

1 North by northwest: climate change and directions of density shifts in birds

2

3 Running head: Climate change and direction of density shift

4

5 Aleksi Lehikoinen<sup>1\*</sup> & Raimo Virkkala<sup>2</sup>

6

7 <sup>1</sup>The Helsinki Lab of Ornithology, Finnish Museum of Natural History, University of  
8 Helsinki, P. O. Box 17, FI-00014 University of Helsinki, Finland.

9 <sup>2</sup>Finnish Environment Institute, Natural Environment Centre, Mechelininkatu 34 a,  
10 P.O. Box 140, FI-00251 Helsinki, Finland.

11 \* corresponding author: email-address: [aleksi.lehikoinen@helsinki.fi](mailto:aleksi.lehikoinen@helsinki.fi), Tel.  
12 +358451375732.

13

14 Abstract

15

16 There is increasing evidence that climate change shifts species distributions towards  
17 poles and mountain tops. However, most studies are based on presence-absence data,  
18 and either abundance or the observation effort have rarely been measured. In addition,  
19 hardly any studies have investigated the direction of shifts and factors affecting them.  
20 Here we show using count data on a 1000 km south-north gradient in Finland, that  
21 between 1970–1989 and 2000–2012, 128 bird species shifted their densities, on  
22 average, 37 kilometres towards the north northeast. The species-specific directions of  
23 the shifts in density were significantly explained by migration behaviour and habitat  
24 type. Although the temperatures have also moved on average towards the north  
25 northeast (186 kilometres), the species-specific directions of the shifts in density and

26 temperature did not correlate due to high variation in density shifts. Findings highlight  
27 that climate change is unlikely the only driver of the direction of species density  
28 shifts, but species-specific characteristics and human land use practices are also  
29 influencing the direction. Furthermore, the alarming results show that former climatic  
30 conditions in the northwest corner of Finland have already moved out of the country.  
31 This highlights the need for an international approach in research and conservation  
32 actions to mitigate the impacts of climate change.

33

34 Keywords: distribution changes, ecological traits, global warming, habitat selection,  
35 monitoring censuses, species distribution models.

36

37

38 Introduction

39

40 Understanding the impact of climate change on species populations is a fundamental  
41 question to mitigate the effects of changing climate. There is an increasing body of  
42 literature showing that species of various taxonomic groups including plants,  
43 invertebrates and vertebrates in both northern and southern hemisphere of the globe  
44 have shifted their distribution during both summer and winter season likely due to  
45 climate change (Parmesan *et al.*, 1999; Parmesan & Yohe, 2003; Hickling, *et al.*,  
46 2006; Kelly & Goulден, 2008; Zuckerberg *et al.*, 2009; Booth *et al.*, 2011; Chen *et*  
47 *al.*, 2011; La Sorte & Jetz, 2012; Breed *et al.*, 2013; Pearce-Higgins & Green, 2014).  
48 Although there is some evidence that species-specific characteristics, such as habitat  
49 preferences, affect how species are responding to climate change (Pöyry *et al.*, 2009)  
50 it is still largely poorly known what factors drive the variation in species-specific  
51 responses.

52         Distribution changes are typically examined at the edges of the distribution  
53 using presence-absence data often ignoring the importance of survey effort (Kujala *et*  
54 *al.*, 2013), whereas changes in the central gravity of the populations using abundance  
55 data has much less frequently been examined (Maclean *et al.*, 2008; Lehikoinen *et al.*,  
56 2013; Virkkala & Lehikoinen, 2014). Furthermore, majority of the studies have only  
57 investigated shifts directly towards the poles despite the fact that isotherms are rarely  
58 placed linearly along latitudes in nature (Huntley *et al.*, 2007, see also Fig. 1).  
59 Therefore, predicted distribution changes of species have also been suggested to occur  
60 nonlinearly towards the poles (Huntley *et al.*, 2007; Burrows *et al.*, 2013).  
61 Interestingly, the direction of the distribution changes has often been neglected  
62 (Gillings *et al.*, 2015). This could underestimate the distance in species distribution

63 changes (Gillings *et al.*, 2015) as most of the earlier studies have often looked at only  
64 on one dimension of the shift (e.g. Thomas & Lennon, 1999; Thomas, 2010).

65 Hockey *et al.* (2011) studied the direction of the species distribution changes in  
66 South Africa using only cardinal directions. On the other hand, Gillings *et al.* (2015)  
67 investigated the actual direction of the shift using presence-absence data from UK. In  
68 view of conservation, it is more important to investigate the changes in species  
69 abundance than occurrence only, as presence-absence data can mask changes in  
70 species abundance (Virkkala & Lehikoinen, 2014). To our knowledge, the directions  
71 of the species' density shifts using long-term abundance data over decades have not  
72 been investigated before. However, Tayleur *et al.* (2015) investigated directions of  
73 density shifts of Swedish birds in 21<sup>st</sup> century and found that shifts were poorly  
74 connected with climatic variables. Furthermore, the impact of potential other  
75 ecological factors than climate on the species-specific variation in the direction of the  
76 density shifts have not been examined.

77 Here we investigate, based on 128 Finnish birds species, the general direction in  
78 shifts of species' central gravity of abundance (hereafter density shift), and whether it  
79 is linked with the direction of the temperature change. Our hypothesis is that  
80 directions of the species-specific temperature and density changes would correlate to  
81 support the impact of climate change as the key driver of distribution changes.  
82 Furthermore, we investigate whether the direction of the shift differs between  
83 functional ecological species groups. We compare density shifts in 147 50-km grid  
84 cells between two periods: 1970–1989 and 2000–2012.

85 We used three different categorizations of species: (i) distribution type, (ii)  
86 habitat type and (iii) migration strategy. We used these groups, because (i) northern  
87 species have shifted their densities toward the north at a faster rate than southern

88 species (Virkkala & Lehikoinen, 2014). We therefore predict that northern species  
89 would show density shifts towards more northerly directions than southern ones, and  
90 the more diverse distribution of directions among southern species would thus explain  
91 the slower speed of density shifts. (ii) Potential habitats for farmland, urban and  
92 montane species are highly restricted, and the first two ones are highly influenced by  
93 human activities, as e.g. farmland practices have strongly affected farmland bird  
94 population trends in Europe including Finland in recent decades (Donald *et al.*, 2001;  
95 Laaksonen & Lehikoinen, 2013). Our hypothesis is that forest species would show  
96 density shifts to more northerly directions than farmland and urban species. Arable  
97 land in Central Finland is concentrated especially on western part of the country  
98 (Ostrobothnia area), which could cause a more western direction of density shifts in  
99 farmland species compared to other species groups. (iii) In residents and partial  
100 migrants a substantial proportion of the individuals remain in the breeding areas and  
101 can thus better track directly changes in their breeding environment compared to  
102 migratory birds, which are also affected by changes on their migratory route and  
103 wintering grounds. European long-distance migrants especially have declined  
104 substantially in recent decades (Sanderson *et al.*, 2006; Laaksonen & Lehikoinen,  
105 2013). In addition to migration distance, the migration direction may affect the  
106 direction of the density shift. Finnish birds have several migration directions from  
107 West Africa to East Asia, and since species are migrating from different directions,  
108 this can affect their direction of the density shift. We predict that southwest, south and  
109 southeast migrants would show density shifts towards northeast, north and northwest,  
110 respectively.

111

112

113 Materials and methods

114

115 Census data and calculation of relative densities

116

117 Line transects have been conducted in Finland regularly since the 1970's (Virkkala &

118 Lehtikoinen, 2014). The line transects are one-visit censuses in which birds are

119 counted along a transect with a length typically 3–6 km, and the locations of the

120 transects have been placed on a map in advance (Lehtikoinen *et al.*, 2014; Virkkala &

121 Lehtikoinen, 2014). The methodology is suitable for counting birds over large areas,

122 and the line transect census can be used to investigate relative densities of species

123 (Järvinen & Väisänen, 1975, 1981). The census period is June and the counts are

124 carried out earlier in southern Finland (between June 1–20) compared to northern

125 Finland (between June 10–30) due to later breeding phenology in northern latitudes.

126 Transects were censused during early morning, when the singing activity of birds is

127 highest in dry weather conditions. The observer walks alone at a speed of 45–60

128 min/km depending on the density of birds along the route using a map, compass or

129 GPS. Each observation is classified as one of the five following categories: (i) singing

130 or displaying, (ii) other calls, (iii) sightings (male, female, pair, brood or nest), (iv)

131 flying bird and (v) flying flock. Flocks are transformed into pairs, normally by

132 dividing by two (male and female) plus the mean species-specific brood size in case

133 of brood flocks. The census unit is a pair of birds, not an individual; thus a male and a

134 female seen separately or together, or a parent with offspring, is transformed into one

135 pair (see Järvinen *et al.*, 1991). The line transect is divided into a main belt and a

136 supplementary belt. The main belt is 50 m wide (25 m on both sides of the transect

137 line) and the supplementary belt is beyond the main belt as far as birds can be

138 detected. Every observation is placed either on the main belt or on the supplementary  
139 belt. Birds crossing the main belt belong to the supplementary belt even if first  
140 observed above the main belt. Together, the main belt and the supplementary belt  
141 form the survey belt. An earlier study showed that species-specific annual proportions  
142 of displaying birds and birds in the main belt were stable during 1987–2010, which  
143 indicates that there are no major changes in species detectability (Lehikoinen, 2013).

144 We divided Finland into 50-km grids and calculated how many kilometres of  
145 line transects have been conducted in each grid during the two different periods,  
146 1970–1989 and 2000–2012 (on average 25 years apart). We omitted the 1990s, since  
147 this period has slightly poorer coverage than other decades in some parts of the  
148 country. Nevertheless, the decadal data has shown that abundances of the 94 most  
149 common species shifted progressively toward higher latitudes (Virkkala &  
150 Lehikoinen, 2014). Altogether 147 grid cells, covering most parts of the country,  
151 included at least 10 kilometres of line transects during both the periods (see Fig. 1a).  
152 During our study periods of 1970–1989 and 2000–2012, altogether 303,647 and  
153 490,474 pairs of birds were observed, respectively. 128 species having at least 20  
154 observations during both periods were included in the analyses (Supplementary  
155 Table 1).

156 We calculated species-specific densities for each grid, based on the number of  
157 pair observations and the length of the line transects in each block and species-  
158 specific correction coefficients (Järvinen & Väisänen, 1983). The relative density of a  
159 species ( $D$ , pairs/km<sup>2</sup>, hereafter density) based on the Finnish line transect census was  
160 calculated as:

$$161 \quad D = K \times N/L, \quad (1)$$

162 where  $K$  = species-specific correction coefficient,  $N$  = numbers of pair observations  
163 of a species on the whole survey belt, and  $L$  = transect length (in km). Species-  
164 specific correction coefficients are based on distance sampling, where ratios of bird  
165 observations on the main belt to those on the supplementary belt are used to calculate  
166 densities of species in a larger (survey belt) line transect (Järvinen & Väisänen, 1983).  
167 We used the earlier published correction coefficients (Virkkala & Lehikoinen, 2014,  
168 Supplementary Table 1) and, using the same data, calculated correction coefficients  
169 for the additional 34 species that were not included in the earlier study  
170 (Supplementary Table 1).

171 Järvinen & Väisänen (1983) have presented correction coefficients based on  
172 data prior to the 1980s. However, since then a lot of new data have been gathered, so  
173 we have revised the coefficients. We calculated species-specific correction  
174 coefficients for southern and northern Finland (divided by the 710 latitude in the  
175 Finnish coordinate system) and for the whole country based on the whole of the  
176 Finnish monitoring data since the 1970s, when both the main belt and the  
177 supplementary belt had been used. The species-specific correction coefficient ( $K$ ) was  
178 calculated as (Järvinen & Väisänen, 1983):

$$179 \quad K = 40 - 40 \sqrt{1-p}, \quad (2)$$

180 where  $p$  = proportion of main belt observations (range 0–1); for details of the  
181 calculations, see Järvinen (1976) and Järvinen & Väisänen (1975, 1976a, 1983).  
182 Observability of species is also affected by the overall density of bird specimens. The  
183 higher the total bird density, the lower the observability on the supplementary belt  
184 (see Järvinen & Väisänen, 1976b). This can be corrected by studying the number of  
185 observations on the main belt. Therefore we also used density dependent correction  
186 coefficient ( $\gamma$ ) calculated as (see Järvinen & Väisänen, 1983):



187  $y = 0.0320x + 0.684$  (3)

188 where x is the number of main belt observations of all species per km. The correction  
189 coefficient (y) receives values above one in regions of high main belt density and  
190 below one in regions of low density. Thus, the density values calculated (equation 1)  
191 were multiplied by the density dependent correction coefficient (y) (Järvinen &  
192 Väisänen, 1983). The density dependent correction coefficient was calculated  
193 separately for each 50-km square for both periods.

194 We used these grid-specific densities to calculate arithmetic central gravity of  
195 densities for each species during both the periods. This was done by first calculating  
196 the northern latitude using mean densities per each latitude grid row (Virkkala &  
197 Lehtikoinen, 2014) and then calculating the longitude using mean densities per each  
198 grid column (species-specific density maps and central gravity of densities are shown  
199 in Supplementary Figs 1–128). In addition, gravity of densities was affected by the  
200 location of censuses inside each grid. The point of each grid cell used in the analyses  
201 was calculated based on mean coordinates of all line transects conducted in the grid  
202 during that particular period. We preferred arithmetic mean instead of median or  
203 geometric mean, since using median the shift would be occurring mainly on grid level  
204 in compass points and intercardinal directions, whereas arithmetic mean allows higher  
205 resolution in direction of the shifts. We declined to use geometric mean, since many  
206 grid cells have zero values which complicates the calculation of geometric mean.

207 Based on latitude and longitude it was possible to calculate direction and  
208 distance of the density shift of species between the two periods. Direction in degrees  
209 could be calculated using inverse hyperbolic tangent and distance using Pythagoras'  
210 Theorem.

211 We divided species into groups using four different classifications  
212 (Supplementary Table 1). First, we divided species into groups based on their general  
213 distribution (southern edge and northern edge species and species which occur in the  
214 larger part of country). This was done using the bird atlas data from Finland from  
215 2006–2010 (see Valkama *et al.*, 2011). Southern and northern species, which had  
216 been observed in less than 20% of the grid cells in Finland during this atlas period,  
217 were classified as edge species. Rest were classified into one group that inhabit larger  
218 geographic areas. Second, we divided species into four categories based on their  
219 habitat use: farmland-urban, forest, wetlands (including rocky outcrops) and montane  
220 (Virkkala *et al.*, 1994; Väisänen *et al.*, 1998; Laaksonen & Lehikoinen, 2013). Third,  
221 species were classified into four groups based on their migration distance (residents,  
222 partial migrants, short- and long-distance migrants (Cramp *et al.*, 1977–1994;  
223 Valkama *et al.*, 2014). We first divided species into two groups, residents-partial  
224 migrants and true migrants (short- and long-distance migrants) and later performed a  
225 more detailed analysis where all four groups were included. Last, we divided species  
226 into three groups based on their main migration direction: southwest (wintering in  
227 West Europe and West Africa), south (South and Central Europe, South and East  
228 Africa) and southeast (Southeast Europe and Asia (Cramp *et al.*, 1977–1994, Valkama  
229 *et al.*, 2014). There was no strong collinearity between groups (all  $|r| < 0.27$ ).

230 The general direction of density shifts could also be caused by the geographical  
231 shape of Finland, since the shape of the country is not a rectangle. We investigated  
232 how this could affect the direction of the density shifts by moving densities of the grid  
233 cells directly towards north. We moved the densities of the first period one grid  
234 northwards (except the most southernmost grids which remained similar) to mimic the  
235 northwards density shifts. In cases where the grid did not have density value on the

236 southern side, we used mean density values of the nearest southwest and southeast  
237 side of the grid (Supplementary Fig. 129). We did these movements of densities for  
238 each species and calculated the direction of density shifts similarly as in the observed  
239 density shifts of species, and thus calculated the hypothetical density shift of each  
240 species.

241 The temperature data originates from the Finnish Meteorological Institute and  
242 included daily values in 10-km grid cells (Fig. 1b). We calculated mean temperatures  
243 for 50-km grids used in the analyses of bird data during the two study periods.  
244 Furthermore, we searched, using temperature of the first period for each 50-km grid,  
245 where the nearest as cold grid cell within Finland was located during the second  
246 period. Based on this information we could calculate which direction the climate has  
247 shifted regionally (Fig. 1c), and thus what would be the direction that species should  
248 have shifted to remain in the same climatic conditions. Last, for each species we  
249 calculated the mean direction and distance of the temperature change from the grid  
250 cells where the species had been observed in the first study period.

251

252 Statistical analyses

253

254 All the statistical analyses were conducted in Matlab R2014a. Significance of the  
255 species-specific density shifts along compass directions and impact of sampling effort  
256 and temperature were tested using log-linear Poisson regression model

257  $N = L + \text{Temp} + \text{Latitude} + \text{Longitude} \quad (4),$

258 where the grid specific change in the number of observed pairs in grid cell (N) is  
259 explained by corresponding change in the length of the line transect (L), temperature  
260 (Temp), latitude and longitude of the same grid cell.

261 The species-specific directions of the density shifts were calculated by using  
262 inverse tangent (Matlab function `atand`) and by using the values of the Finnish  
263 uniform coordinate system, where a change of one unit corresponds distance of 10  
264 kilometres (see Fig. 1). For circular analyses, Circular Statistics Toolbox was used.  
265 All the functions of the toolbox and their codes are freely available on the web  
266 (Berens, 2009). The mean direction was calculated using the function `circ_mean` and  
267 the 95 % confidence intervals were calculated using the function `circ_confmean`.  
268 Rayleigh's test (function `circ_rtest`; test for the significance of the mean direction in  
269 the cycle histogram) was used to test whether the directions differ from an even  
270 distribution. Furthermore, the Harrison-Kanji test (function `circ_hktest`; circular  
271 analog of two-factor ANOVA) was used to analyse whether the direction of different  
272 groups differed. The Watson-Williams test (function `circ_wwtest`; circular analog of  
273 the one-factor ANOVA) was used to test whether the direction of temperature and  
274 density shifts differed, and the function `circ_corrcc` was used to test whether the  
275 species-specific directions in temperature and density correlate. Last, because closely  
276 related species may show similar type of responses, we investigated whether the  
277 findings were linked to the phylogeny of the species. We tested whether the residuals  
278 of results were correlated with the relative phylogenetic distance on the order and  
279 family level. We did this by correlating the differences in residuals of a pair of species  
280 with the corresponding relative phylogenetic distance between the species. The  
281 phylogeny was based on the taxonomy of AERC TAC (<http://www.aerc.eu/tac.html>).  
282 Function `circ_corrcl` was used to test the potential influence of phylogeny by  
283 correlating the differences in residuals of each pair of species with the corresponding  
284 relative phylogenetic distance between the species. In addition, the average direction

285 and distance of shifts (vector) was calculated by using the arithmetic mean of a  
286 species' latitude and longitude change.

287         Since the analyses of the significance of the density shifts (128 tests per  
288 variable) and the investigation of impacts of different groups required multiple testing  
289 (5 tests) we used a sequential Bonferroni correction to adjust the P-values (Rice,  
290 1989).

291

292

293 Results

294

295 The findings show that the mean direction of the density shift was on average towards  
296 the north northeast ( $\alpha = 12^\circ$ ,  $0^\circ$  is north with rotation clockwise). The distribution of  
297 directions differed significantly from an even distribution (Rayleigh's test,  $z = 17.7$ ,  
298  $n = 128$ ,  $P < 0.001$ ), but not from the direct north direction (Fig. 2a). On average,  
299 species densities shifted 35.9 kilometres towards the north and 7.0 kilometres toward  
300 the east in 25 years (36.6 km in total, 1.5 km / year). However, there was a large  
301 variation in the density shift between species. Among the 128 study species, 96  
302 species shifted their densities northward (mean  $\alpha = 17^\circ$ , north northeast, c.i.  $7-27^\circ$ )  
303 with an average of 60.2 kilometres shift north and 18.9 km shift east (mean average  
304 total length of density shift of 82.1 km, 3.3 km / year). About half of these species, 49  
305 species, shifted their densities northward more than 50 kilometres, and for only 25  
306 species the shift towards north was less than 20 kilometres (Supplementary Table 1).

307 Correspondingly, 32 species shifted their densities in the southern directions  
308 (mean  $\alpha = 216^\circ$ , c.i.  $197-235^\circ$ ) with an average of 33.8 km shift south and of 34.7 km  
309 shift west (mean average total length of density shift of 72.7 km, 2.9 km/ year). Half  
310 of these species (16) shifted their densities less than 20 kilometres towards south and  
311 only seven species shifted their densities more than 50 kilometres southwards  
312 (Supplementary Table 1). The glm test revealed that 63 of the species shifted their  
313 densities significantly towards north and 17 significantly towards south  
314 (Supplementary Table 1). Correspondingly 11 species shifted their densities  
315 significantly towards east and ten towards west. Grid-specific changes in temperature  
316 explained only shifts of four species, and changes in length of line transects did not  
317 showed significant results.

318           The modelled northwards movement of densities of species produced on  
319 average density shift towards the north ( $\alpha = 9^\circ$ , c.i. 358–20°), which did not differ  
320 either from the direct north or the corresponding observed density shift of species ( $\alpha$   
321 = 12°).

322           The mean direction of the temperature shift was north northeast ( $\alpha = 13^\circ$ , Fig.  
323 2a) and did not differ from mean direction of the species' density shift (Watson-  
324 Williams test,  $F_{1,254} = 0.02$ ,  $P = 0.90$ ). There was however a clear geographical pattern  
325 in the direction of the temperate shift. In the southern half of Finland, the direction  
326 was on average toward the northeast, whereas in the northern part of the country the  
327 temperatures shifted westward toward the mountainous region in the northwest (Fig.  
328 1c). In the northwest corner, the climatic conditions of the 1970's and 1980's, in the  
329 resolution of 50-km grids, have already moved outside the borders of Finland (Fig.  
330 1c). Despite the similar mean direction of both the temperature and density shifts of  
331 species, the species-specific directions did not correlate significantly ( $\rho = -0.03$ ,  $n =$   
332 128,  $P = 0.71$ ). Furthermore, the distance of the temperature change was on average  
333 186 km (min-max 143–301 km), which is more than five times the mean distance that  
334 all species have shifted toward the north.

335           Habitat type and migration distance significantly explained the difference in  
336 distribution of directions (Harrison-Kanji test,  $\chi^2_2 = 17.92$ ,  $P = 0.0064$ ,  $\chi^2_6 = 8.84$ ,  
337  $P = 0.012$ , respectively, Fig. 2b-c). Despite the high variation in the directions,  
338 farmland-urban, wetland and montane species shifted their densities towards the north  
339 northwest ( $\alpha = 335^\circ$ ,  $\alpha = 339^\circ$ , and  $\alpha = 350$ , respectively; Fig. 2b-c), whereas forest  
340 species moved towards the north northeast ( $\alpha = 32^\circ$ , Fig. 2b, Supplementary Fig.  
341 130). For instance typical farmland species like Lapwing *Vanellus vanellus*, Skylark  
342 *Alauda arvensis*, Barn Swallow *Hirundo rustica* and Eurasian Starling *Sturnus*

343 *vulgaris* shifted their densities more than 40 km westward. In contrast, Eurasian  
344 Sparrowhawk *Accipiter nisus*, Osprey *Pandion haliaetus*, Merlin *Falco columbarius*,  
345 Red-breasted Flycatcher *Ficedula parva*, Willow Tit *Poecile montanus*, Coal Tit  
346 *Periparus ater* and Common Crossbill *Loxia curvirostra* showed the strongest shifts  
347 among forest birds towards north and east (all shifted more than 150 km,  
348 Supplementary Table 1). Among montane birds, the strongest shifts were observed in  
349 Long-tailed Skua *Stercorarius longicaudus* and Lapland Longspur *Calcarius*  
350 *lapponicus* which shifted towards northeast more than 100 kilometres and Snow  
351 Bunting *Plectrophenax nivalis* whose densities shifted towards the highest mountains  
352 in the northwest more than 80 kilometres.

353         Furthermore, when grouping species into residents-partial migrants and true  
354 migrants, there was a significant difference in the directions between groups (Fig. 2d).  
355 Almost all resident and partial migratory species shifted their densities towards the  
356 northeast ( $\alpha = 39^\circ$ , Fig. 2d), whereas many migratory species showed density shifts  
357 towards the west and southwest ( $\alpha = 358^\circ$ , Fig. 2d, Supplementary Fig. 131).  
358 However, a more complicated model with the four migration type categories did not  
359 explain species-specific variation in the shift of the densities (H-K test,  $\chi^2_6 = 9.54$ ,  
360  $P = 0.15$ ). This was likely because both residents and partial migrants moved towards  
361 the northeast and short- and long-distance migrants towards the north (Supplementary  
362 Fig. 132a–d). In the case of either habitat type or the migration distance the residuals  
363 of the models were not correlated with the phylogeny either at the order or family  
364 level (all  $P$ 's  $> 0.26$ ).

365         There was some evidence that migration direction explains part of the variation  
366 in density shifts (H-K test,  $\chi^2_4 = 11.1$ ,  $P = 0.086$ ). Species wintering in the southwest  
367 shifted their densities on average towards the north northeast direction ( $\alpha = 13^\circ$ ),



368 whereas species wintering in the south and southeast shifted their densities towards  
369 north northwest ( $\alpha = 339^\circ$  and  $\alpha = 335^\circ$ , respectively, Fig. 2e), as would have been  
370 expected based on their migration routes. The distribution of the directions did not  
371 differ between southern edge ( $\alpha = 323^\circ$ ) or northern edge ( $\alpha = 72^\circ$ ) species or species  
372 that occur in the large part of the country ( $\alpha = 8^\circ$ , H-K test,  $\chi^2_4 = 7.12$ ,  $P = 0.13$ ;  
373 Fig. 2f). In general, the group of species that shifted their densities westwards  
374 included several types of species, such as migrants wintering in Asia (e.g. Blyth's  
375 Reed Warbler *Acrocephalus dumetorum* and Greenish Warbler *Phylloscopus*  
376 *trochiloides*), farmland species (mentioned above), and other species with declining  
377 population dynamics (e.g. Common Buzzard *Buteo buteo*, Honey Buzzard *Pernis*  
378 *apivorus*, Hen Harrier *Circus cyaneus* and Sedge Warbler *Acrocephalus*  
379 *schoenobaenus*) (see Supplementary Table 1).

380

381

382

383 Discussion

384

385 The findings reveal that directions of species' density and temperature shifts are not  
386 directly towards the north, but most often towards the north northeast and north  
387 northwest. Although these directions can partly be driven by the geographical shape  
388 of the country, this underlines that the rate of species density shifts are  
389 underestimated, if the shift is only measured using one north-south dimension.  
390 However, the speed of the temperature change has been much faster than  
391 corresponding speed in the change of bird species densities, which has also been  
392 found in some earlier studies both in Europe and North America (Devictor *et al.*,  
393 2008, 2012; La Sorte & Jetz, 2012). Importantly, although the species and  
394 temperature had on average the same direction, the species-specific values were not  
395 significantly correlated as we predicted. This is probably due to the large variation in  
396 the species density shifts, since 25% of the species show a move towards southern  
397 directions. In a recent work, Tayleur *et al.* (2015) showed that only 20% of the  
398 Swedish bird species had shifted their densities towards the expected direction during  
399 21<sup>th</sup> century according to the temperature change and changes in rainfall had hardly  
400 any impact on density changes. On the other hand, Virkkala *et al.* (2014) showed that  
401 observed changes in Finnish bird distributions between 1974–89 and 2006–2010 were  
402 largely in the same direction as predicted range shifts by 2051–2080 based on  
403 bioclimatic envelope models. Understanding causes of the variation in species-  
404 specific directions and the speed of change is crucial for making predictions in species  
405 distributions and for conservation actions.

406 This study shows that forest bird species have on average shifted towards a  
407 northeastern direction, whereas species of other habitats have on average shifted their

408 densities towards northwestern directions. Finland is situated on the western edge of  
409 the Eurasian boreal forest zone (see e.g. Huntley *et al.*, 2007; Virkkala *et al.*, 2008),  
410 which is why it is logical that forest species show density shift towards the northeast.  
411 Nevertheless, management of forest can also affect species ability to move their  
412 distributions (Felton *et al.*, 2014). On the other hand, declining montane species  
413 (Lehikoinen *et al.*, 2014) were moving on average towards the north northwest, where  
414 the highest and coldest montane areas are situated in Finland. Thus, the physiography  
415 of Finland explains some of the shifts. Northwards density shifts of bird species have  
416 also been observed in Finnish protected areas, where human-caused land use is  
417 prohibited, suggesting that climate change was the main cause for species density  
418 shifts in natural habitats (forests, wetlands and montane habitats) (Virkkala &  
419 Rajasärkkä, 2011). In addition, land use changes also influence our results. Farmland  
420 birds have generally declined in Finland since the 1970's, mainly due to changes in  
421 farmland practices (Rintala & Tiainen, 2007; Laaksonen & Lehikoinen, 2013). Mean  
422 density shifts of farmland species towards a northwestern direction is supported by  
423 our predictions, as the largest arable land areas in the northern and central part of the  
424 country are situated on the western side. Moreover, densities of several farmland  
425 species have shifted towards the southwest indicating that these species have retracted  
426 towards their core breeding areas. In the UK, land use changes have been shown to be  
427 more important drivers of the farmland bird species than climatic factors (Eglington &  
428 Pearce-Higgins, 2012).

429       Furthermore, migration behaviour, especially the comparison between residents  
430 (including partial migrants) and true migrants explained the differences in species-  
431 specific variation in the shift direction. Residents and partial migrants shifted their  
432 densities very strongly toward the northeast, whereas among migrants, many species

433 showed western or southwestern density shifts. This could indicate that residents and  
434 partial migrants could better track climatic changes than migratory species, which are  
435 away for the winter (Pearce-Higgins & Green, 2014).

436 Many south-eastern and southern migrants tend to spread in western directions,  
437 whereas southwestern migrants tend to spread towards the north northeast. Although  
438 these groups did not differ between each other significantly, this kind of pattern would  
439 make sense as species migration direction classifies the angle along which birds tend  
440 to move most during their life cycle. One of the widely known impact of climate  
441 change is advanced spring arrival dates of many bird species (Jonzén *et al.*, 2006;  
442 Lehtikoinen & Sparks, 2010, Vaitkuviene *et al.* 2015). The advanced spring migration  
443 potentially together with more favourable migration conditions could be one of the  
444 mechanisms behind climate induced distribution shifts due prolonged to migration  
445 distances (Otterlind, 1954; Berthold, 2001). This emphasizes that the migration  
446 direction and route of dispersal should be investigated in more detail. However, since  
447 our study showed that residents and partial migrants shifted more towards northeast  
448 than true migrants other mechanisms are also acting here.

449 Although this study is based on large-scale data covering over 1000 km in a  
450 north-south direction through the boreal zone and over 600 kilometres in a west-east  
451 direction, it is still conducted within one country and does not cover the whole  
452 population of any of the study species. Such analyses dealing with abundance shifts at  
453 a whole population level are very rare (see, however, Lehtikoinen *et al.*, 2013; Pavón-  
454 Jordan *et al.*, 2015), and require harmonious monitoring schemes. Furthermore, the  
455 conservation decisions and management actions are typically done on a national level,  
456 which is why these borders need to be taken into account although species do not  
457 recognize border lines (Pouzols *et al.*, 2014).

458           Unfortunately corresponding long-term census data from the border countries,  
459 especially from the Russian side, are lacking. Furthermore, the alarming results show  
460 that the former climatic conditions in the northwest corner of Finland have already  
461 moved out of Finland at least on the 50-km grid scale. Although in this mountainous  
462 region, in the short-term species could cope with climate change by shifting their  
463 densities uphill, in the long-term their currently declining populations (Lehikoinen *et*  
464 *al.*, 2014) may become extirpated from northwestern Europe (Huntley *et al.*, 2007;  
465 Virkkala *et al.*, 2008). This underlines that international collaboration should be  
466 increased to improve our understanding of species abundance and distribution  
467 changes (Jiguet *et al.*, 2010; Lehikoinen *et al.*, 2014) and to design management  
468 actions to conserve biodiversity in the face of changing climate (Pearce-Higgins &  
469 Green, 2014; Pouzols *et al.*, 2014).

470

#### 471 Acknowledgements

472

473 We thank the hundreds of birdwatchers who participated in the data collection. Risto  
474 A. Väisänen coordinated the censuses at the Finnish Museum of Natural History for  
475 decades. The Ministry of the Environment provided financial support for the counts  
476 and A.L. received financial support from the Academy of Finland (project 275606).  
477 The detailed comments by three anonymous reviewers are greatly acknowledged.  
478 Benjamin Steele kindly checked the language.

479

480

#### 481 References

482 Berens P (2009) CircStat: A Matlab Toolbox for Circular Statistics. *Journal of*  
483 *Statistica Software*, **31**, 10. (available at [www.jstatsoft.org/v31/i10](http://www.jstatsoft.org/v31/i10))

484 Berthold P (2001) *Bird migration*. Oxford University Press, Oxford.

485 Booth DJ, Bond N, Maccreadie P (2011) Detecting range shifts among Australian  
486 fishes in response to climate change. *Marine and Freshwater Research*, **62**,  
487 1027–1042.

488 Breed GA, Stichter S, Crone EE (2013) Climate-driven changes in northeastern US  
489 butterfly communities. *Nature Climate Change*, **3**, 142–145.

490 Burrows, MT, Schoeman DS, Richardson AJ *et al.* (2014) Geographical limits to  
491 species-range shifts are suggested by climate velocity. *Nature*, **507**, 492–495.

492 Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of  
493 species associated with high levels of climate warming. *Science*, **333**, 1024–  
494 1026.

495 Cramp S, Simmons KEL, Perrins CM (1977–1994) *Handbook of the birds of Europe,*  
496 *Middle East and North America: Birds of the Western Palaearctic*. Oxford  
497 University Press.

498 Devictor V, Julliard R, Couvet D, Jiguet F (2008) Birds are tracking climate change,  
499 but not fast enough. *Proceedings of the Royal Society B-Biological Sciences*,  
500 **254**, 2743–2748.

501 Devictor V, van Swaay C, Brereton T *et al.* (2012). Differences in the climate debt of  
502 birds and butterflies at a continental scale. *Nature Climate Change*, **2**, 121–124.

503 Donald PF, Green RE, Heath MF (2001) Agricultural intensification and the collapse  
504 of Europe's farmland bird populations. *Proceedings of the Royal Society B-*  
505 *Biological Sciences*, **268**, 25–29.

506 Eglington SM, Pearce-Higgins JW (2012) Disentangling the relative importance of  
507 changes in climate and land-use intensity in driving recent bird population  
508 trends. *PLoS One*, **7**, e30407.

509 Felton A, Lindbladh M, Elmberg J, Felton AM, Andersson E, Sekercioglu CH,  
510 Collingham Y, Huntley B (2014) Projecting impacts of anthropogenic climatic  
511 change on the bird communities of southern Swedish spruce monocultures: will  
512 the species poor get poorer? *Ornis Fennica* **91**, 1–13.

513 Gillings S, Balmer DE, Fuller RJ (2015) Directionality of recent bird distribution  
514 shifts and climate change in Great Britain. *Global Change Biology* **21**, 2155–  
515 2168.

516 Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide  
517 range of taxonomic groups are expanding polewards. *Global Change Biology*,  
518 **12**, 450–455.

519 Hockey PAR, Sirami C, Ridley AR, Midgley GF, Babiker HA (2011) Interrogating  
520 recent range change in South African birds: confounding signals from land use  
521 and climate change present a challenge for attribution. *Diversity and*  
522 *Distributions*, **17**, 254–261.

523 Huntley B, Green RE, Collingham YC, Willis SG (2007) *A climatic atlas of European*  
524 *breeding birds*. Durham University, The RSPB and Lynx Edicions, Barcelona.

525 Järvinen O (1976) Estimating relative densities of breeding birds by the line transect  
526 method. II. Comparison between two methods. *Ornis Scandinavica*, **7**, 43–48.

527 Järvinen O, Väisänen, RA (1975) Estimating relative densities of breeding birds by the  
528 line transect method. *Oikos*, **26**, 316–322.

529 Järvinen O, Väisänen, RA (1976a) Finnish line transect censuses. *Ornis Fennica*, **53**,  
530 115–118.

- 531 Järvinen O, Väisänen, RA (1976b) Estimating relative densities of breeding birds by  
532 the line transect method. IV. Geographical constancy of the proportion of main  
533 belt observations. *Ornis Fennica*, **53**, 87–91.
- 534 Järvinen O, Väisänen, RA (1981) Methodology for censusing land bird faunas in large  
535 regions. *Studies in Avian Biology*, **6**, 146–151.
- 536 Järvinen O, Väisänen RA (1983) Correction coefficients for line transect censuses of  
537 breeding birds. *Ornis Fennica*, **60**, 97–104.
- 538 Järvinen O, Koskimies P, Väisänen RA (1991) Line transect census of breeding land  
539 birds. In: *Monitoring bird populations: a manual of methods applied in Finland*  
540 (eds Koskimies P, Väisänen RA). Zoological Museum, Finnish Museum of  
541 Natural History, pp. 33–40.
- 542 Jiguet F, Devictor V, Ottvall R, Van Turnhout C, Van der Jeugd H, Lindström, Å  
543 (2010) Bird population trends are linearly affected by climate change along  
544 species thermal ranges. *Proceedings of the Royal Society B-Biological Sciences*,  
545 **277**, 3601–3618.
- 546 Jonzén N, Lindén A, Ergon, T *et al.* (2006) Rapid advance of spring arrival dates in  
547 long-distance migratory birds. *Science*, **312**, 1959–1961
- 548 Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate  
549 change. *Proceedings of the National Academy of Sciences of the United States*  
550 *of America*, **105**, 11823–11826.
- 551 Kujala H, Vepsäläinen V, Zuckerberg B, Brommer JE (2013) Range margin shifts of  
552 birds revisited - the role of spatiotemporally varying survey effort. *Global*  
553 *Change Biology*, **19**, 420–430.



- 554 Laaksonen T, Lehikoinen A (2013) Population trends in boreal birds: Continuing  
555 declines in agricultural, northern, and long-distance migrant species. *Biological*  
556 *Conservation*, **168**, 99–107.
- 557 La Sorte FA, Jetz W (2012) Tracking of climatic niche boundaries under recent  
558 climate change. *Journal of Animal Ecology*, **81**, 914–925.
- 559 Lehikoinen A (2013) Climate change, phenology and species detectability in a  
560 monitoring scheme. *Population Ecology*, **55**, 315–323.
- 561 Lehikoinen A, Green M, Husby M, Kålås JA, Lindtröm, Å (2014). Common montane  
562 birds are declining in northern Europe. *Journal of Avian Biology*, **45**, 3–14.
- 563 Lehikoinen A, Jaatinen K, Vähätalo AV *et al.* (2013) Rapid climate-driven shifts in  
564 wintering distributions of three common waterbird species. *Global Change*  
565 *Biology*, **19**, 2071–2081.
- 566 Lehikoinen E, Sparks TH (2010) Changes in migration. In *Effects of climate change*  
567 *on birds* (A. Møller, W. Fiedler, & P. Berthold, eds), Oxford Univ. Press,  
568 Oxford, UK, pp. 89–112.
- 569 Maclean IMD, Austin GE, Rehfisch MM *et al.* (2008) Climate change causes rapid  
570 changes in the distribution and site abundance of birds in winter. *Global Change*  
571 *Biology*, **14**, 2489–2500.
- 572 Otterlind G (1954) Flyttning och utbredning. *Vår Fågelvärld*, **13**, 1–261.
- 573 Parmesan C, Ryrholm N, Stefanescu C, *et al.* (1999) Poleward shifts in geographical  
574 ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–  
575 583.
- 576 Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change  
577 impacts across natural systems. *Nature*, **421**, 37–42.

578 Pavón-Jordán D, Fox AD, Clausen P *et al.* (2015). Climate driven changes in winter  
579 abundance of a migratory waterbird in relation to EU protected areas. *Diversity*  
580 *and Distributions*, **21**, 571–582

581 Pearce-Higgins J, Green, RE (2014) *Birds and Climate Change: impacts and*  
582 *conservation responses*. University of Cambridge.

583 Pouzols FM, Toivonen T, Di Minin E *et al.* (2014) Global protected area expansion is  
584 compromised by protected land-use and parochialism. *Nature*, **516**, 383–386.

585 Pöyry J, Luoto M, Heikkinen RK, Kuussaari M, Saarinen K (2009) Species traits  
586 explain recent range shifts of Finnish butterflies. *Global Change Biology*, **15**,  
587 732–743.

588 Rice WR (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.

589 Rintala J, Tiainen J (2007) A model incorporating a reduction in carrying capacity  
590 translates brood size trends into a population decline: the case of Finnish  
591 starlings, 1951–2005. *Oikos*, **117**, 47–59.

592 Sanderson FJ, Donald PF, Pain DJ, Burfield, IJ, van Bommel FPJ (2006) Long-term  
593 population declines in Afro-Palaearctic migrant birds. *Biological Conservation*,  
594 **131**, 93–105.

595 Tayleur C, Caplat P, Massinino D, Johnston A, Jonzén N, Smith HG, Lindström Å  
596 (2015) Swedish birds are tracking temperature but not rainfall: evidence from a  
597 decade of abundance changes. *Global Ecology and Biogeography*, **24**, 859–872.

598 Thomas CD (2010) Climate, climate change and range boundaries. *Diversity and*  
599 *Distributions*, **16**, 488–495.

600 Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. *Nature*, **399**,  
601 213–213.

602 Väisänen RA, Lammi E, Koskimies P (1998) *Distribution, numbers and population*  
603 *changes of Finnish breeding birds*. Otava.

604 Vaitkuviene D, Gagys M, Bartkeviciene G, Romanovskaja D (2015) The effect of  
605 weather variables on the White Stork (*Ciconia ciconia*) spring migration  
606 phenology. *Ornis Fennica* **92**, 43–52.

607 Valkama J, Vepsäläinen V, Lehikoinen A (2011) The Third Finnish Breeding Bird  
608 Atlas. Finnish Museum of Natural History and Ministry of Environment  
609 (<http://atlas3.lintuatlas.fi/english>), Helsinki.

610 Valkama J, Saurola P, Lehikoinen A, Lehikoinen, E, Piha, M, Sola, P, Velmala, W  
611 (2014) *The Finnish Bird Ringing Atlas. Vol. II*. Finnish Museum of Natural  
612 History and Ministry of Environment.

613 Virkkala R, Heikkinen RK, Leikola N, Luoto M (2008) Projected large-scale range  
614 reductions of northern-boreal land bird species due to climate change.  
615 *Biological Conservation*, **141**, 1343–1353.

616 Virkkala R, Lehikoinen A (2014) Patterns of climate-induced density shifts of  
617 species: poleward shifts faster in northern boreal birds than in southern birds.  
618 *Global Change Biology*, **20**, 2995–3003.

619 Virkkala R, Pöyry J, Heikkinen RK, Lehikoinen A, Valkama J (2014) Protected areas  
620 alleviate climate change effects on northern bird species of conservation  
621 concern. *Ecology and Evolution*, **4**, 2991–3003.

622 Virkkala R, Rajasärkkä A (2011) Northward density shift of bird species in boreal  
623 protected areas due to climate change. *Boreal Environment Research*, **16** (suppl.  
624 B), 2–13.

625 Virkkala R, Rajasärkkä A, Väisänen RA, Vickholm M, Virolainen E (1994) The  
626 significance of protected areas for the land birds of southern Finland.  
627 *Conservation Biology*, **8**, 532–544

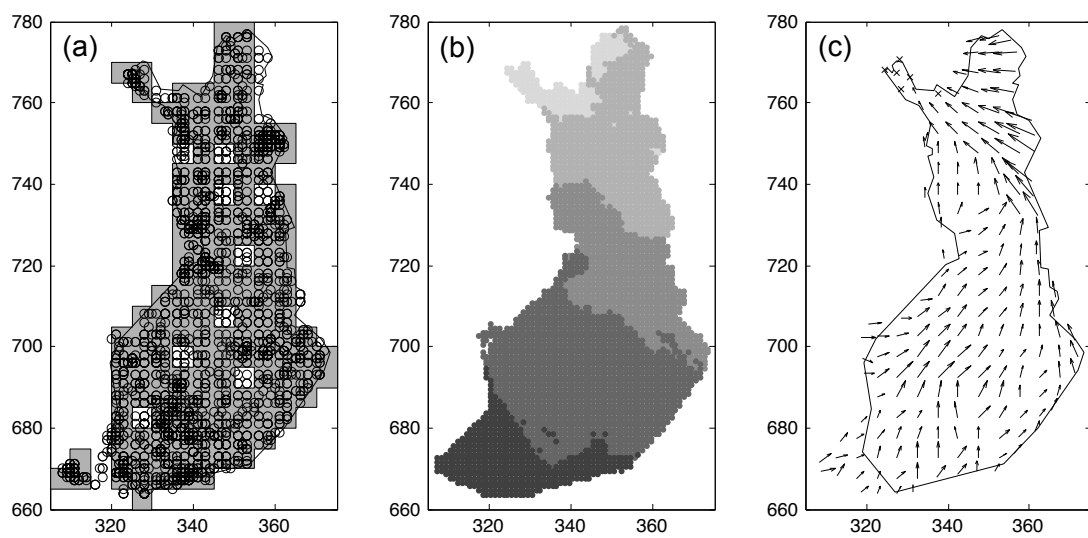
628 Zuckerberg B, Woods AM, Porter WF (2009) Poleward shifts in breeding bird  
629 distributions in New York State. *Global Change Biology*, **15**, 1866-1883.

630

631

632

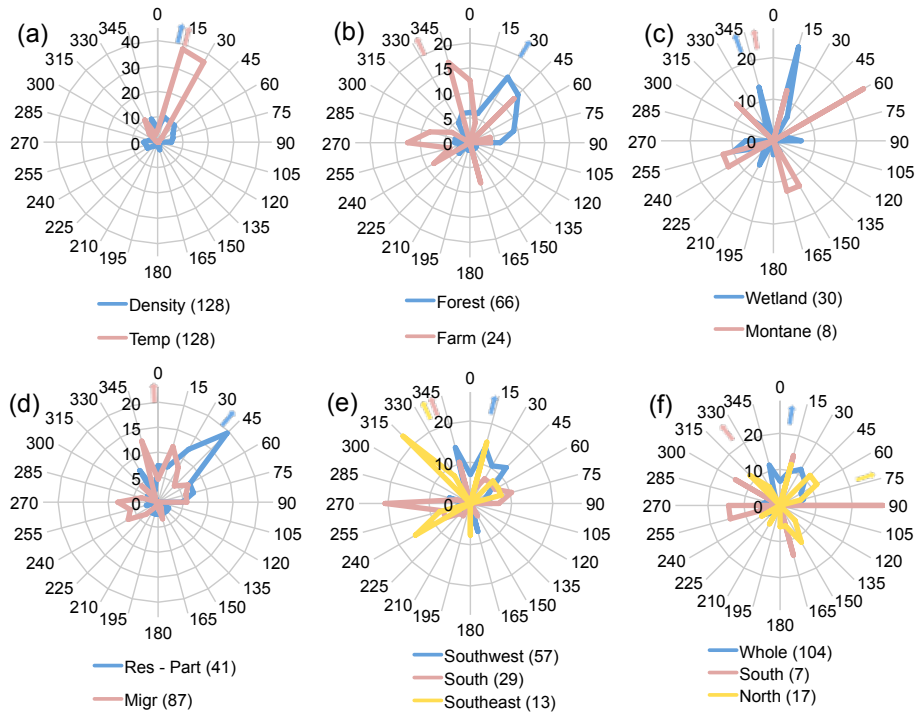
633



634  
635

636 Fig. 1. Map of Finland showing a) 50-km grid cells in grey and individual census sites  
637 in circles in the 1970s, 1980s and 2000s, b) isotherms in annual temperature during  
638 1970–1989 (darker colour indicate warmer temperature) and c) directions that

639 temperature has changed in Finland between 1970–1989 and 2000–2012. Longer  
 640 arrows indicate stronger temperature shifts. ‘x’-marks show grids where climate in the  
 641 1970s and 1980s no longer exists in Finland during the second study period.  
 642



643  
 644 Fig. 2. Distribution of directions of density shifts. (a) Densities of all species (95% c.  
 645 i. of the mean direction 358–30°) and corresponding temperature (95 % c. i. 8–17°) in  
 646 their same breeding range from 1970–1989 to 2000–2012. Distribution of directions  
 647 of density shifts according to main habitat type of the species [b] farmland and forest  
 648 species and c) wetland and montane species], migration behaviour [d] residents -  
 649 partial migrants and fully migratory species], spring migration direction [e] southwest,  
 650 south or southeast] and general distribution of the species [f] southern edge, large part  
 651 of the country and northern edge]. The colour lines show the distribution of directions  
 652 in 15° intervals and the colour arrows next to the degrees show the mean direction of  
 653 the particular distribution.

654

655 Supporting information

656

657 Supplementary Table 1. Species-specific data with sample sizes, habitat, migration  
658 and distribution classifications, central gravity of density expressed as latitudes and  
659 longitudes during both study periods, direction of the density shift, total distance of  
660 shift density shift along latitude and longitude directions and direction of the species-  
661 specific temperature shift.

662

663 Supplementary Figs. 1–128. Species-specific density maps during the first (1970-  
664 1989, left panel) and second (2000-2012, right panel) study period.

665

666 Supplementary Fig. 129. Illustration of moved densities of species to estimate the  
667 potential effect of shape of the country on the direction of density shifts.

668

669 Supplementary Fig. 130. Grid specific changes of relative densities of groups of  
670 species classified based on their main habitat type.

671

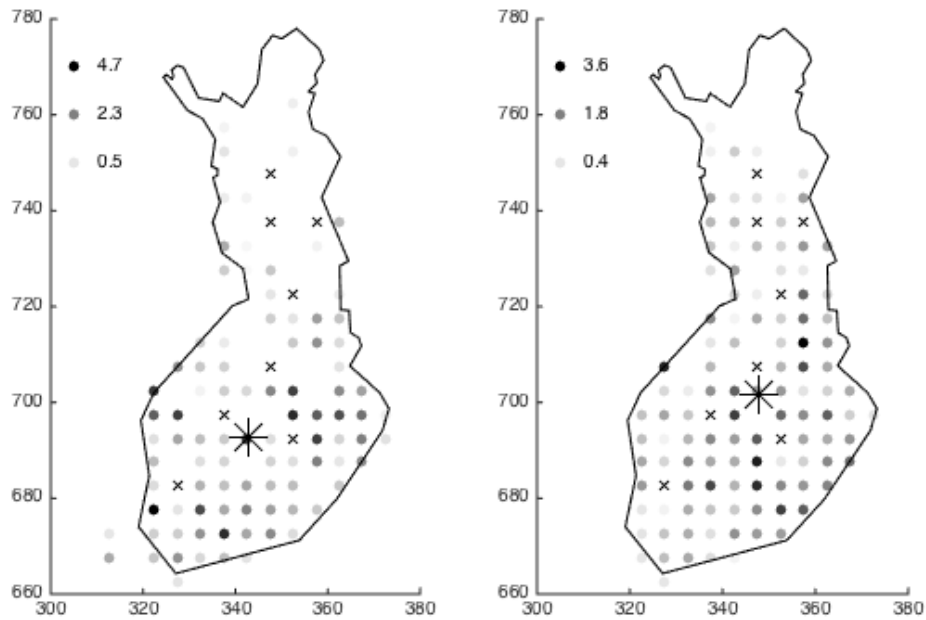
672 Supplementary Fig. 131. Grid specific changes of relative densities of groups of  
673 species classified based on their migration type.

674

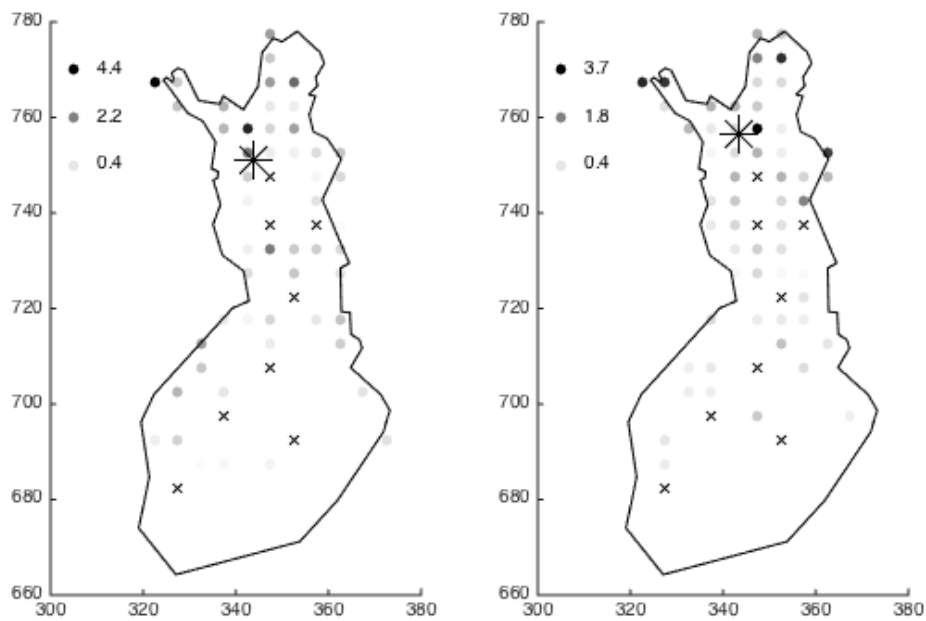
675 Supplementary Fig. 132. Distribution of directions of changes in densities based on  
676 four migration groups.

677

Supplementary figs 1–128. Species-specific density maps during the first (1970-1989, left panel) and second (2000-2012, right panel) study period. The 50-km grid-specific densities are shown in grey scale illustrated by three values on the up left corner of each panel. Large asterisk shows the central gravity of the densities and small black crosses are grids that did not have enough data (excluded from the analyses).

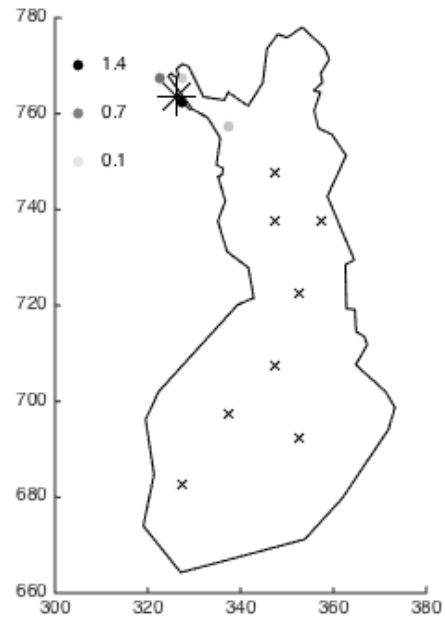
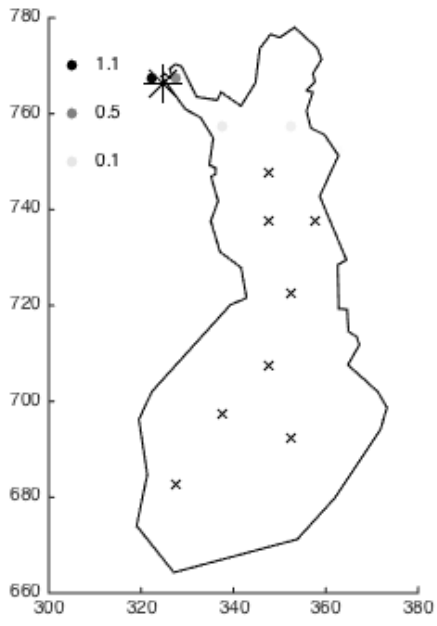


Supplementary fig. 1. *Tetrastes bonasia*

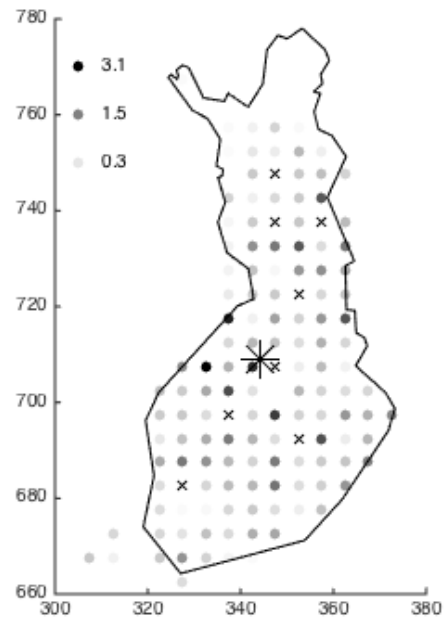
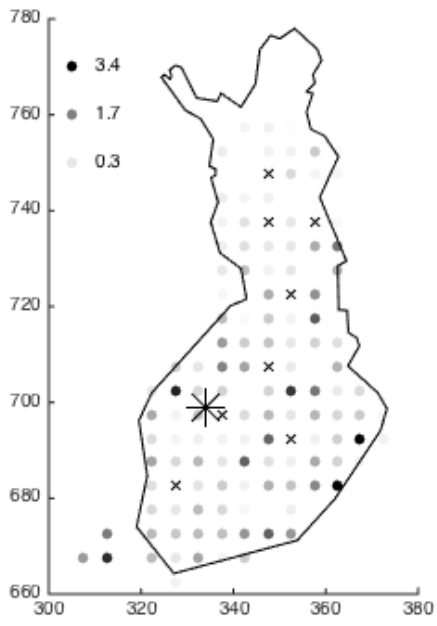


Supplementary fig. 2. *Lagopus lagopus*

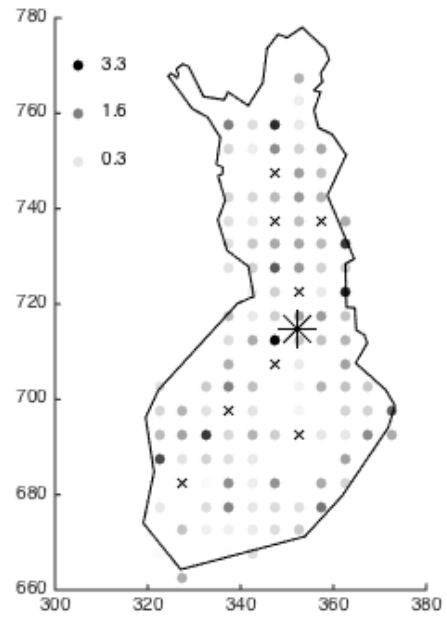
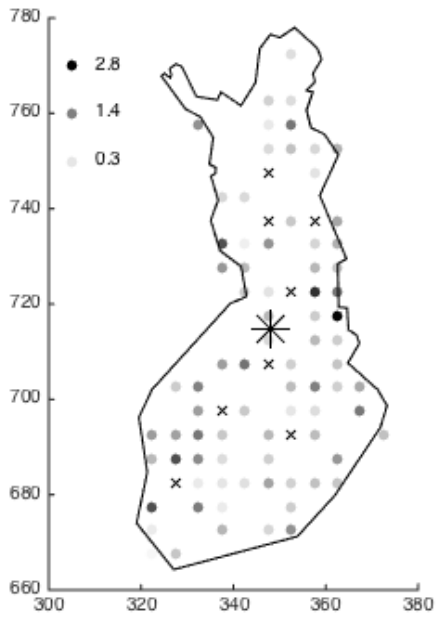




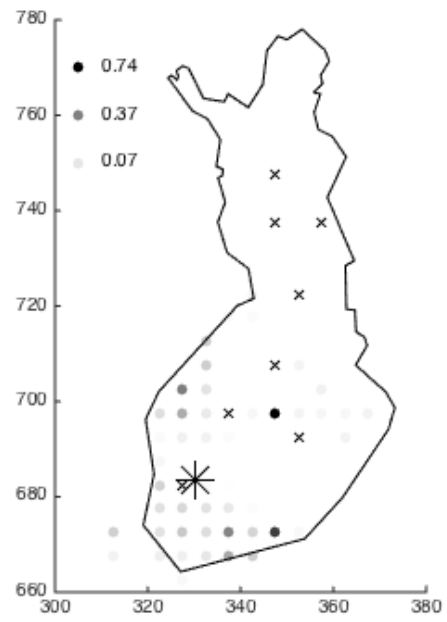
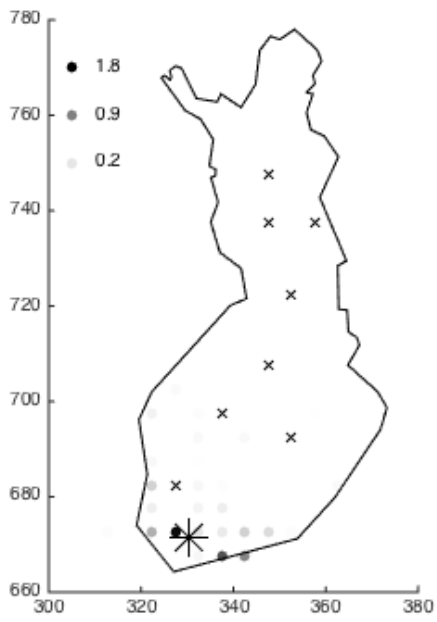
Supplementary fig. 3. *Lagopus muta*



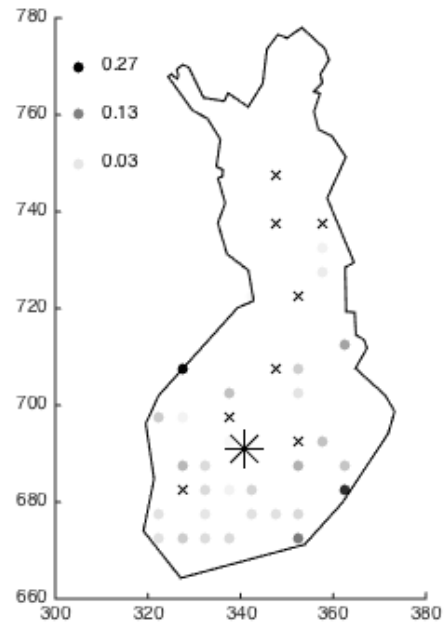
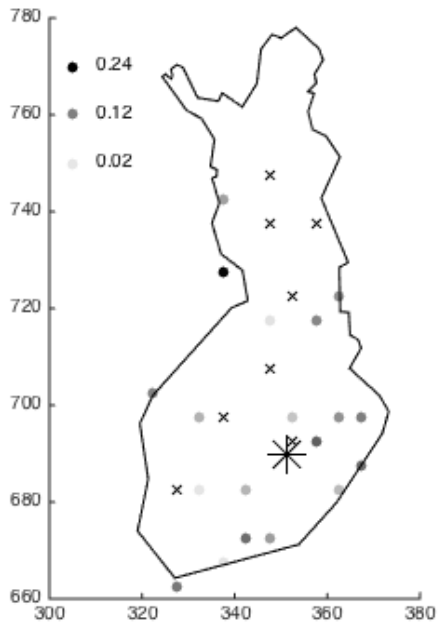
Supplementary fig. 4. *Tetrao tetrix*



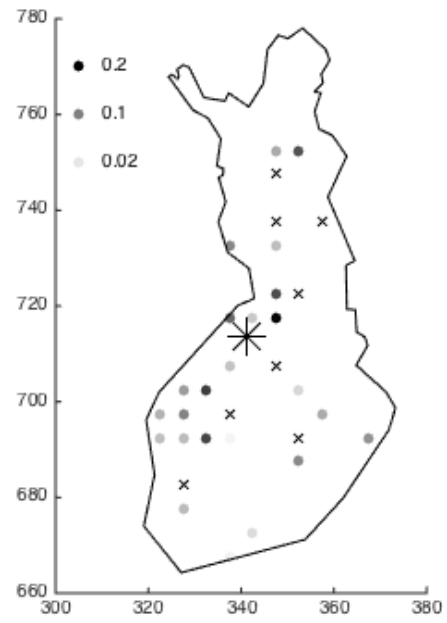
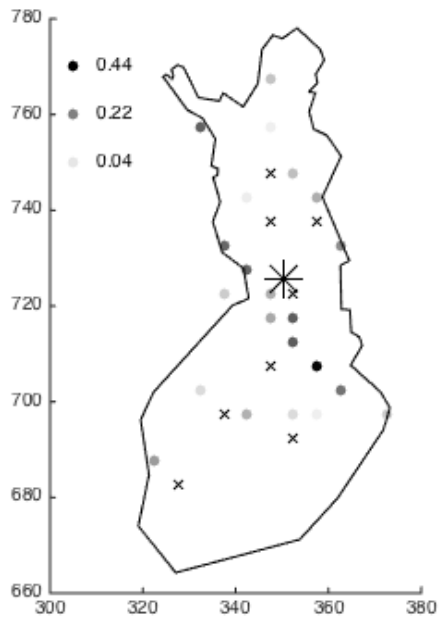
Supplementary fig. 5. *Tetrao urogallus*



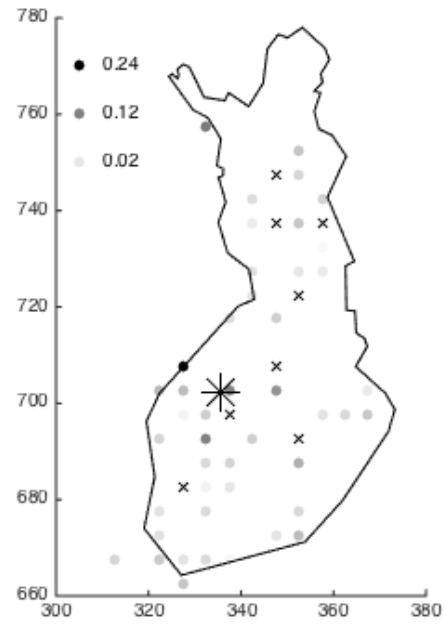
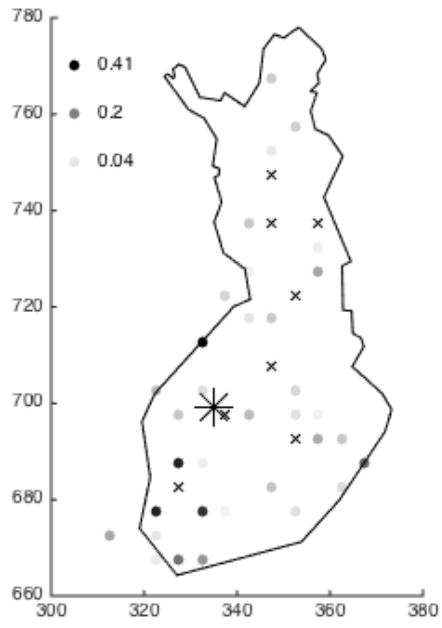
Supplementary fig. 6. *Phasianus colchicus*



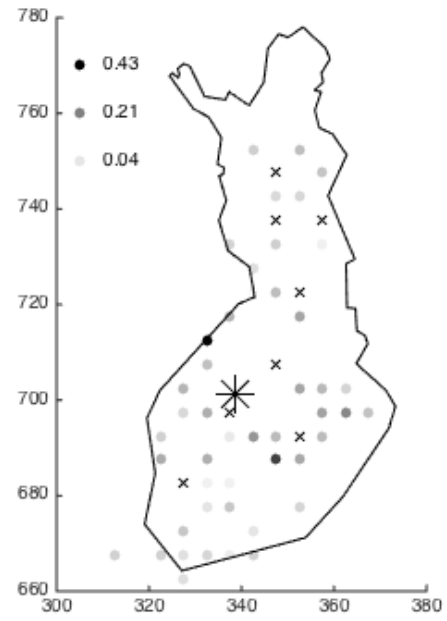
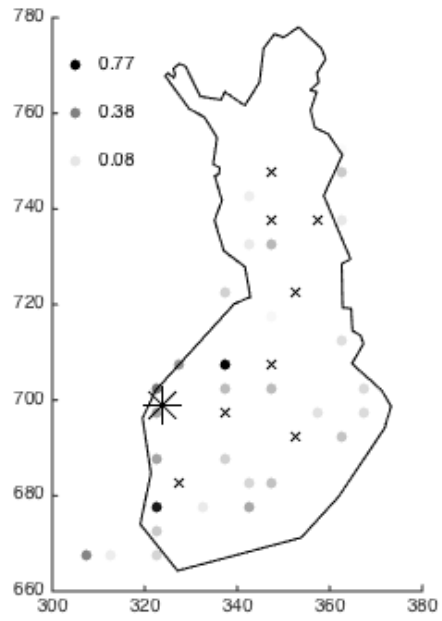
Supplementary fig. 7. *Pernis apivorus*



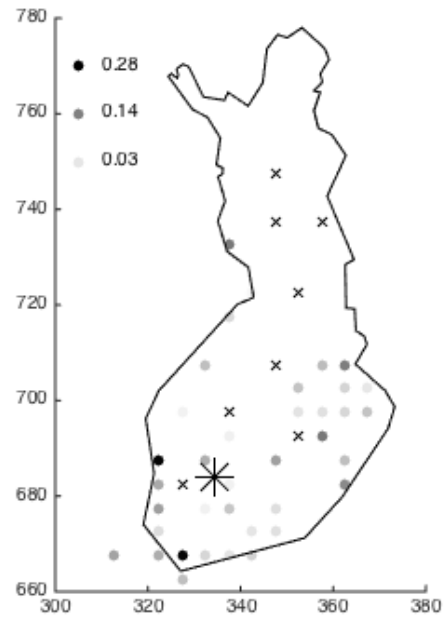
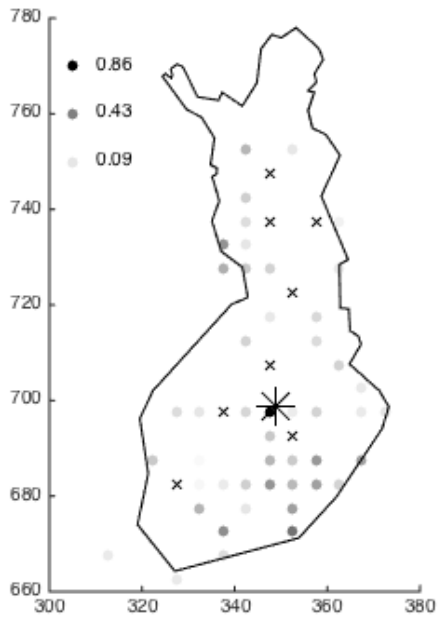
Supplementary fig. 8. *Circus cyaneus*



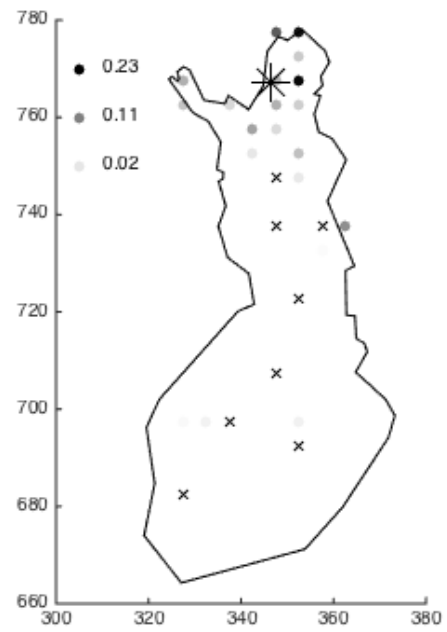
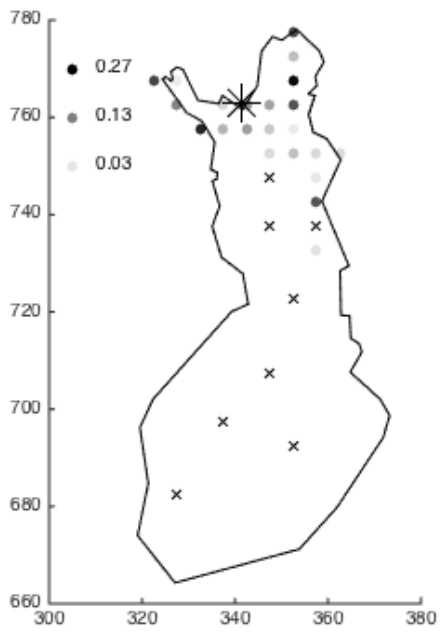
Supplementary fig. 9. *Accipiter gentilis*



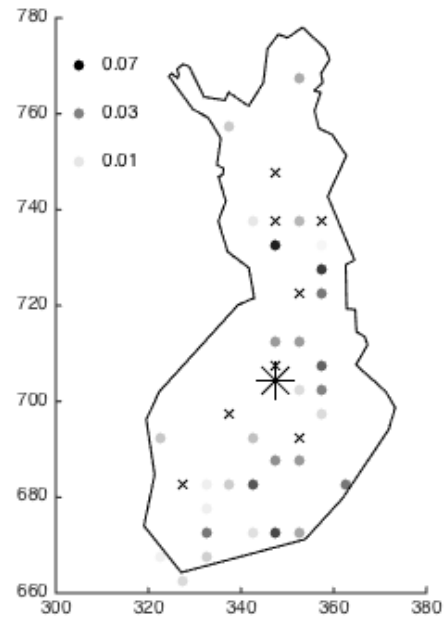
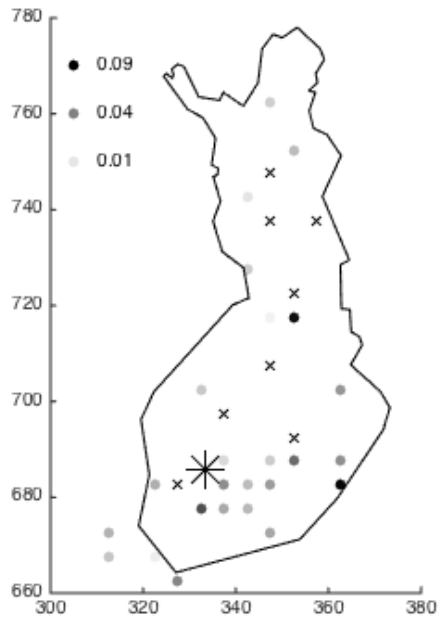
Supplementary fig. 10. *Accipiter nisus*



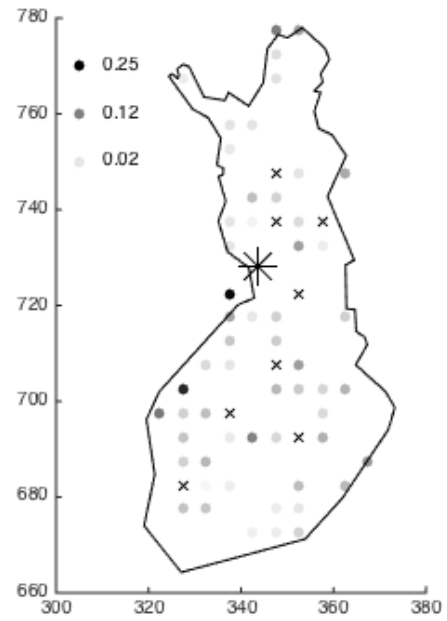
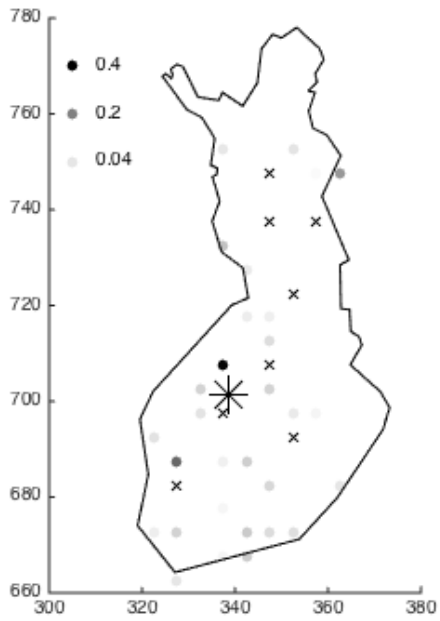
Supplementary fig. 11. *Buteo buteo*



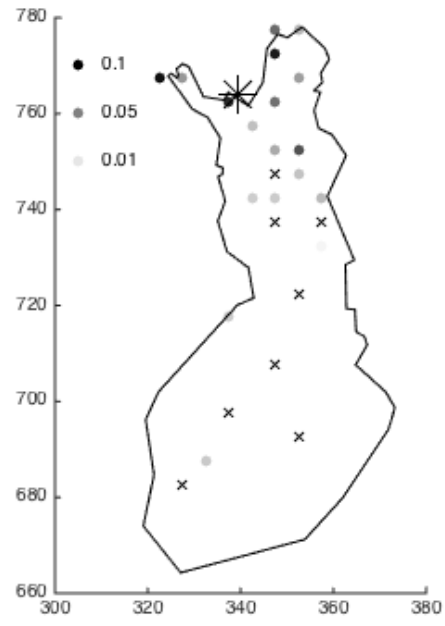
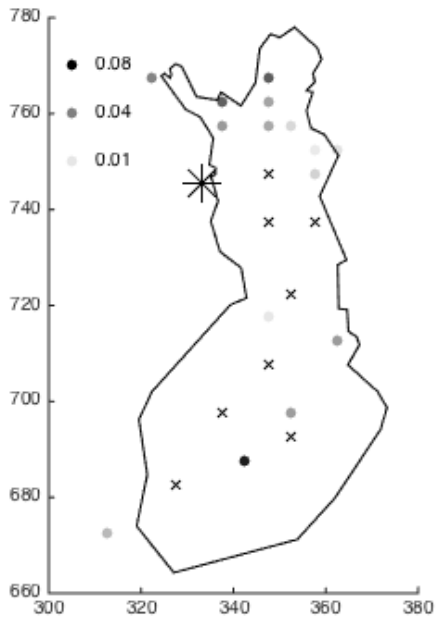
Supplementary fig. 12. *Buteo lagopus*



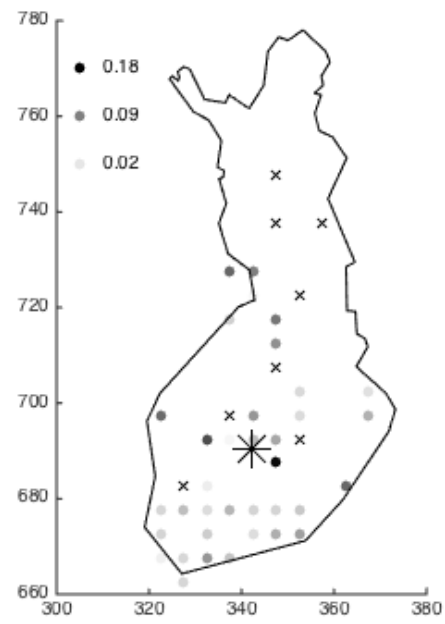
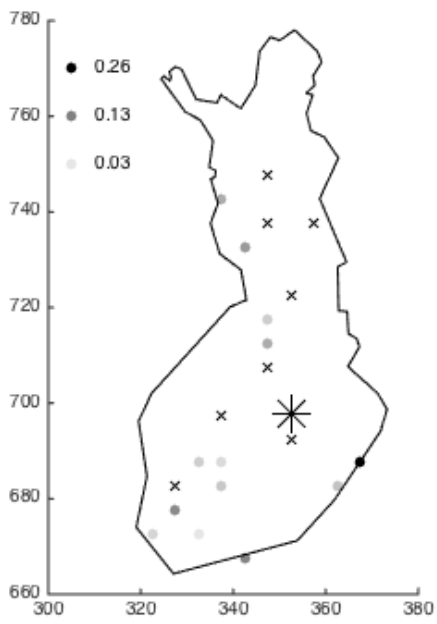
Supplementary fig. 13. *Pandion haliaetus*



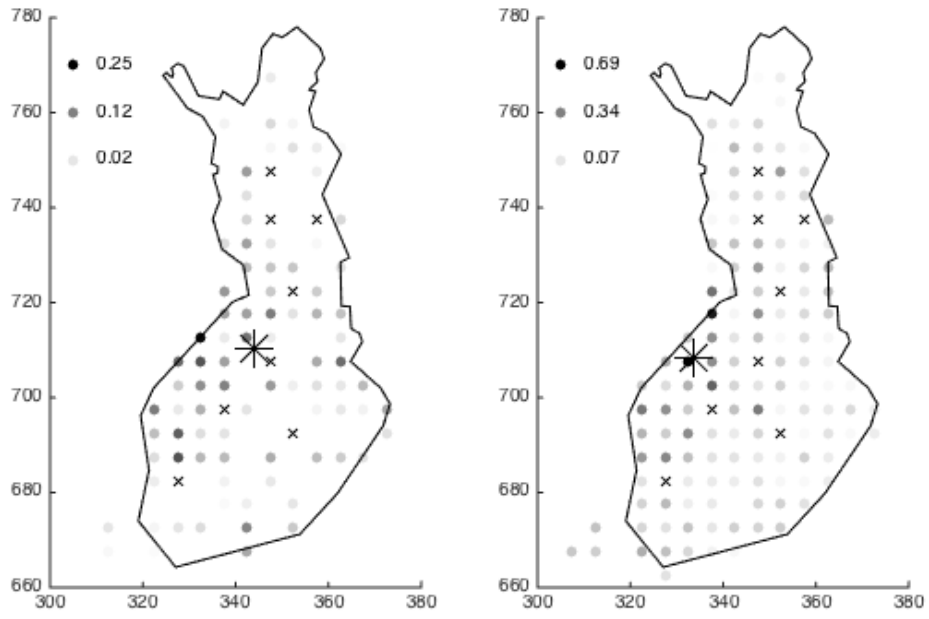
Supplementary fig. 14. *Falco tinnunculus*



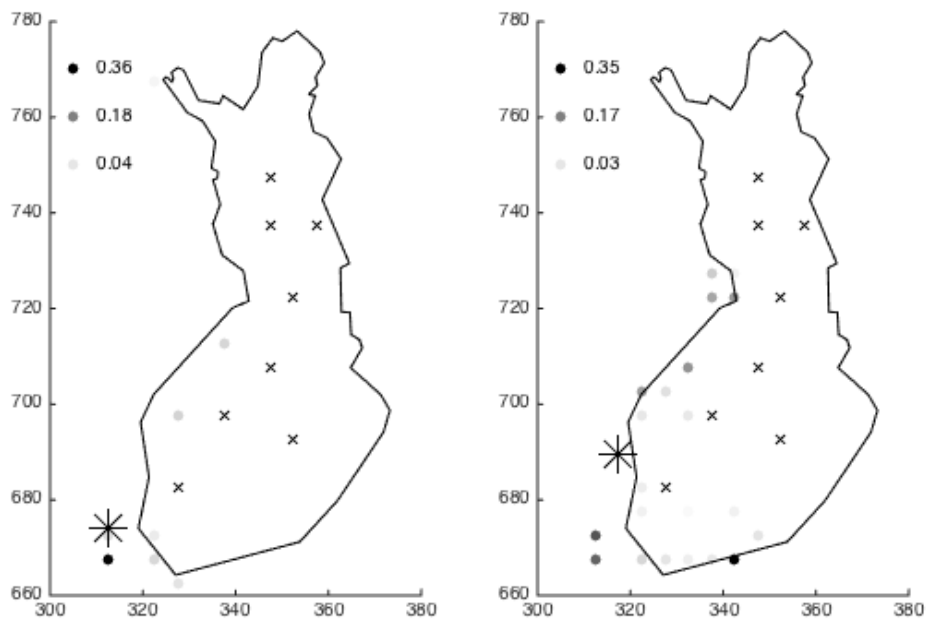
Supplementary fig. 15. *Falco columbarius*



Supplementary fig. 16. *Falco subbuteo*

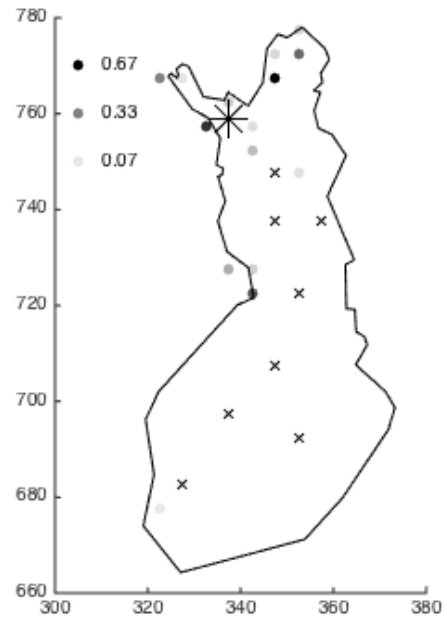
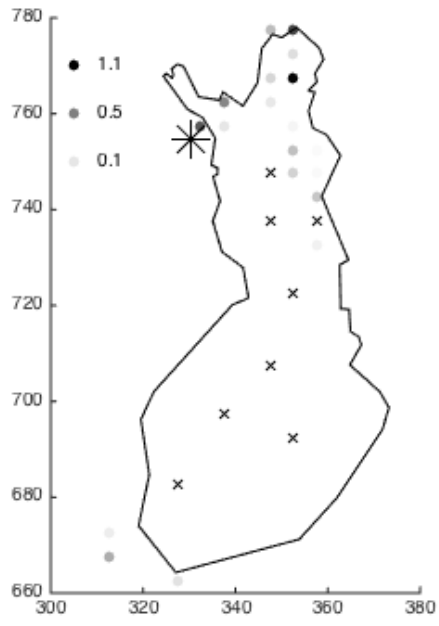


Supplementary fig. 17. *Grus grus*

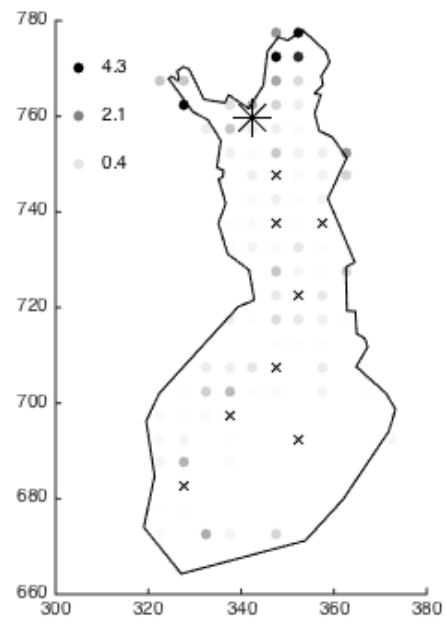
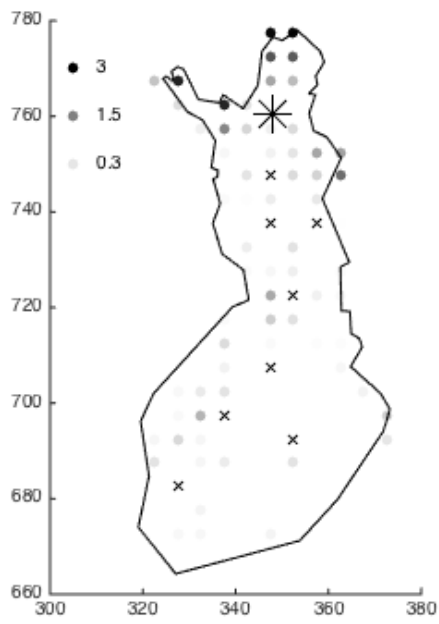


Supplementary fig. 18. *Haematopus ostralegus*

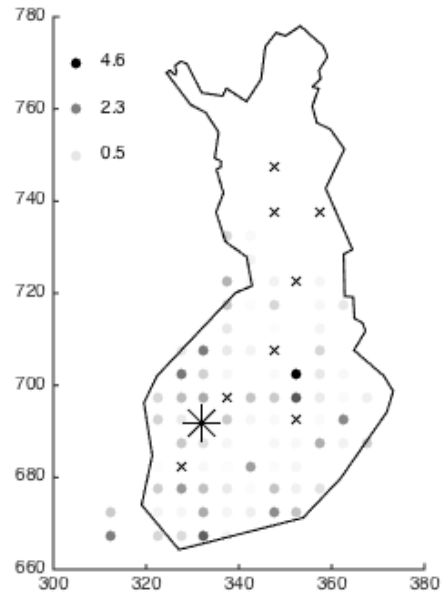
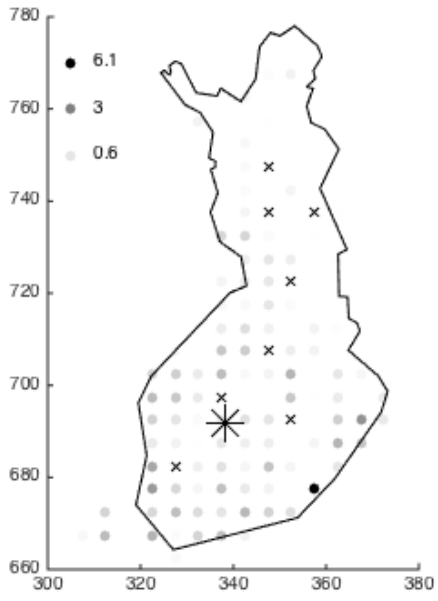




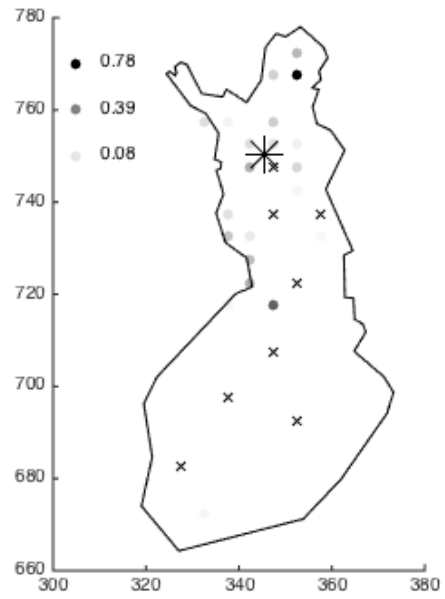
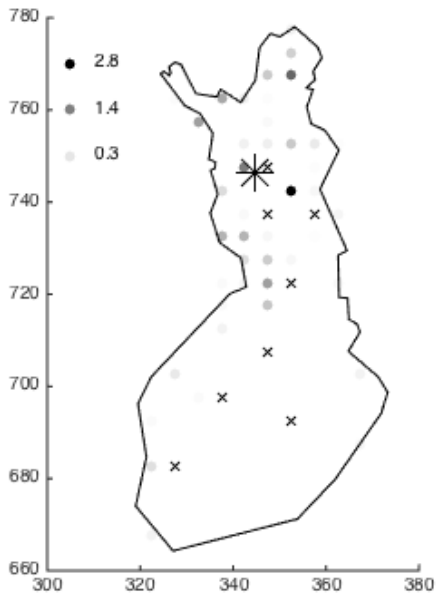
Supplementary fig. 19. *Charadrius hiaticula*



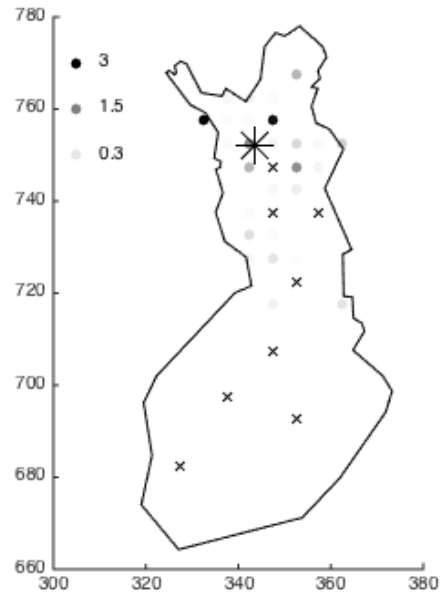
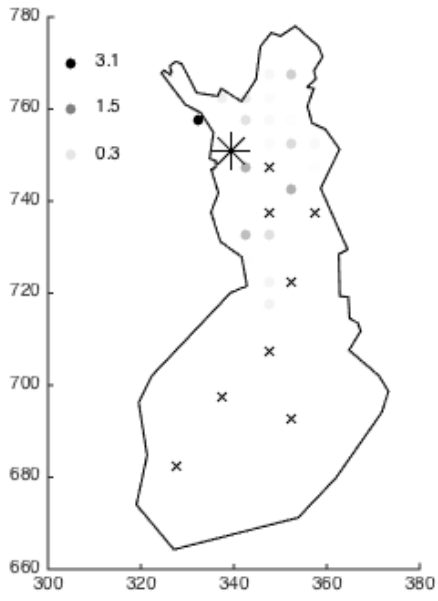
Supplementary fig. 20. *Pluvialis apricaria*



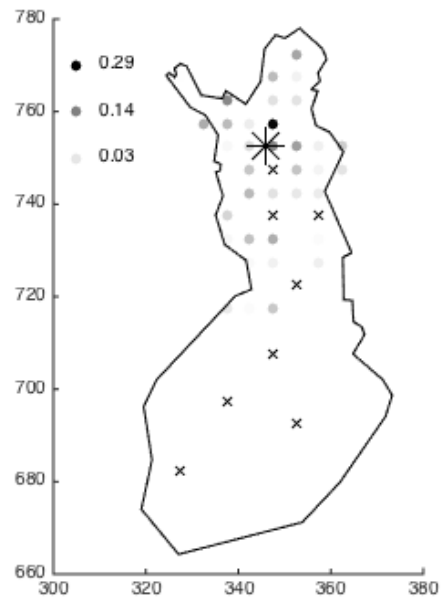
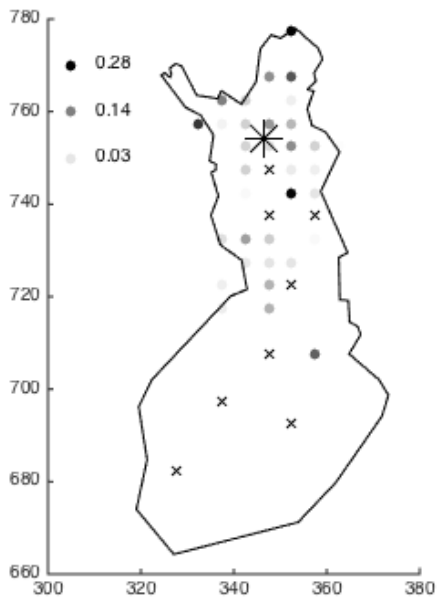
Supplementary fig. 21. *Vanellus vanellus*



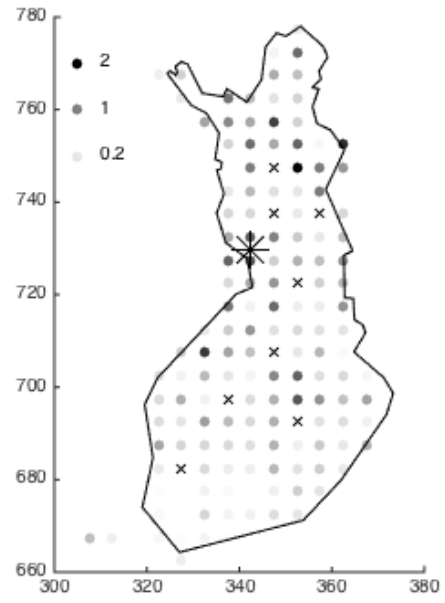
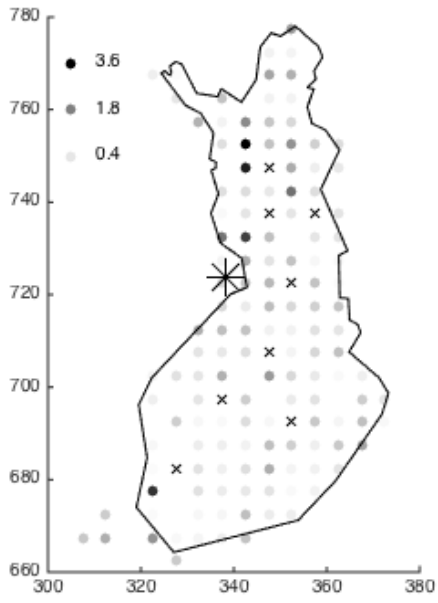
Supplementary fig. 22. *Calidris pugnax*



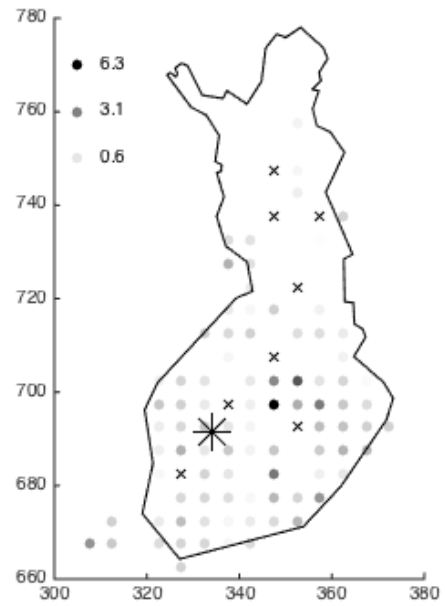
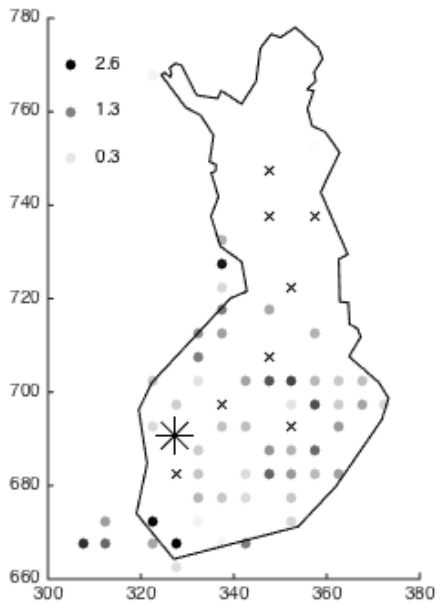
Supplementary fig. 23. *Calidris falcinellus*



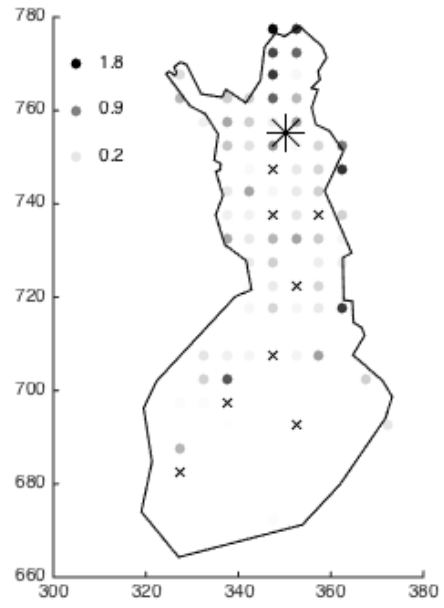
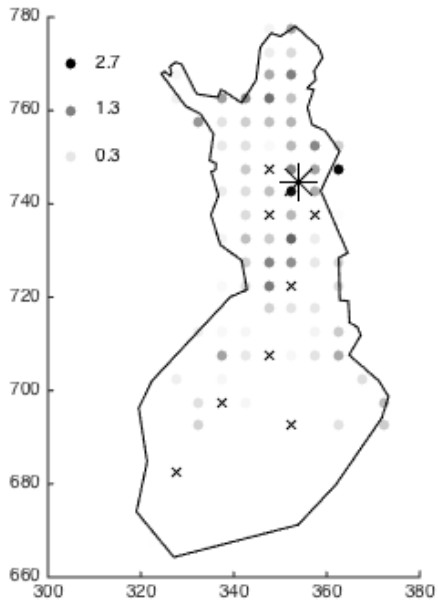
Supplementary fig. 24. *Lymnocyptes minumus*



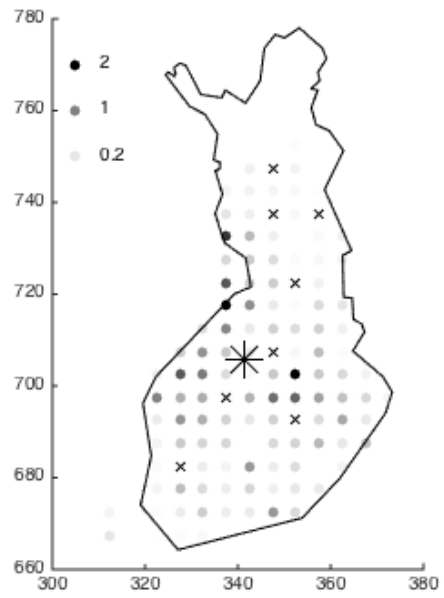
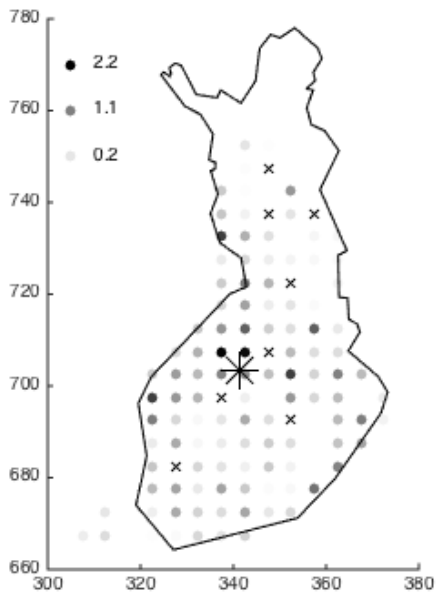
Supplementary fig. 25. *Gallinago gallinago*



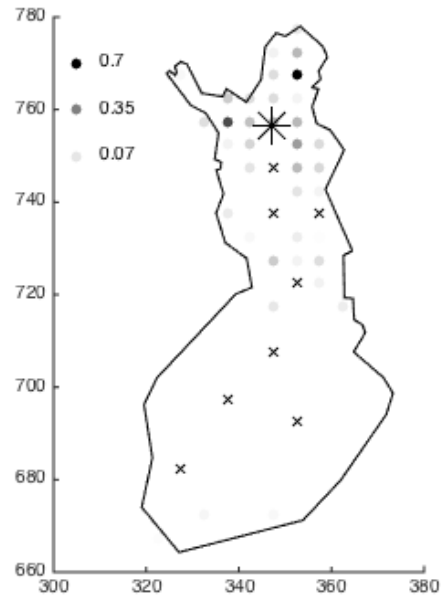
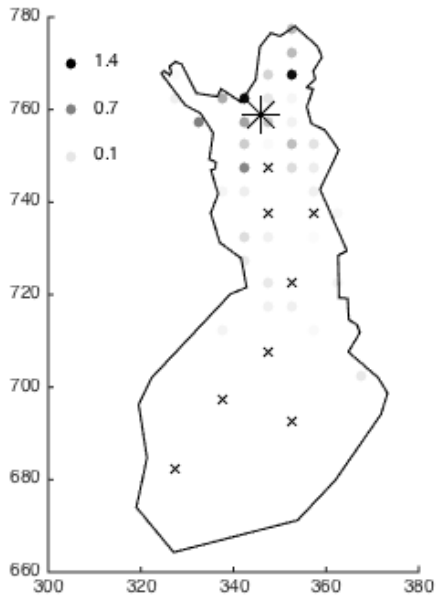
Supplementary fig. 26. *Scolopax rusticola*



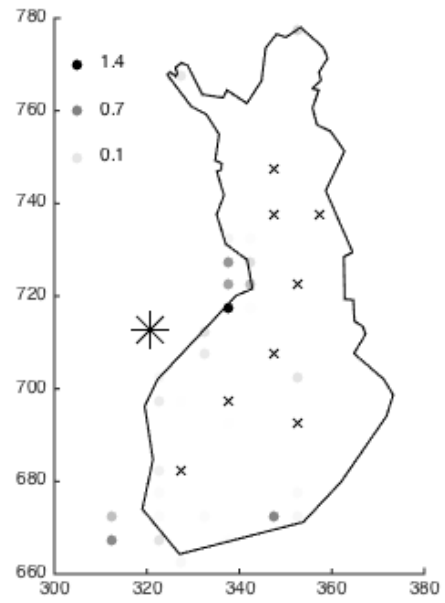
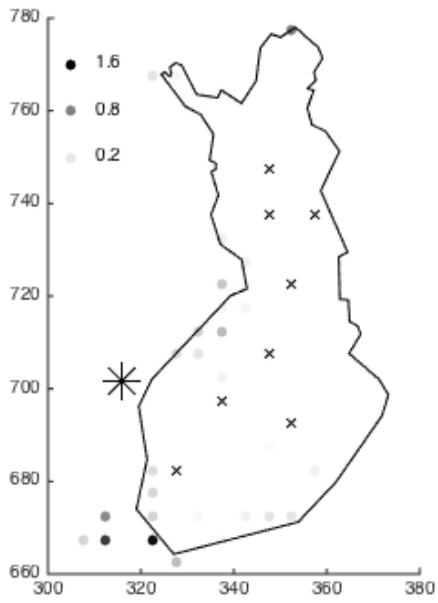
Supplementary fig. 27. *Numenius phaeopus*



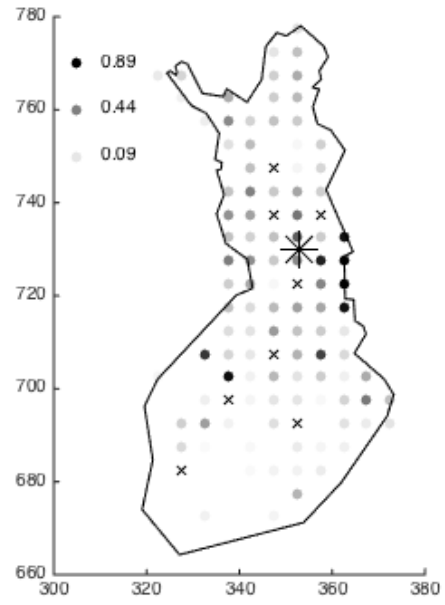
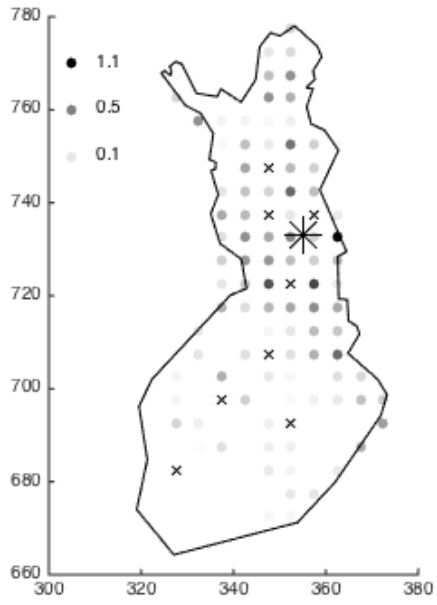
Supplementary fig. 28. *Numenius arquata*



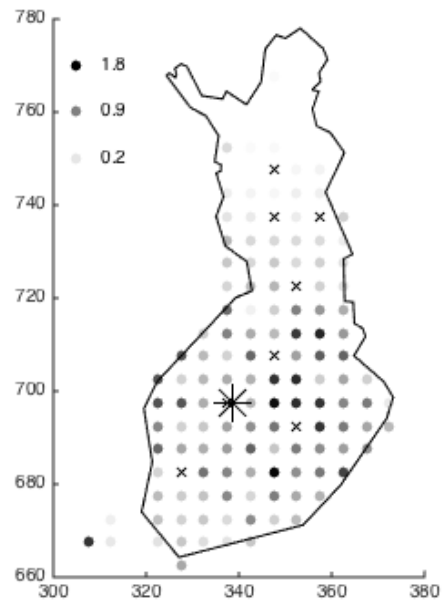
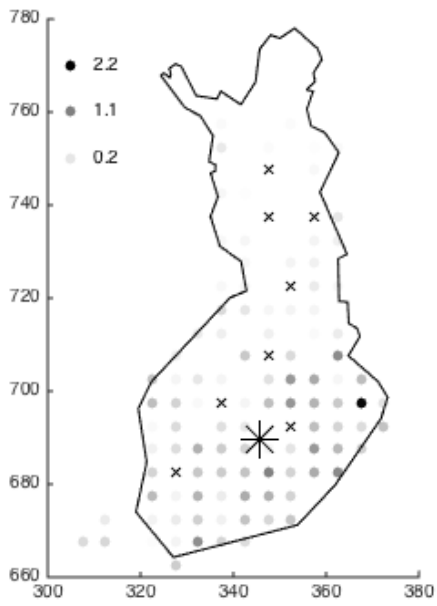
Supplementary fig. 29. *Tringa erythropus*



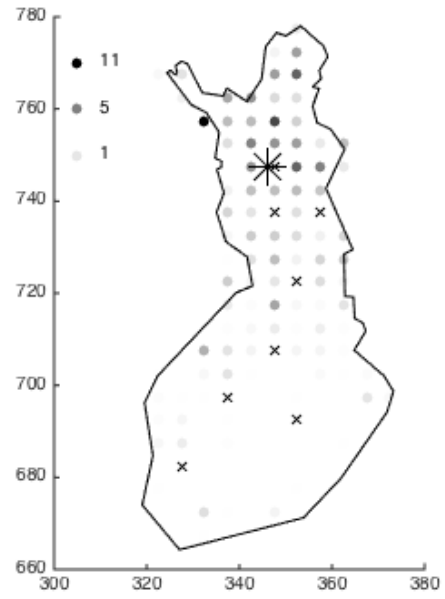
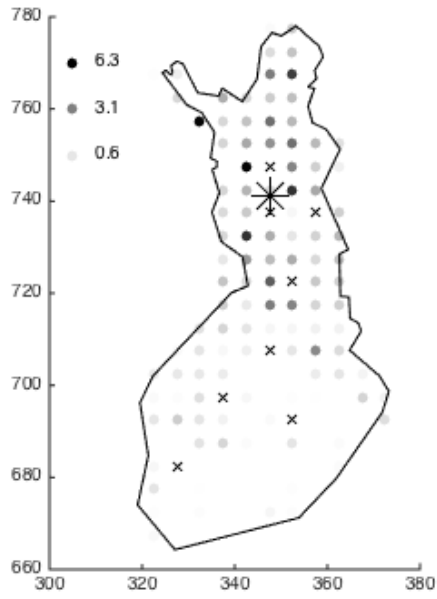
Supplementary fig. 30. *Tringa totanus*



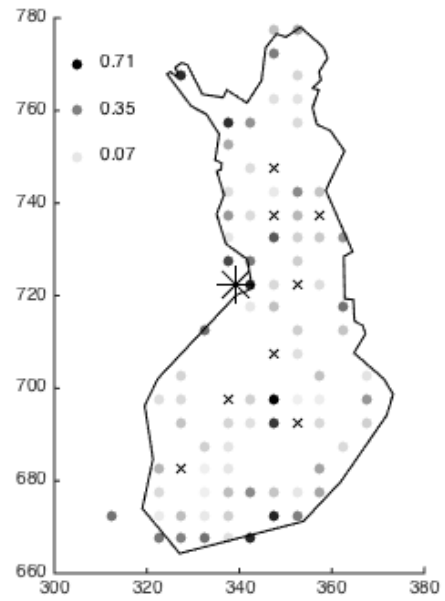
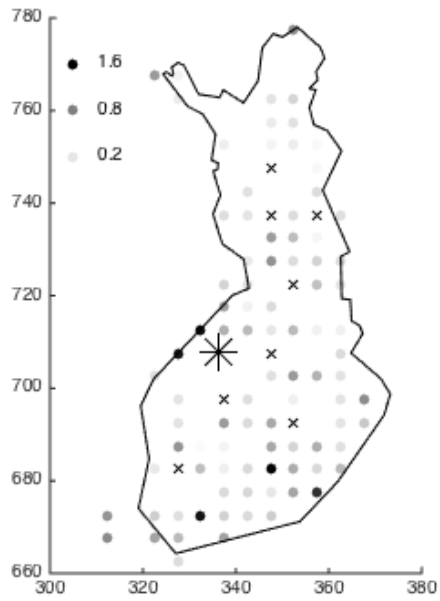
Supplementary fig. 31. *Tringa nebularia*



Supplementary fig. 32. *Tringa ochropus*

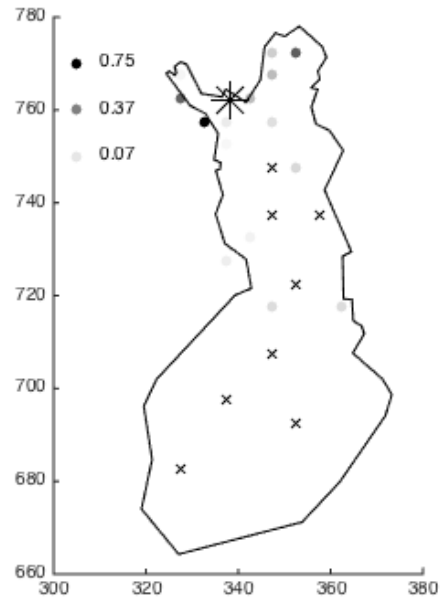
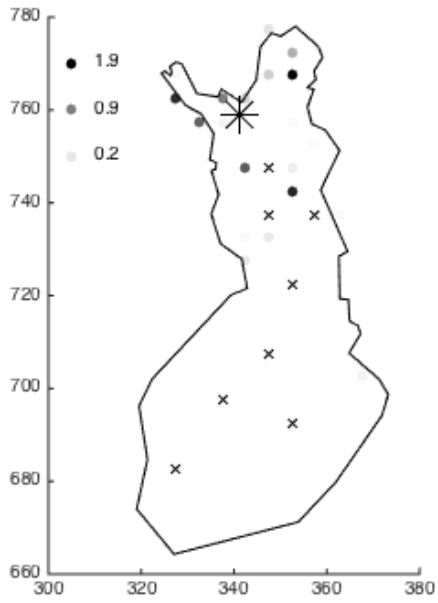


Supplementary fig. 33. *Tringa glareola*

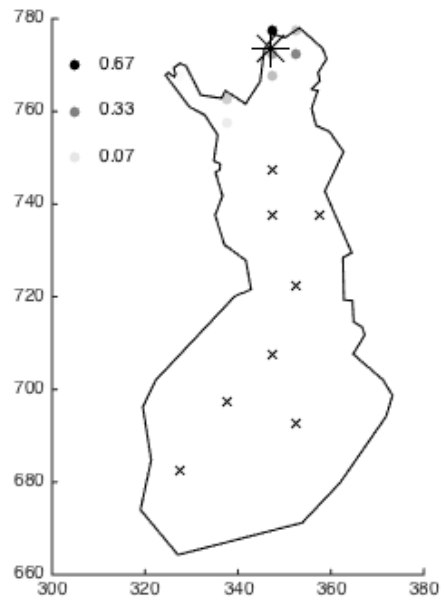
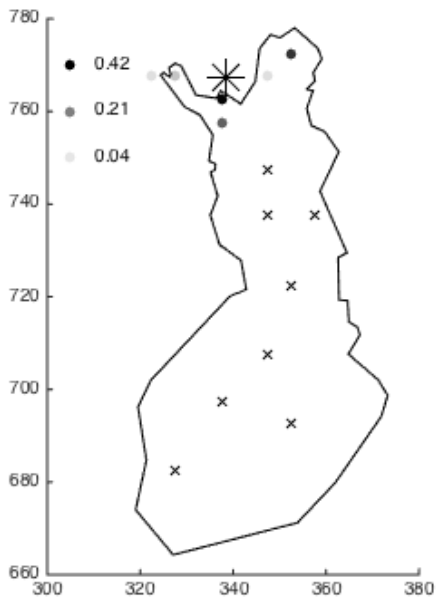


Supplementary fig. 34. *Actitis hypoleucos*

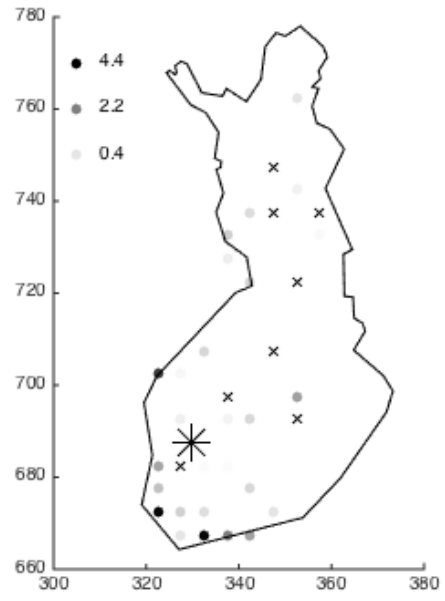
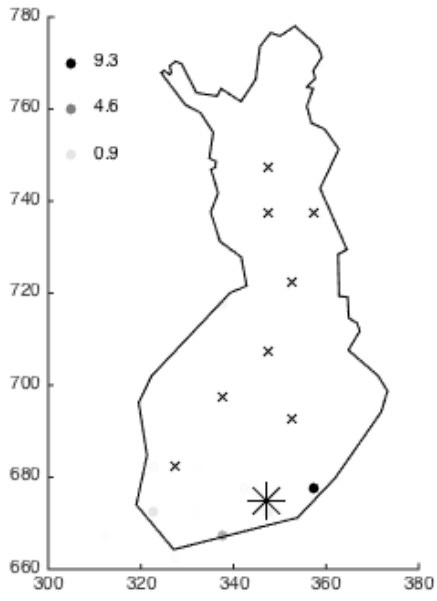




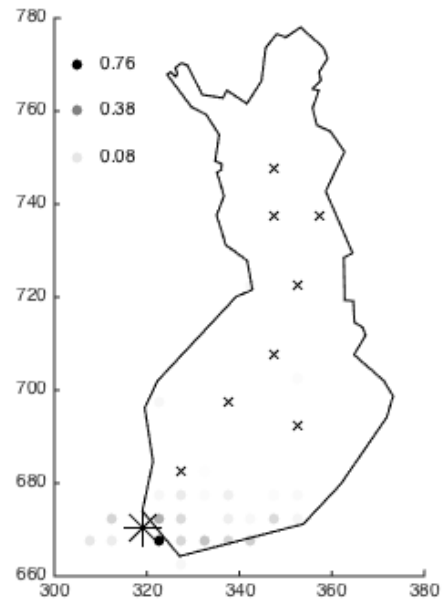
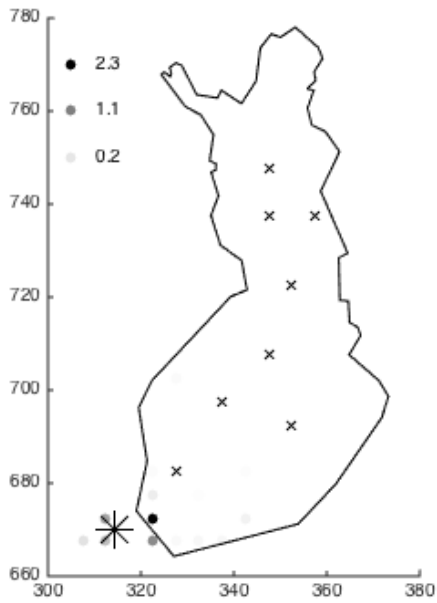
Supplementary fig. 35. *Phalaropus lobatus*



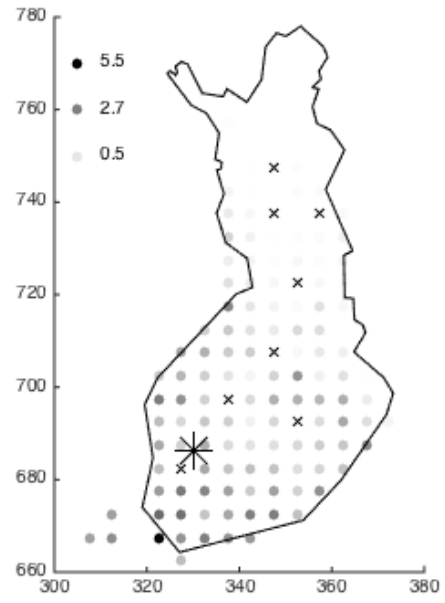
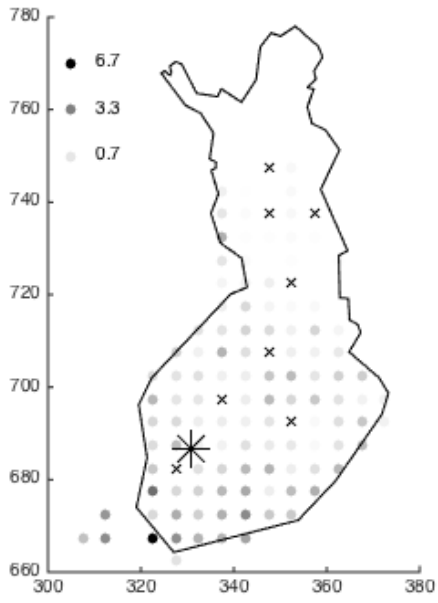
Supplementary fig. 36. *Stercorarius longicaudus*



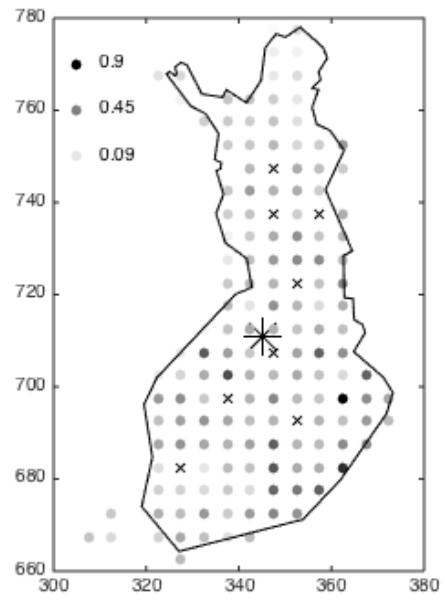
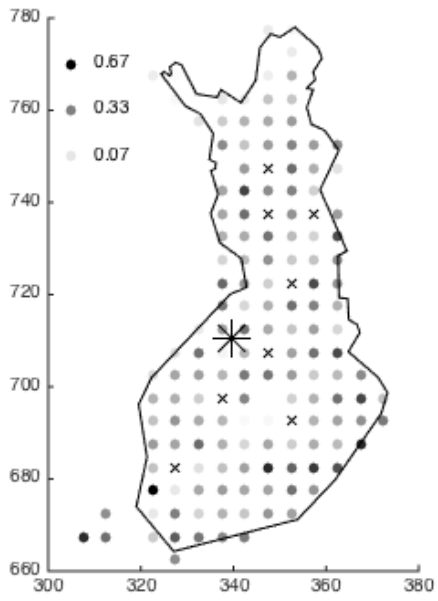
Supplementary fig. 37. *Columba livia*



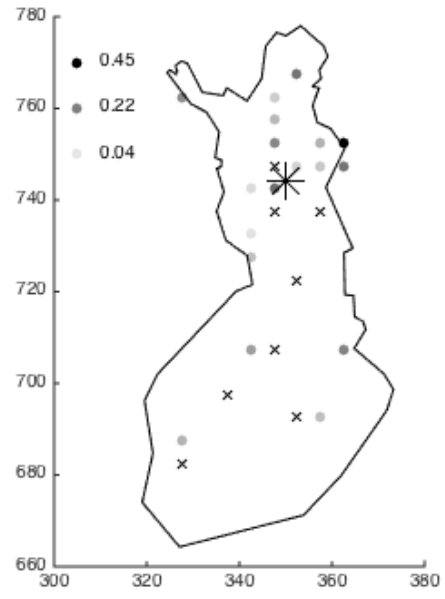
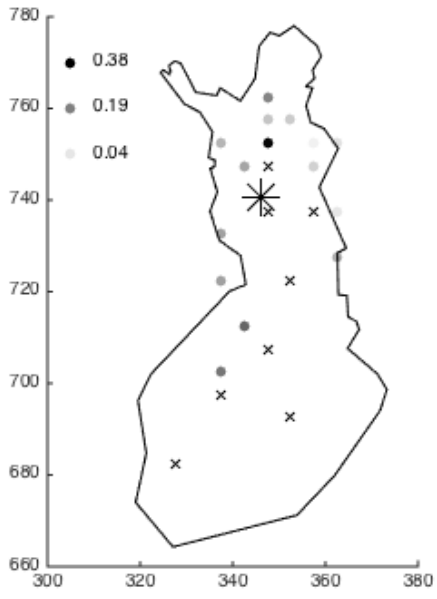
Supplementary fig. 38. *Columba oenas*



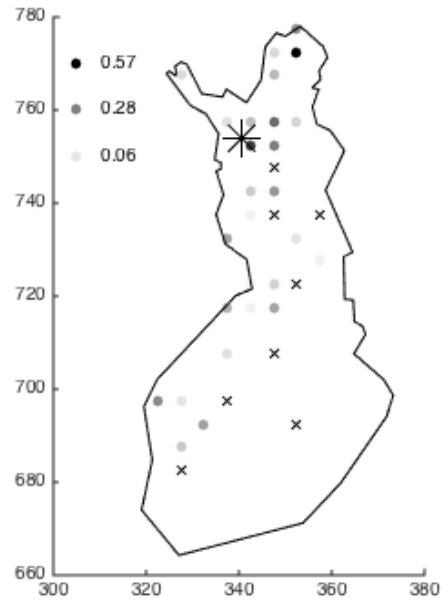
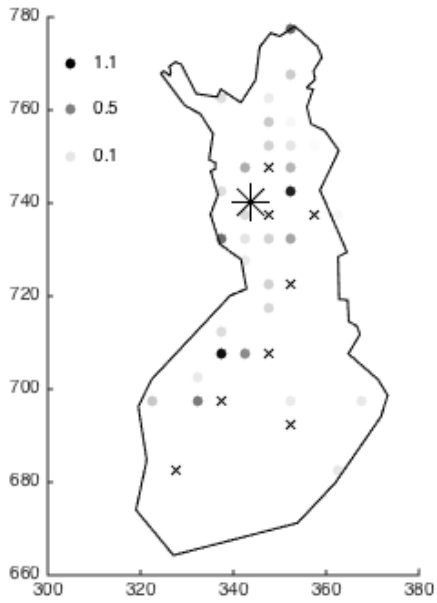
Supplementary fig. 39. *Columba palumbus*



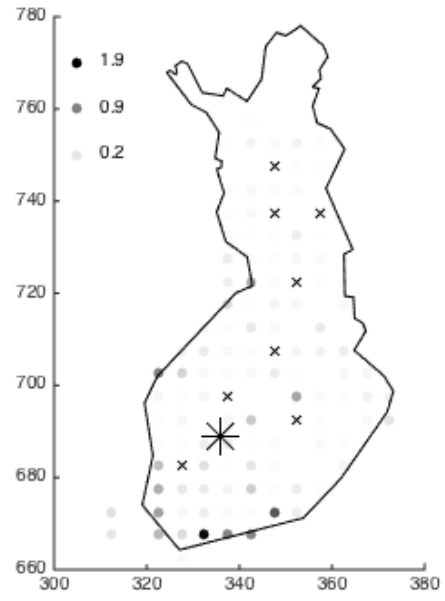
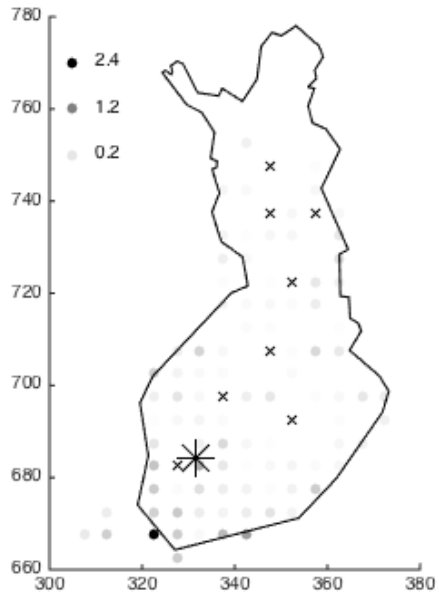
Supplementary fig. 40. *Cuculus canorus*



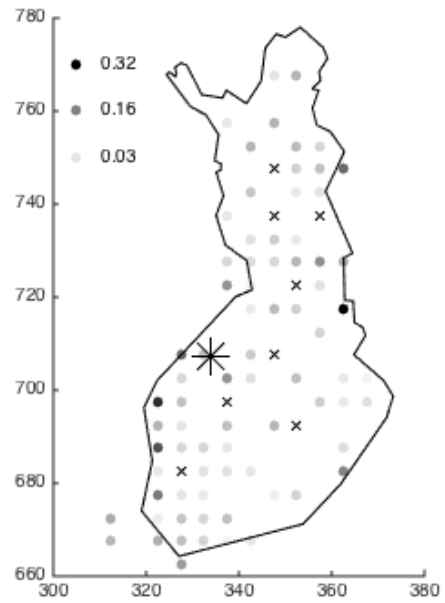
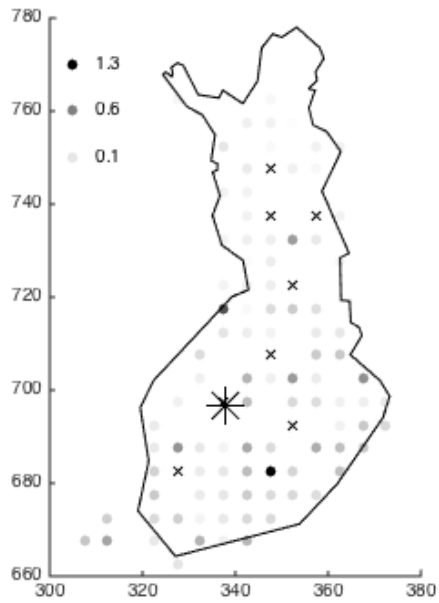
Supplementary fig. 41. *Surnia ulula*



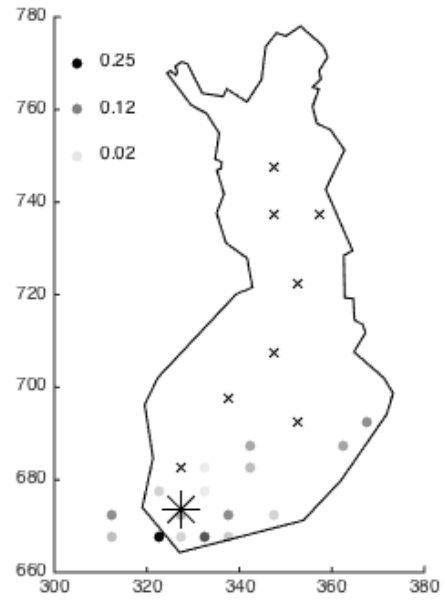
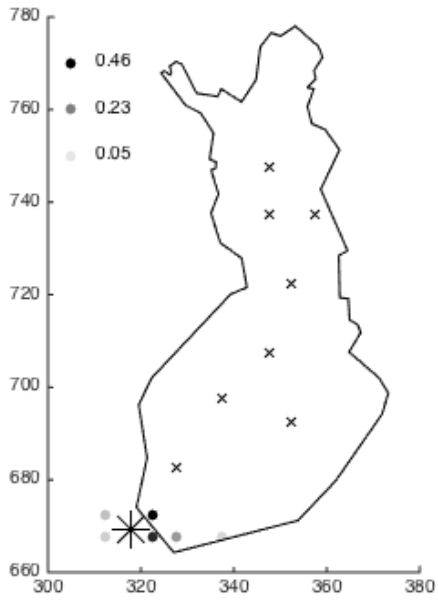
Supplementary fig. 42. *Asio flammeus*



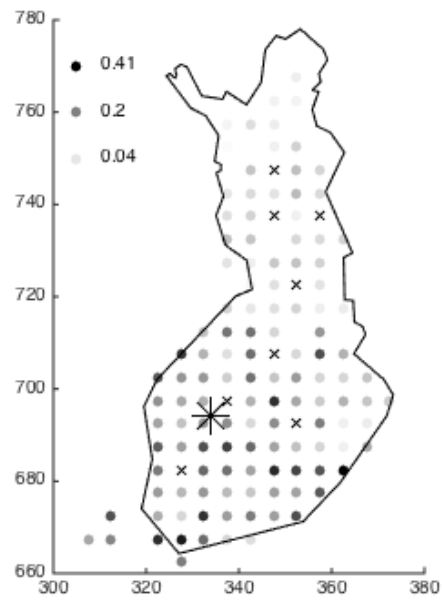
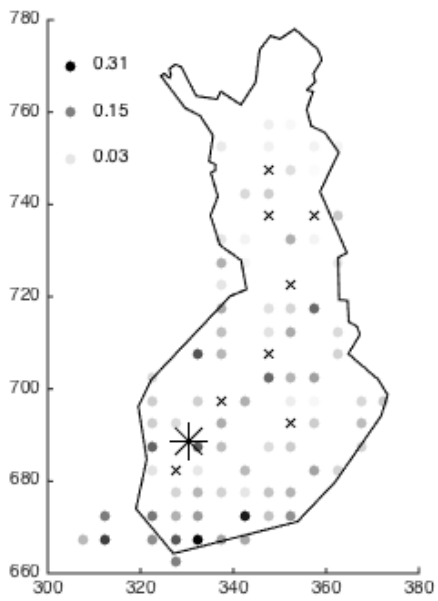
Supplementary fig. 43. *Apus apus*



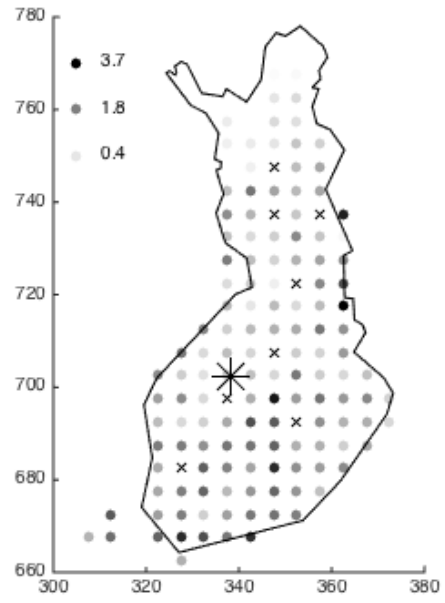
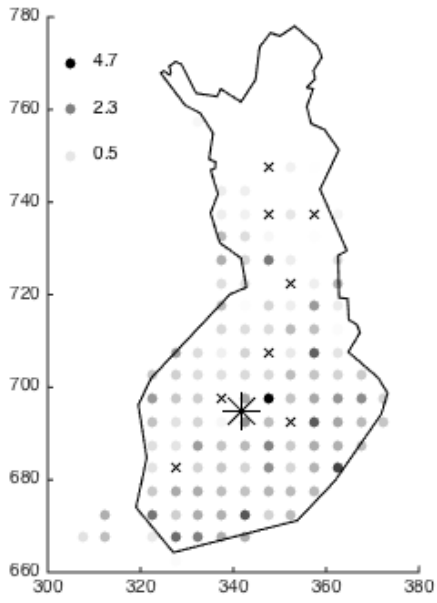
Supplementary fig. 44. *Jynx torquilla*



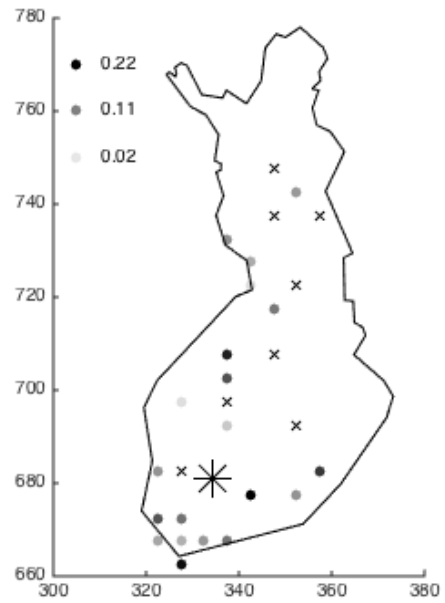
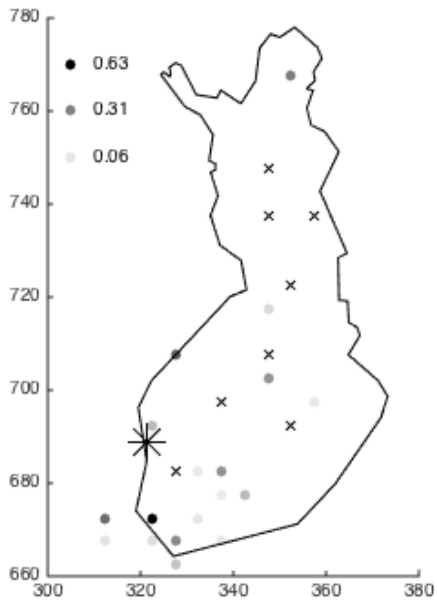
Supplementary fig. 45. *Picus canus*



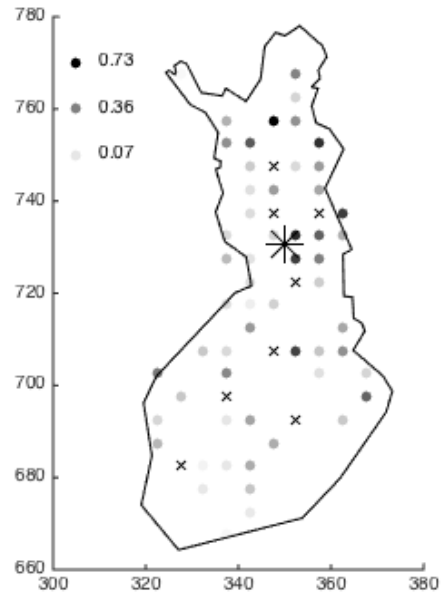
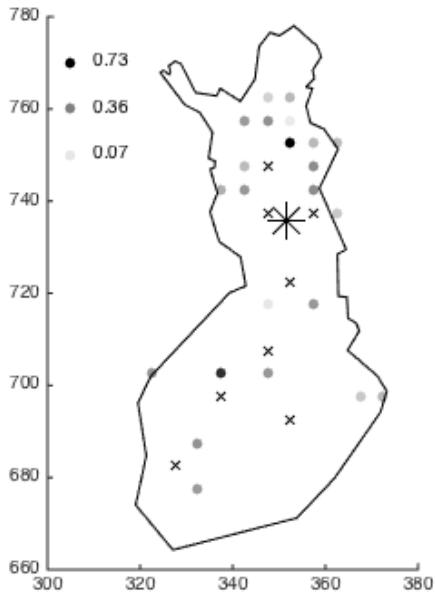
Supplementary fig. 46. *Dryocopus martius*



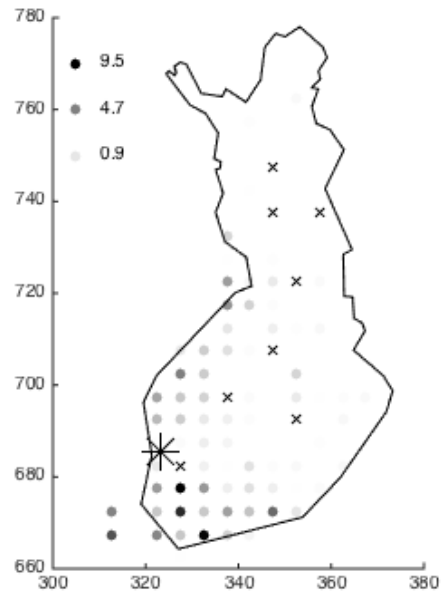
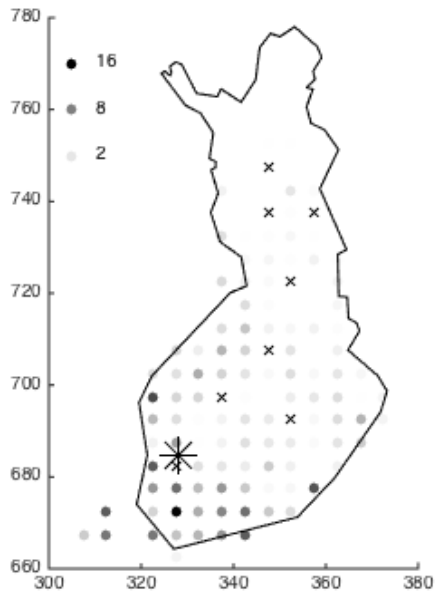
Supplementary fig. 47. *Dendrocopos major*



Supplementary fig. 48. *Dendrocopos minor*

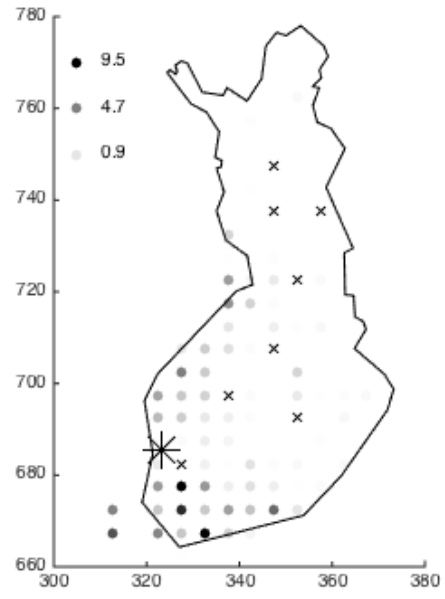
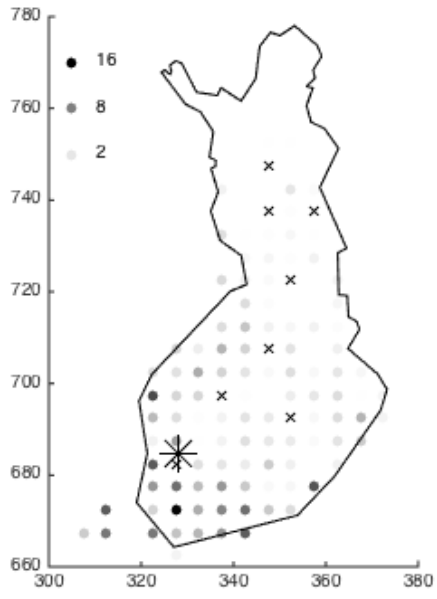


Supplementary fig. 49. *Picoides tridactylus*

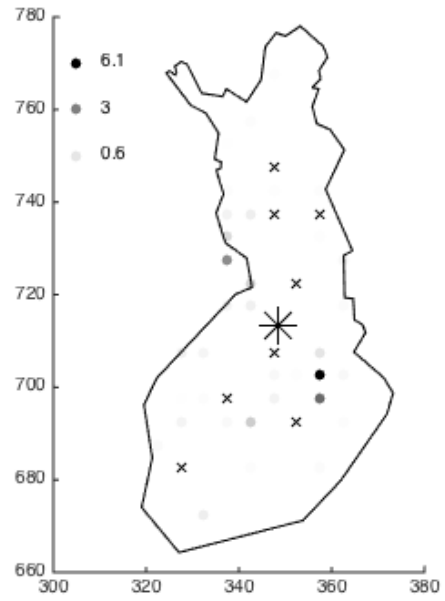
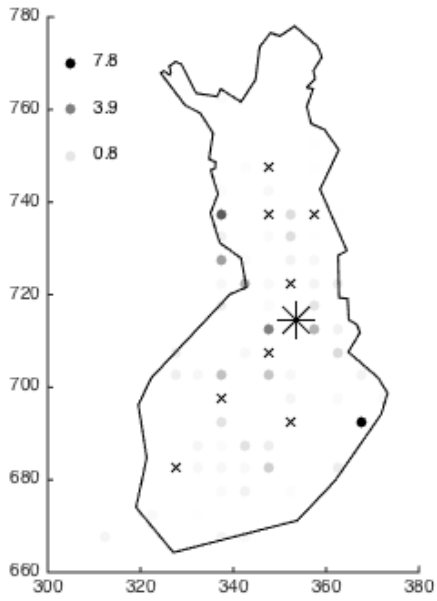


Supplementary fig. 50. *Lullula arborea*

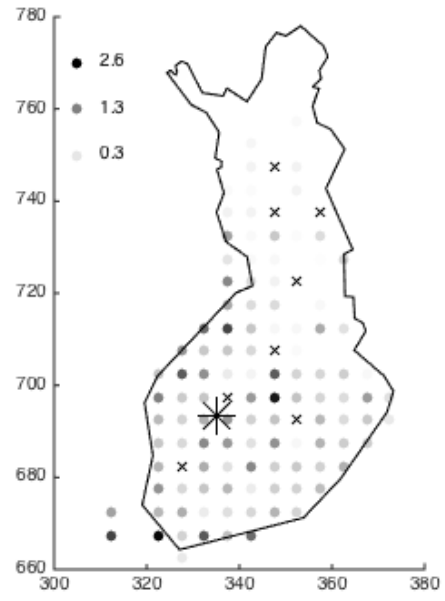
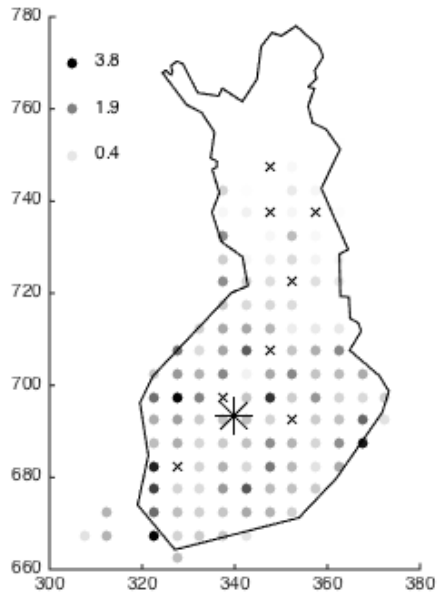




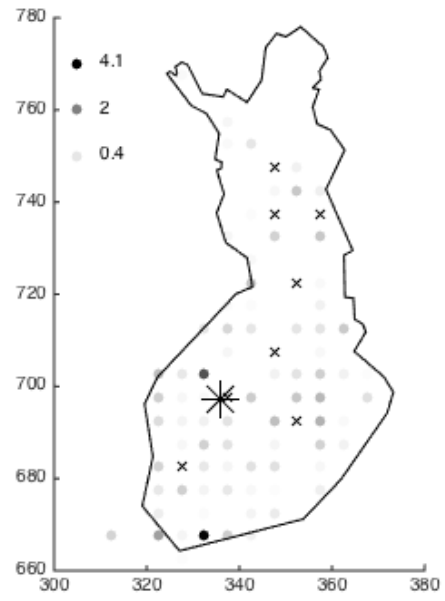
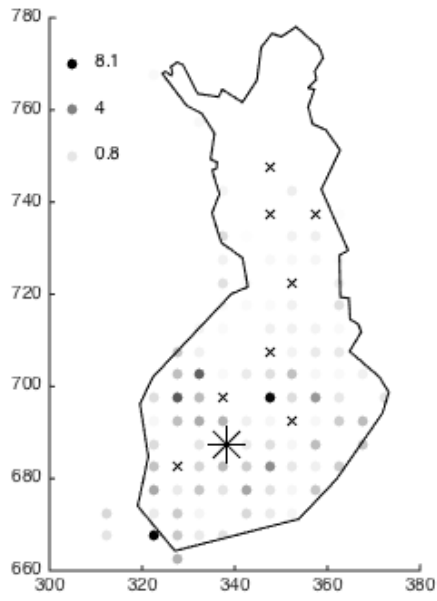
Supplementary fig. 51. *Alauda arvensis*



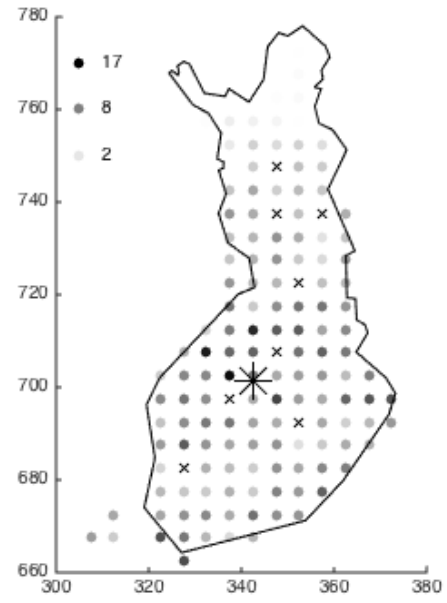
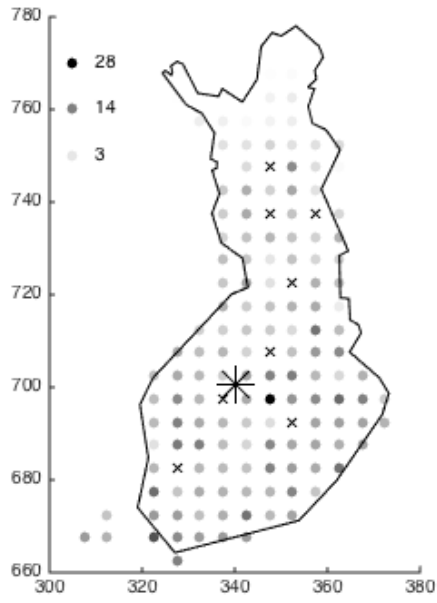
Supplementary fig. 52. *Riparia riparia*



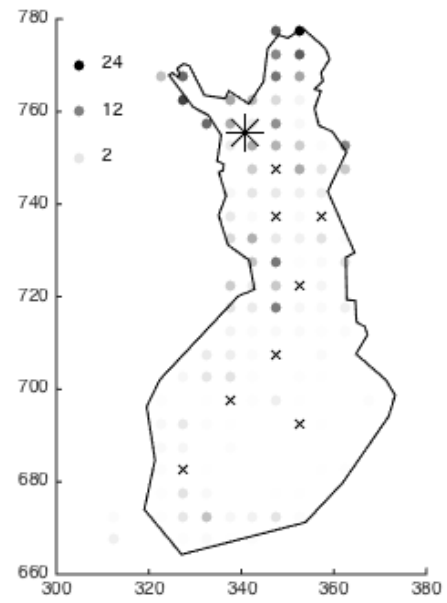
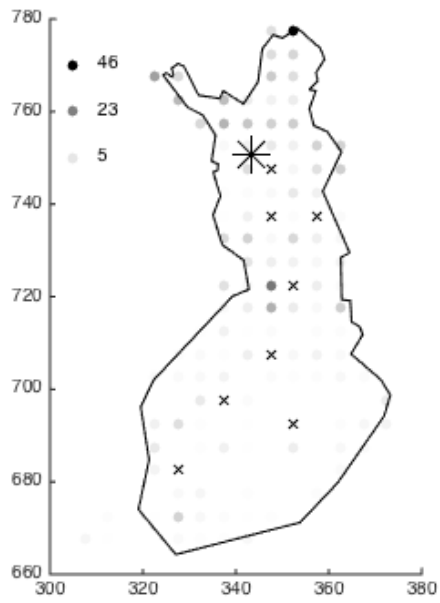
Supplementary fig. 53. *Hirundo rustica*



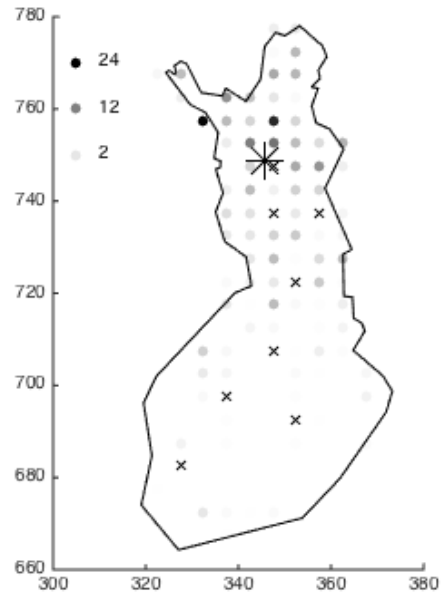
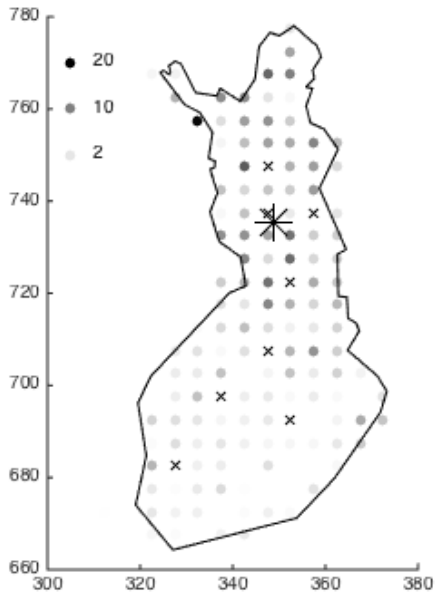
Supplementary fig. 54. *Delichon urbicum*



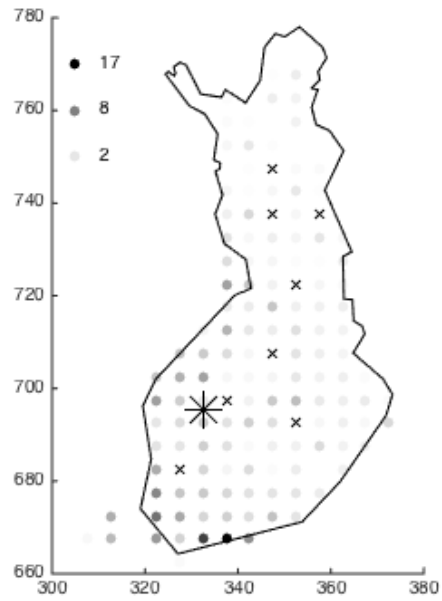
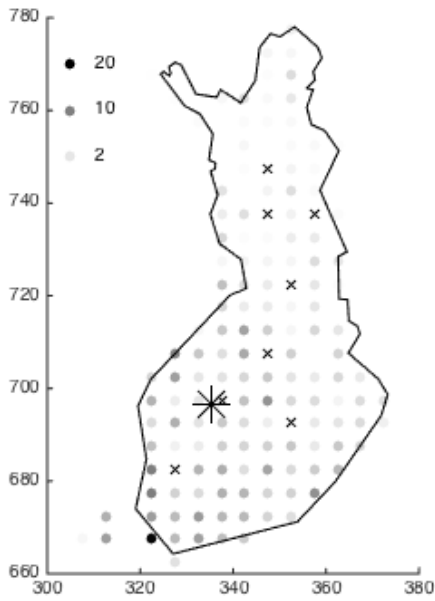
Supplementary fig. 55. *Anthus trivialis*



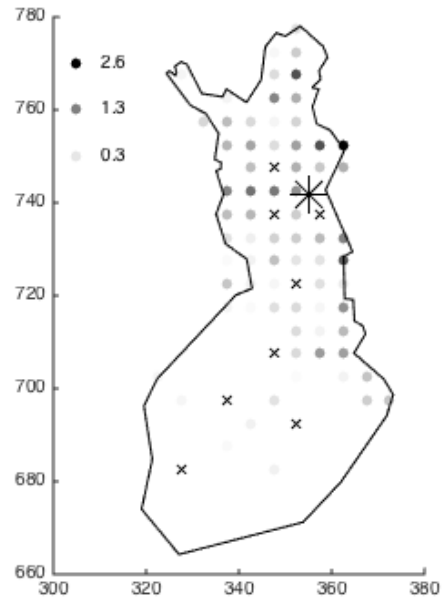
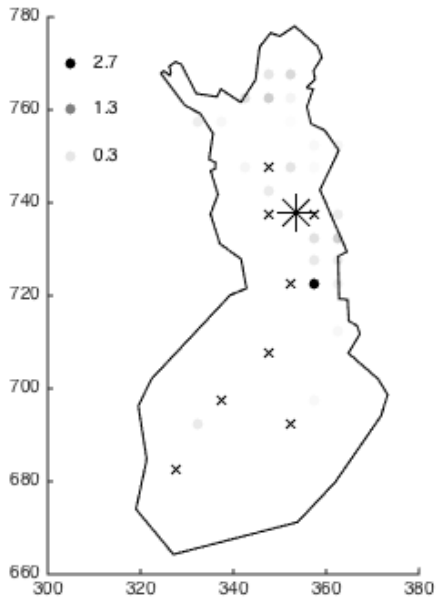
Supplementary fig. 56. *Anthus prantensis*



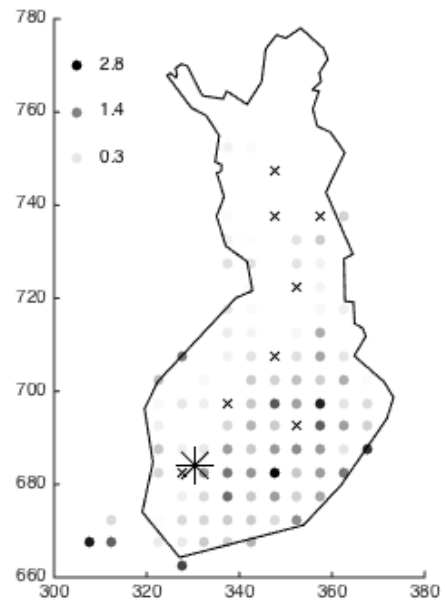
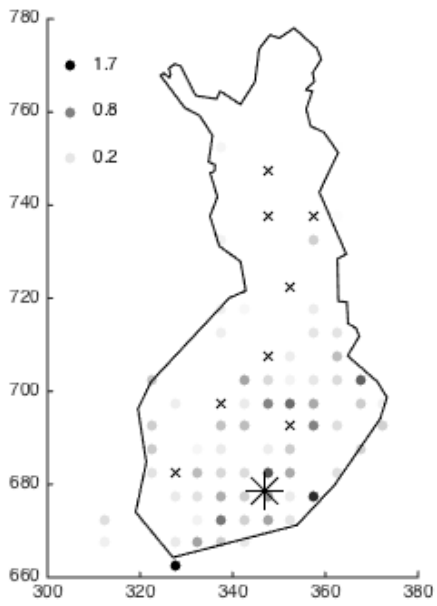
Supplementary fig. 57. *Motacilla flava*



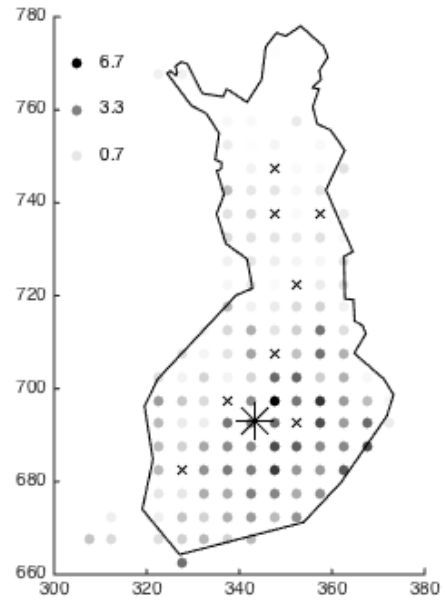
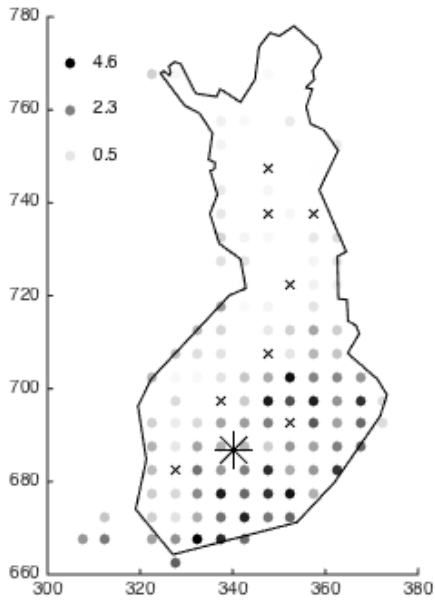
Supplementary fig. 58. *Motacilla alba*



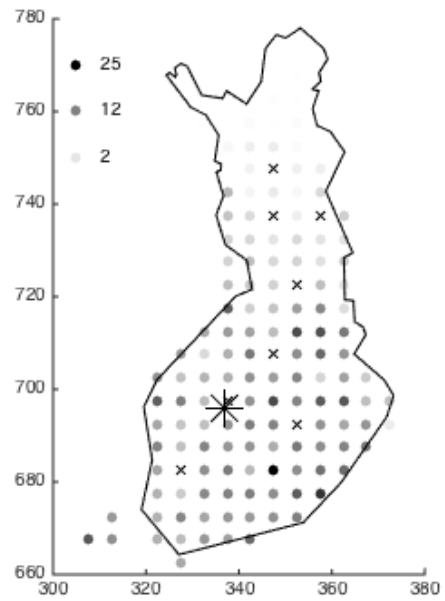
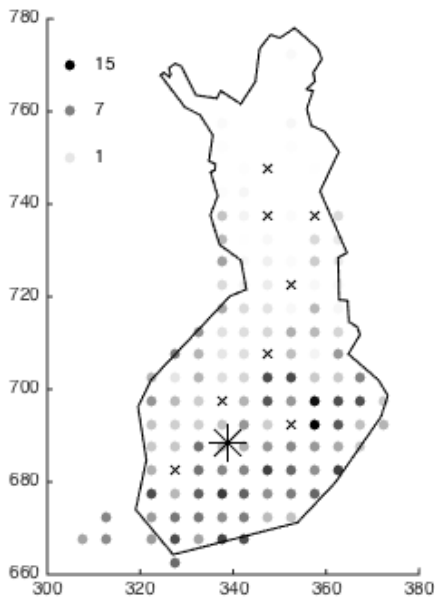
Supplementary fig. 59. *Bombycilla garrulus*



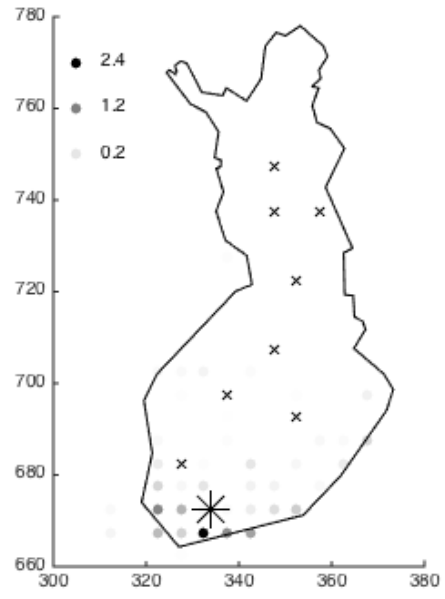
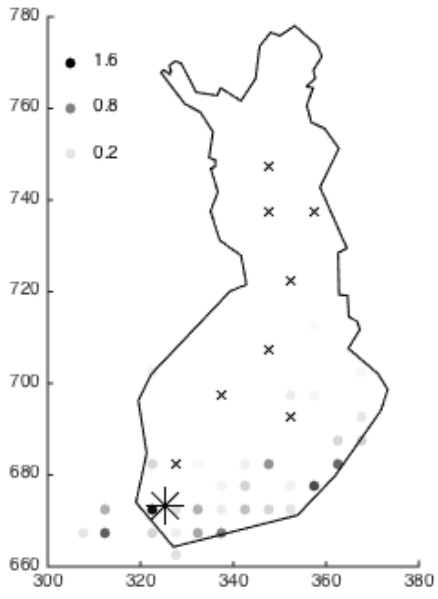
Supplementary fig. 60. *Troglodytes troglodytes*



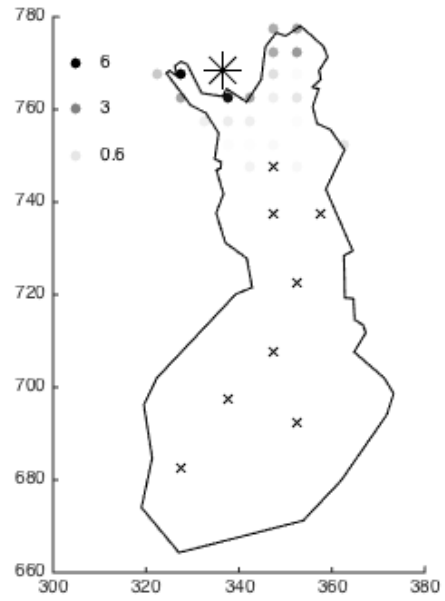
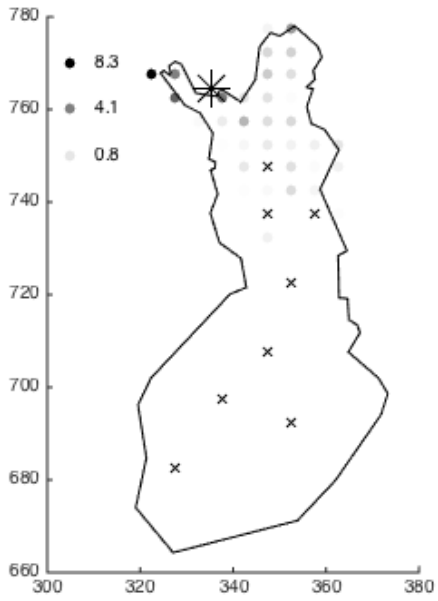
Supplementary fig. 61. *Prunella modularis*



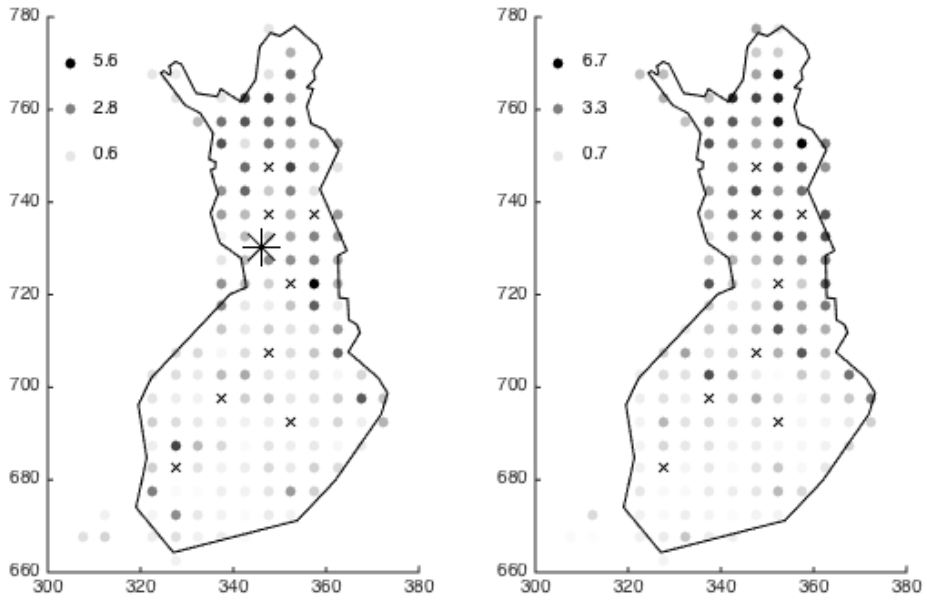
Supplementary fig. 62. *Erithacus rubecula*



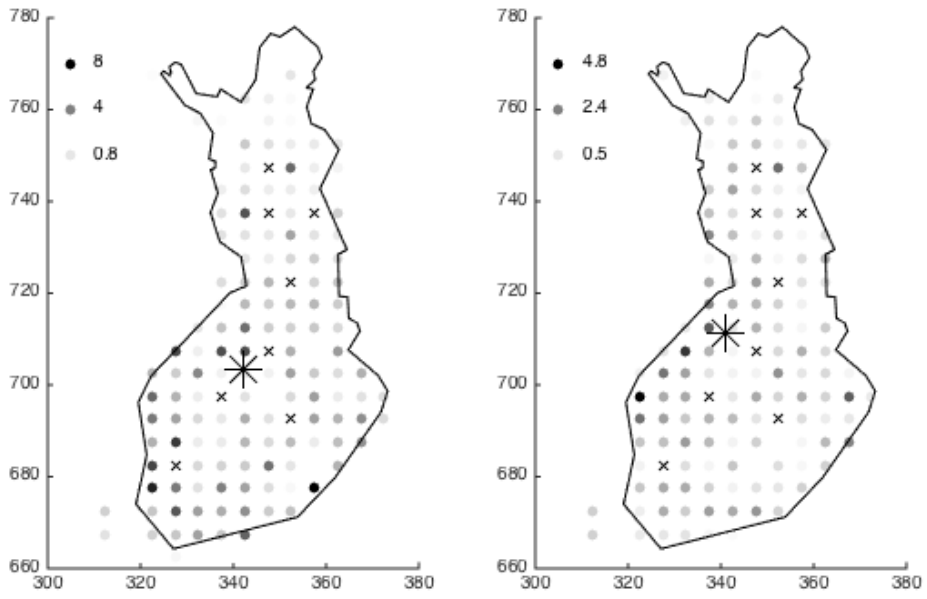
Supplementary fig. 63. *Luscinia luscinia*



Supplementary fig. 64. *Luscinia svecica*

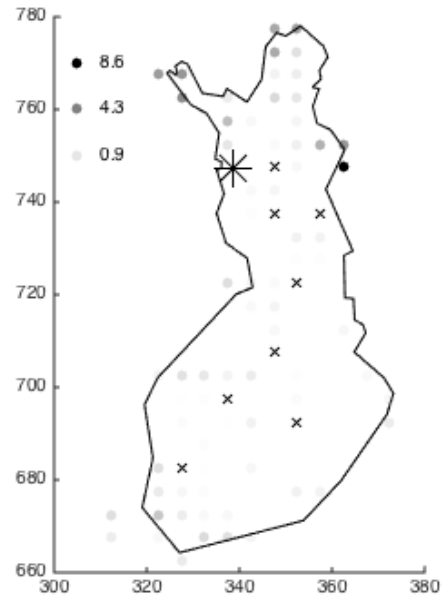
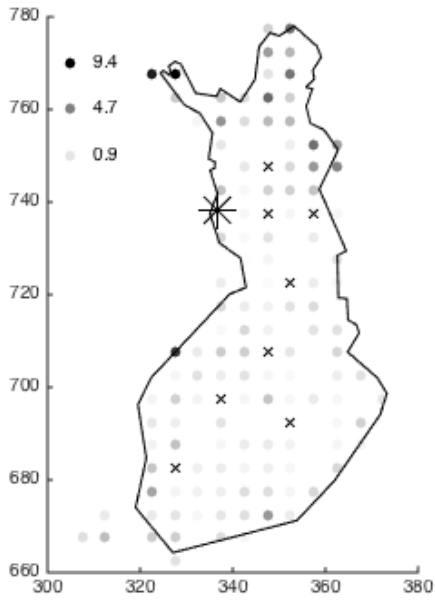


Supplementary fig. 65. *Phoenicurus phoenicurus*

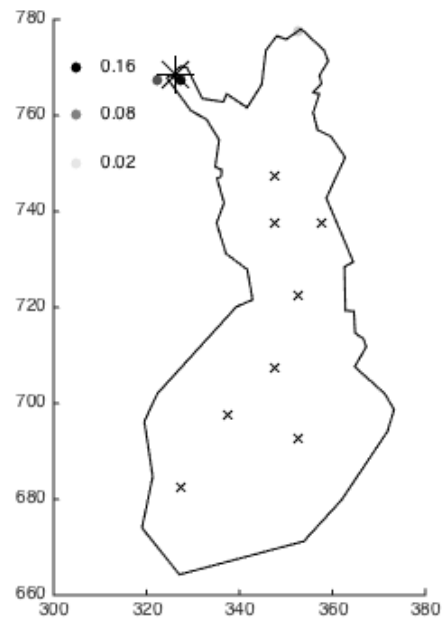
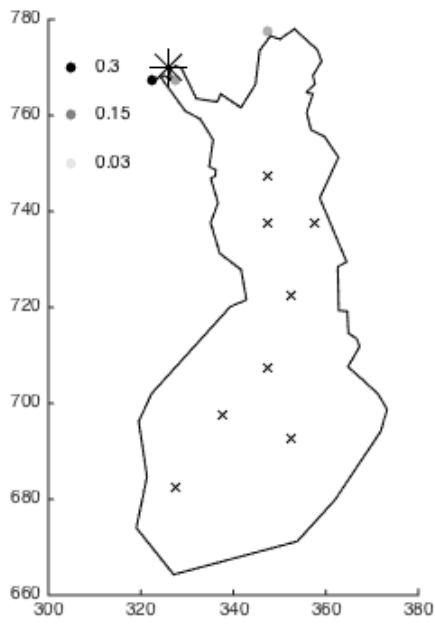


Supplementary fig. 66. *Saxicola rubetra*

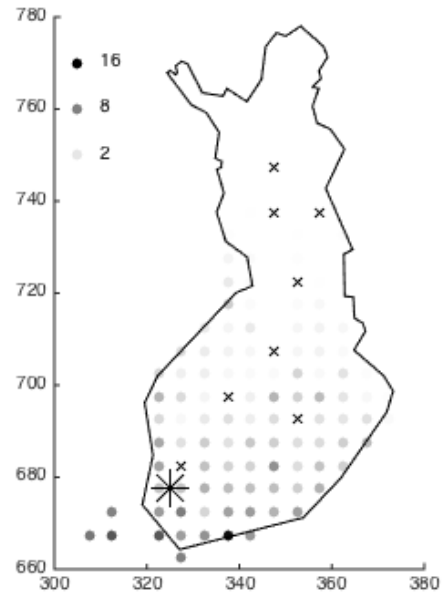
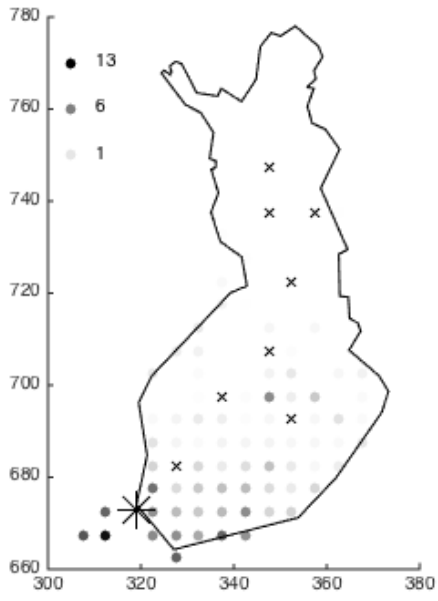




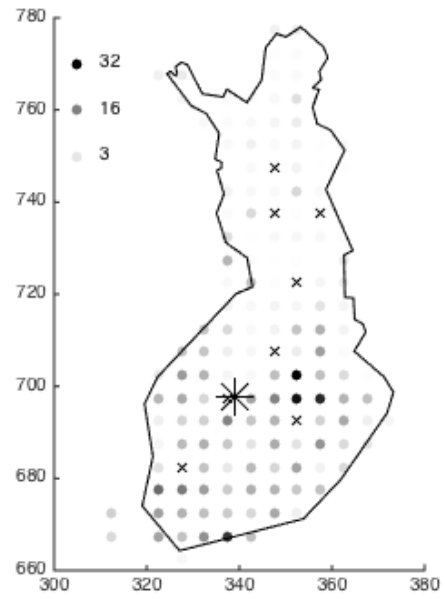
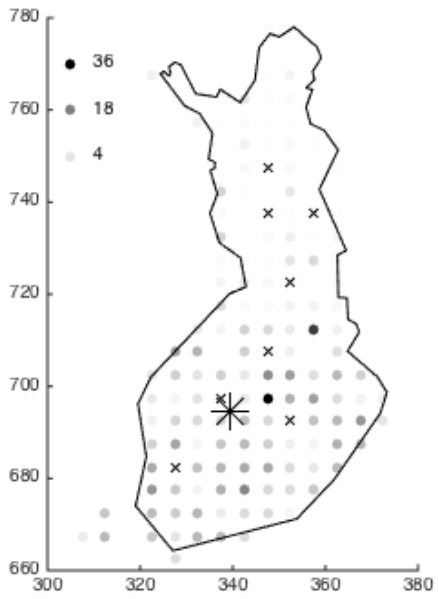
Supplementary fig. 67. *Oenanthe oenanthe*



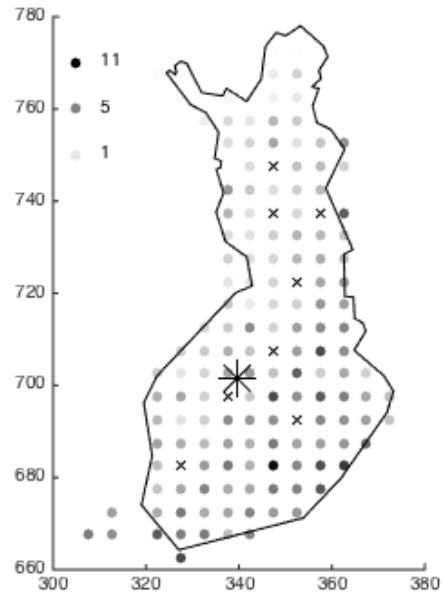
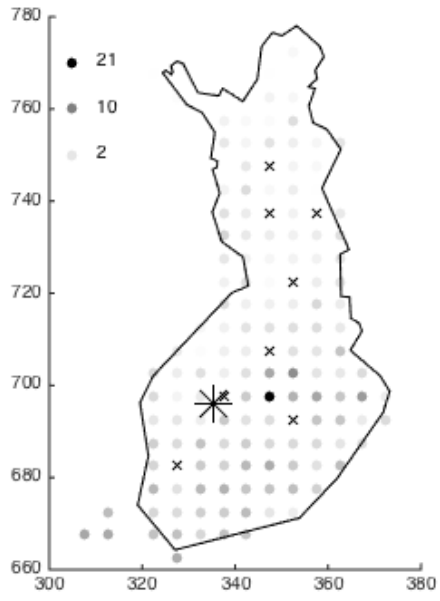
Supplementary fig. 68. *Turdus torquatus*



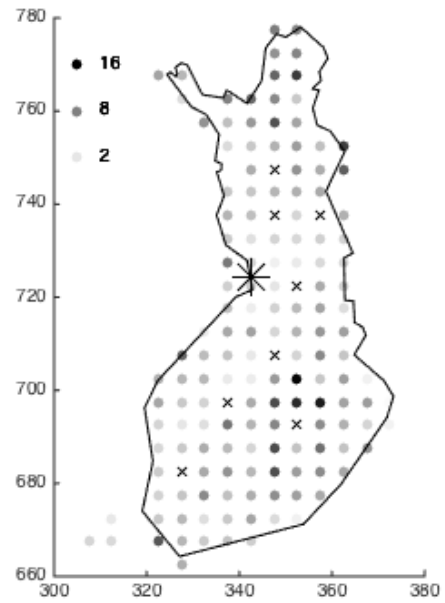
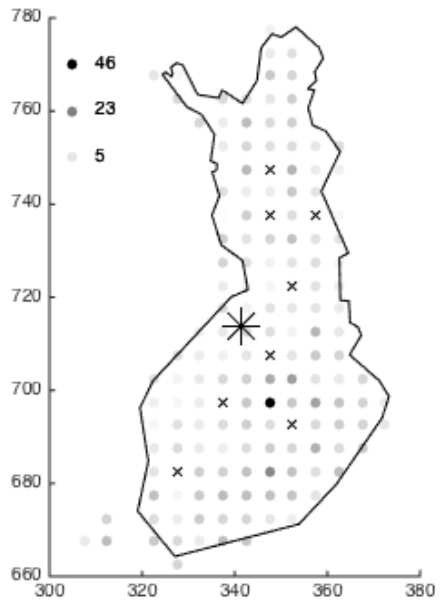
Supplementary fig. 69. *Turdus merula*



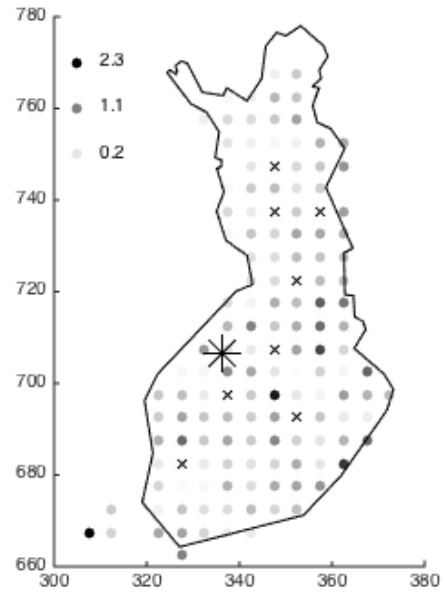
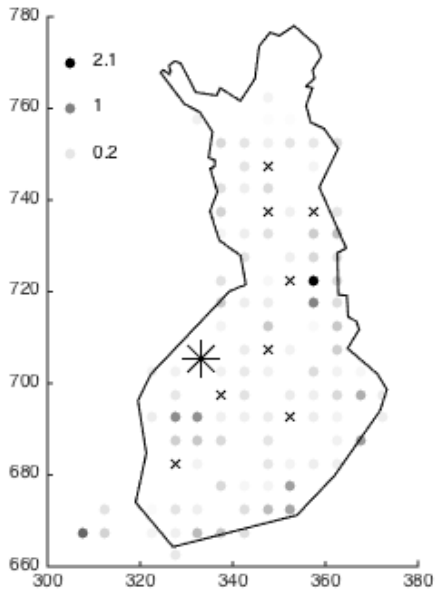
Supplementary fig. 70. *Turdus pilaris*



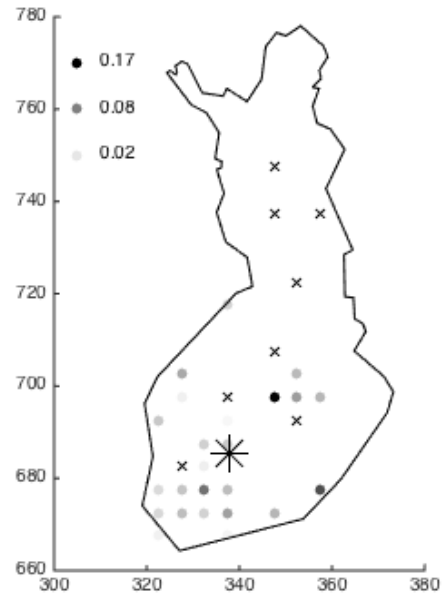
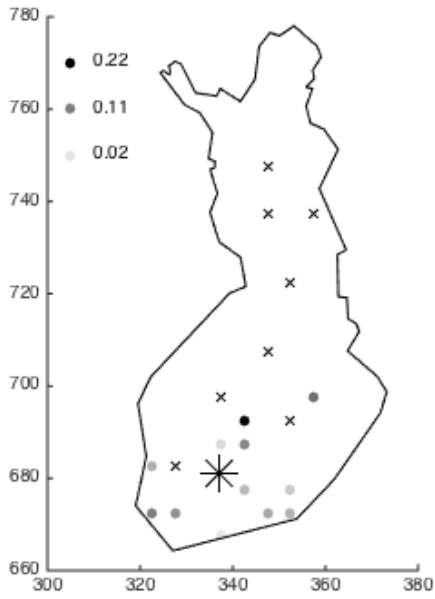
Supplementary fig. 71. *Turdus philomelos*



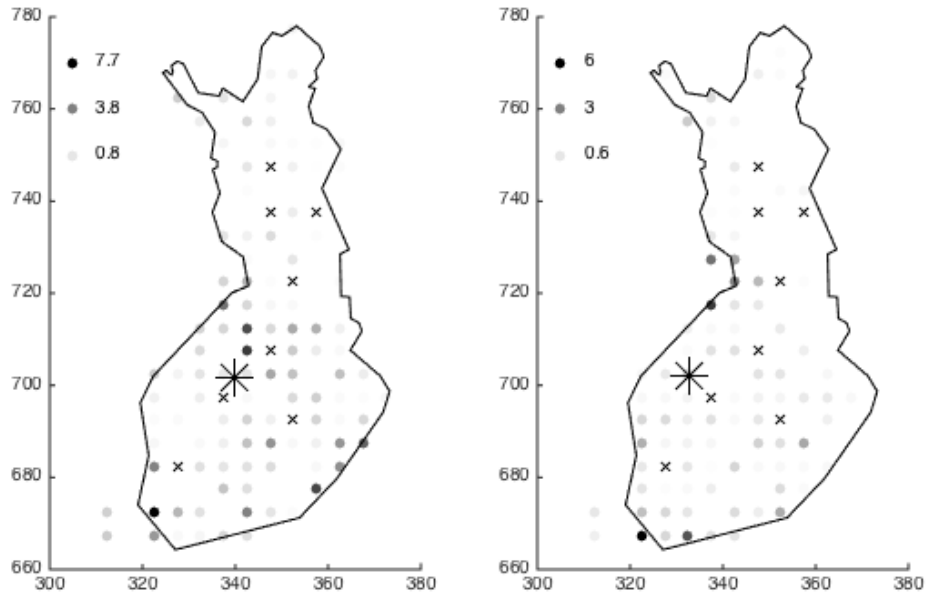
Supplementary fig. 72. *Turdus iliacus*



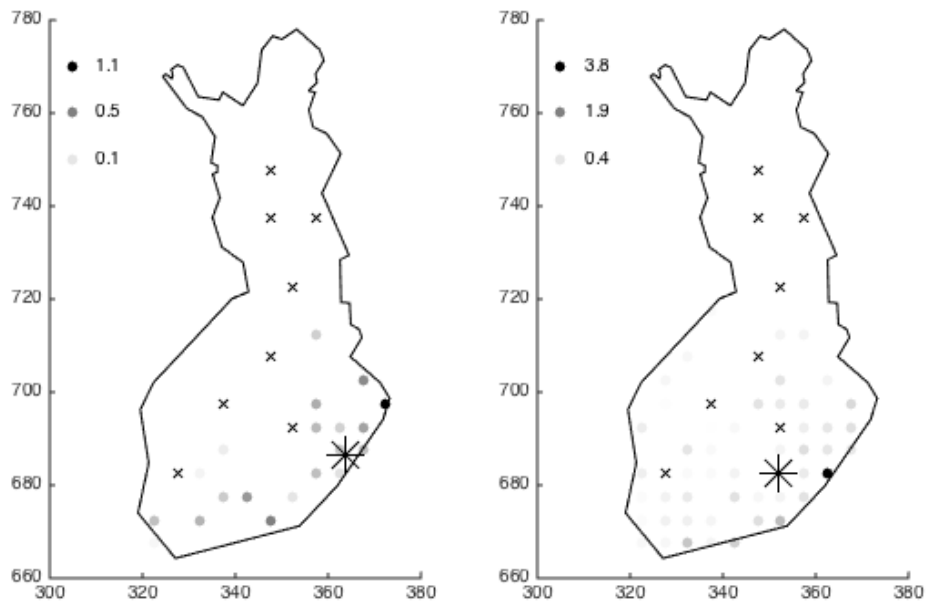
Supplementary fig. 73. *Turdus viscivorus*



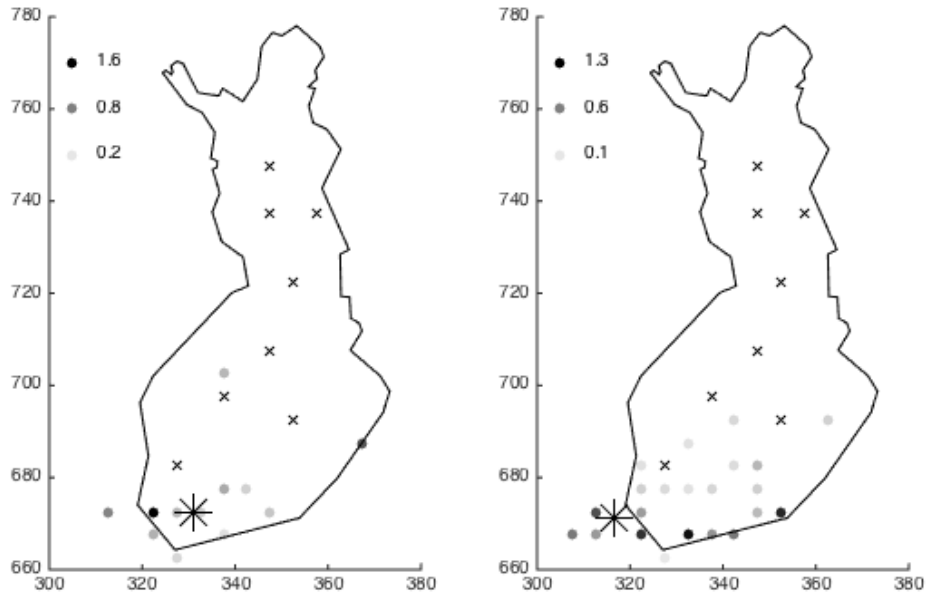
Supplementary fig. 74. *Locustella naevia*



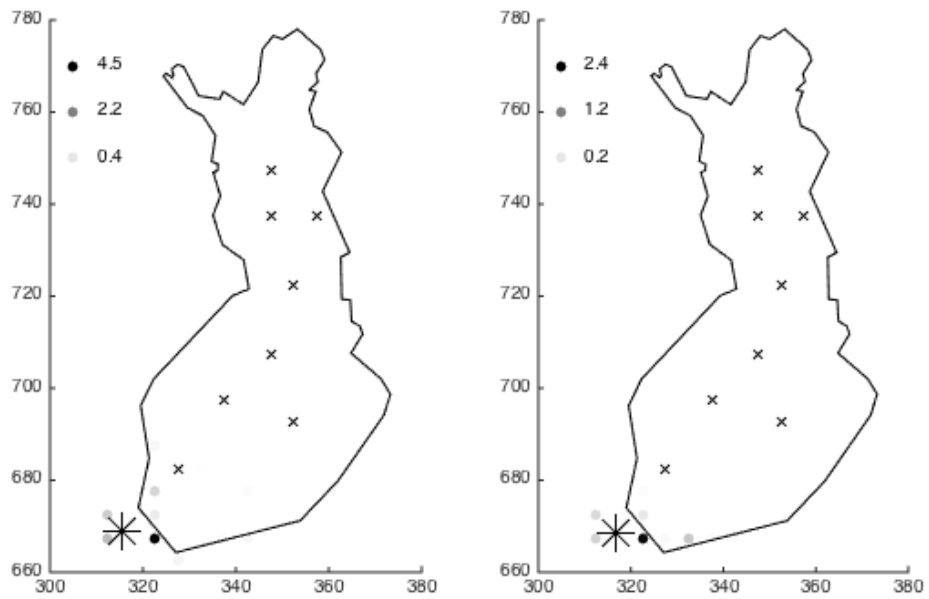
Supplementary fig. 75. *Acrocephalus schoenobaenus*



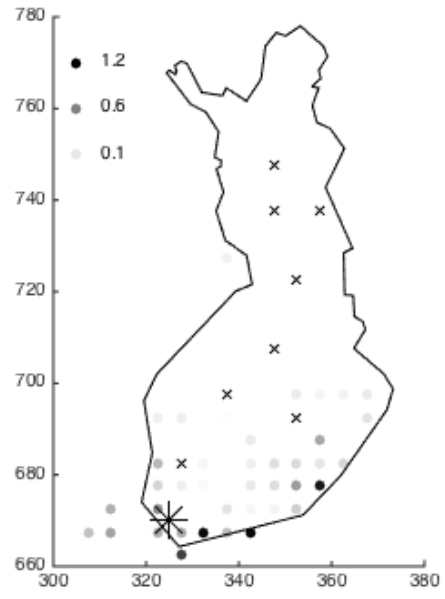
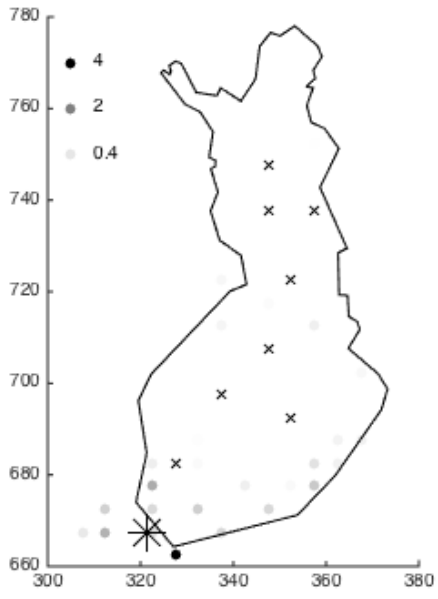
Supplementary fig. 76. *Acrocephalus dumetorum*



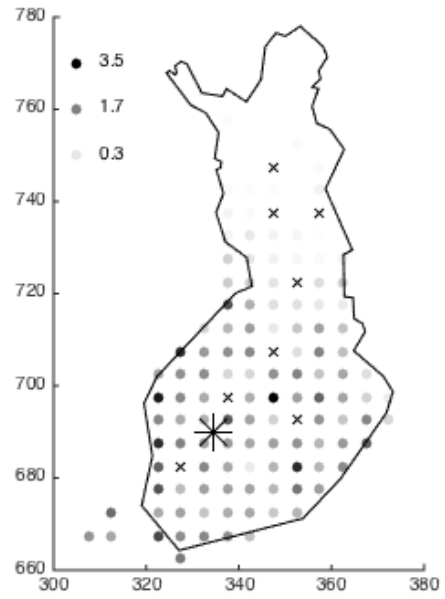
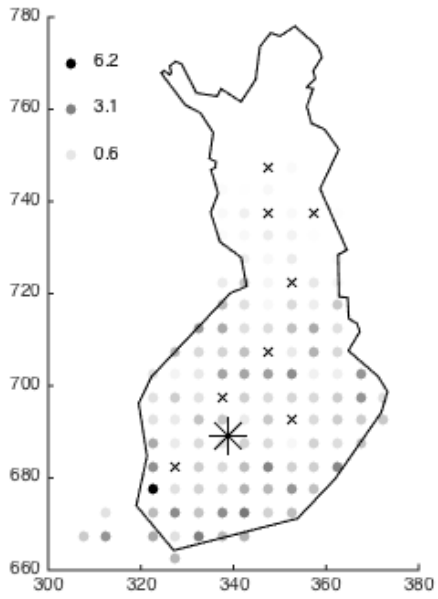
Supplementary fig. 77. *Acrocephalus palustris*



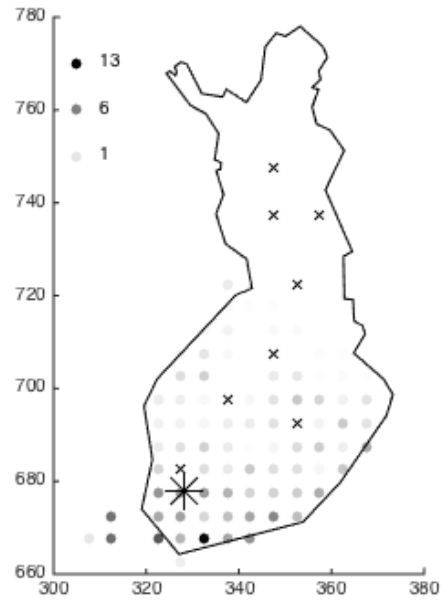
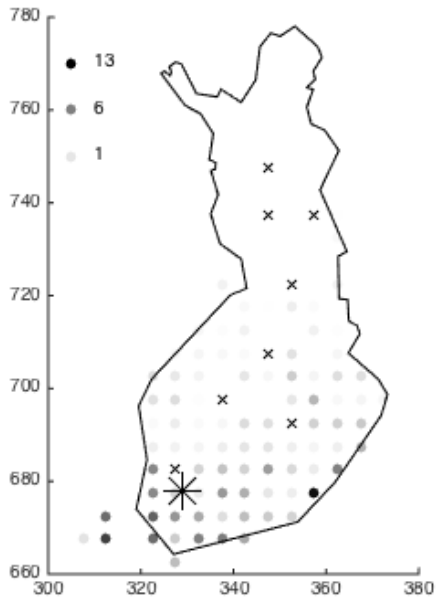
Supplementary fig. 78. *Acrocephalus scirpaceus*



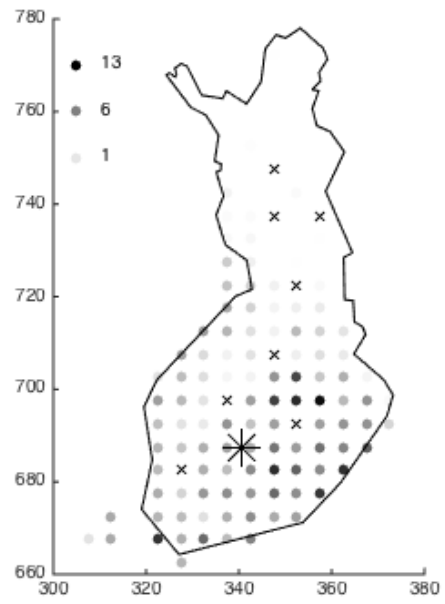
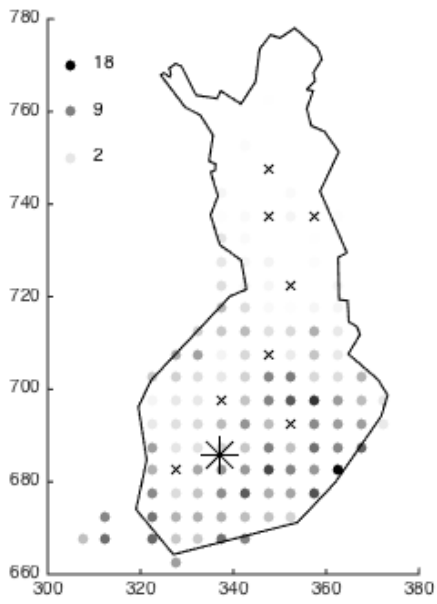
Supplementary fig. 79. *Hippolais icterina*



Supplementary fig. 80. *Sylvia curruca*

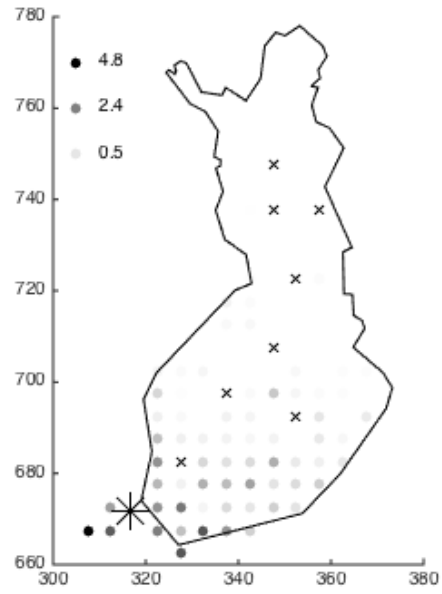
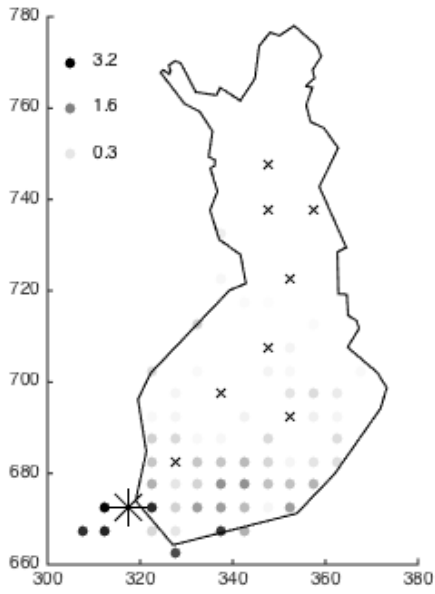


Supplementary fig. 81. *Sylvia communis*

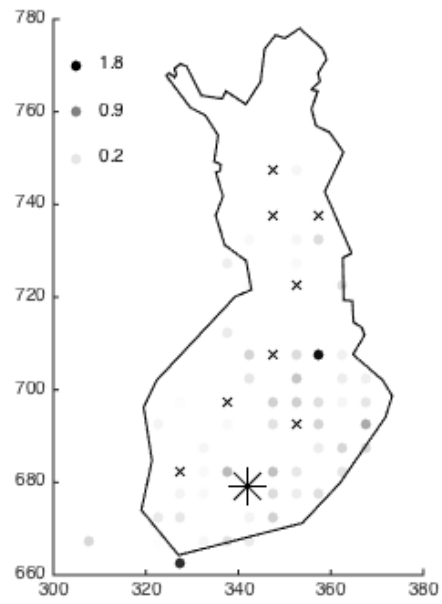
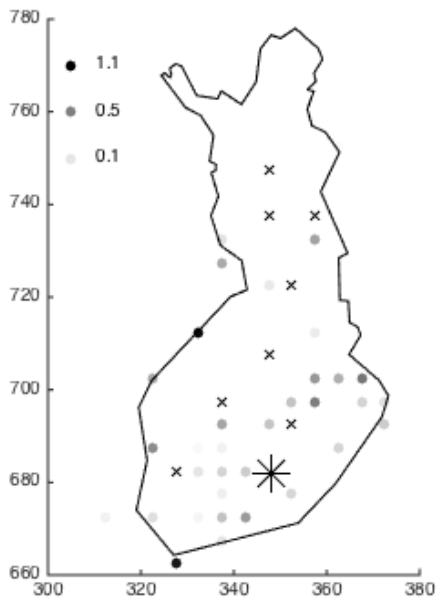


Supplementary fig. 82. *Sylvia borin*

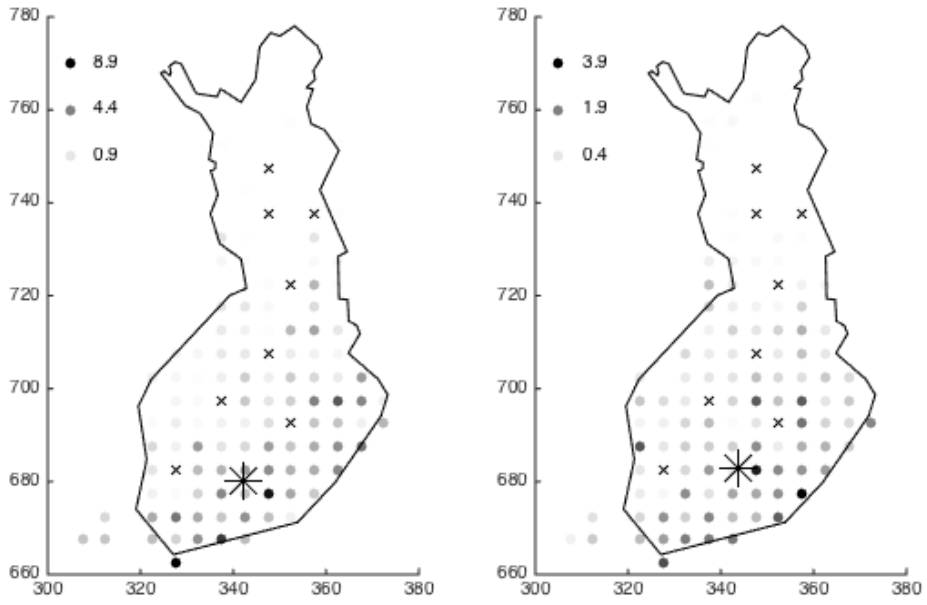




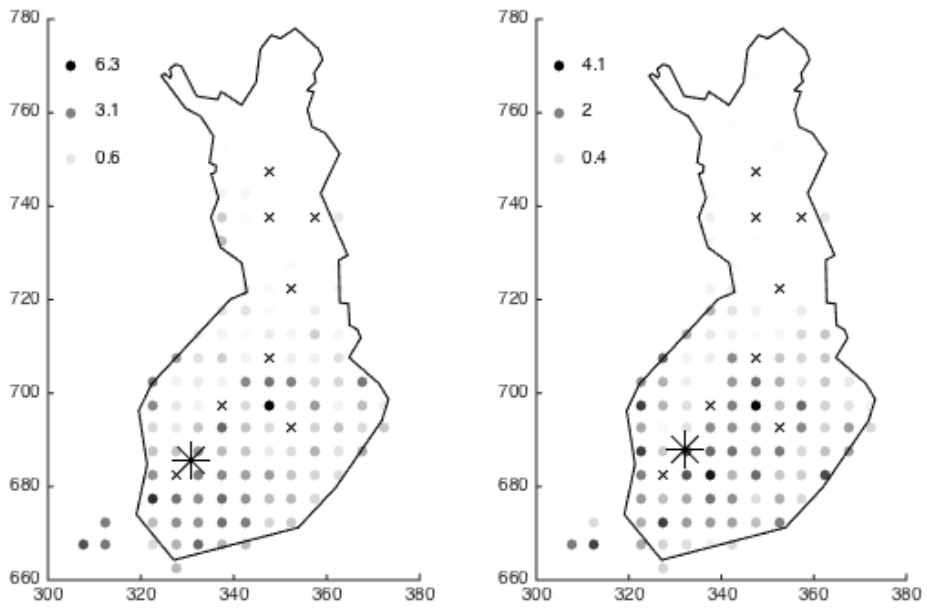
Supplementary fig. 83. *Sylvia atricapilla*



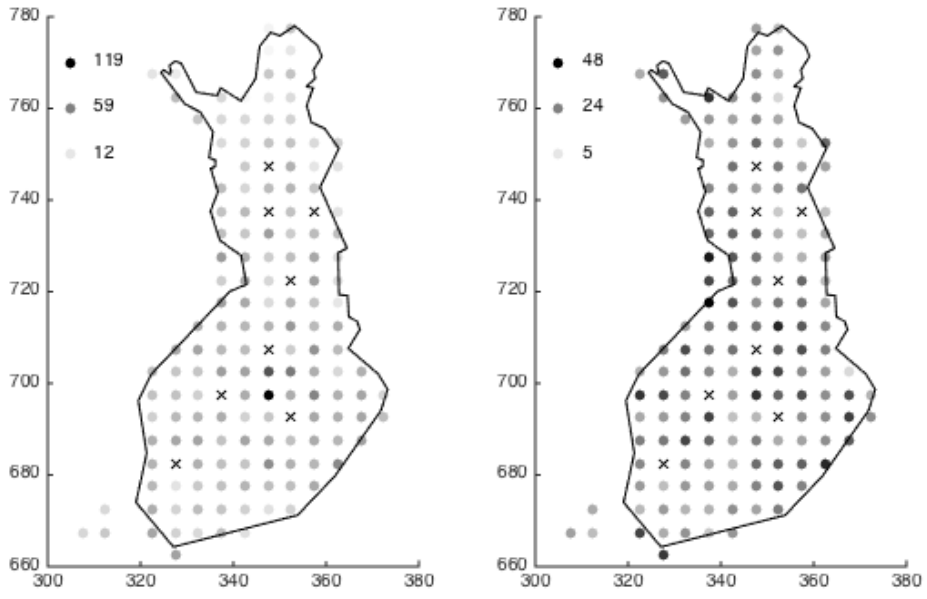
Supplementary fig. 84. *Phylloscopus trochiloides*



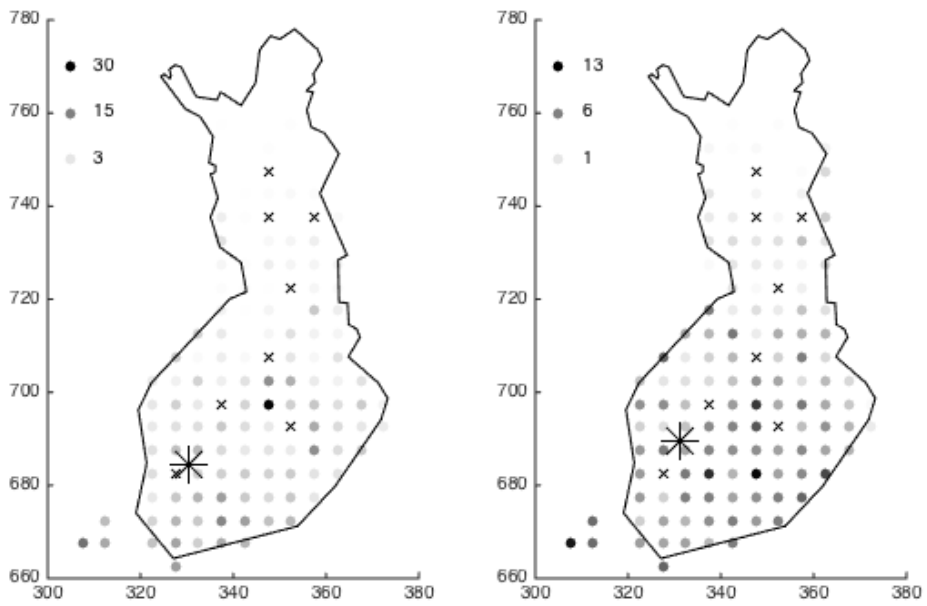
Supplementary fig. 85. *Phylloscopus sibilatrix*



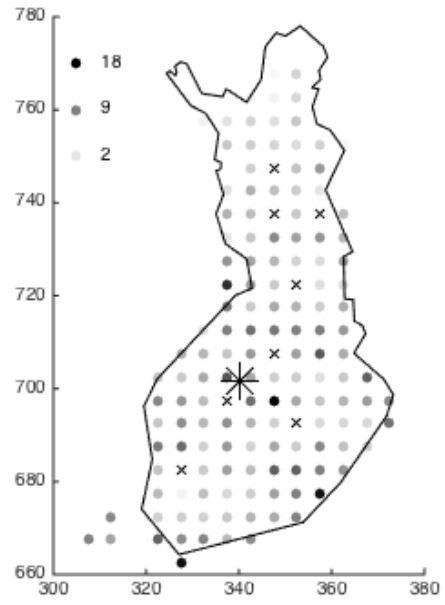
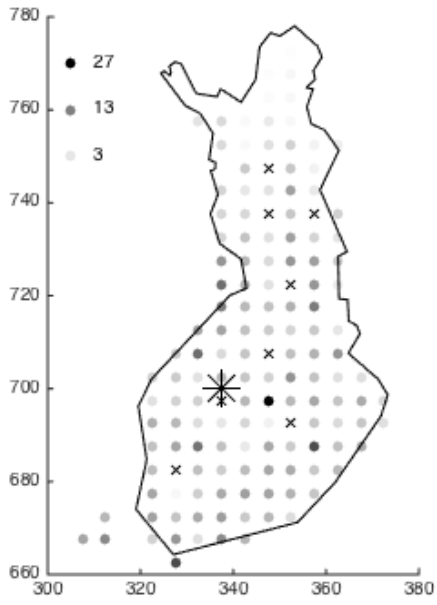
Supplementary fig. 86. *Phylloscopus collybita*



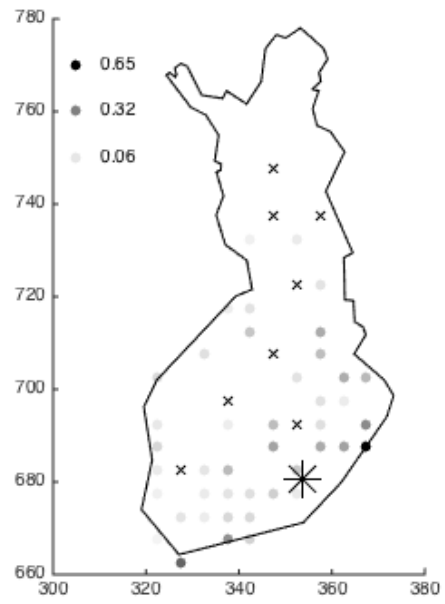
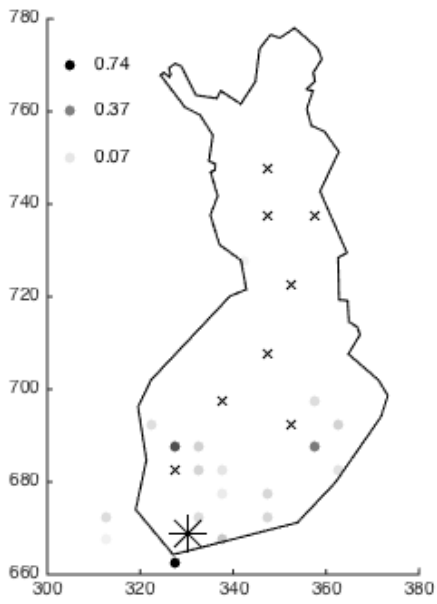
Supplementary fig. 87. *Phylloscopus trochilus*



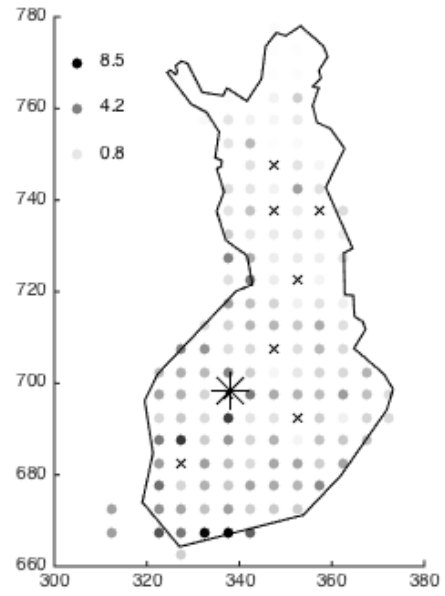
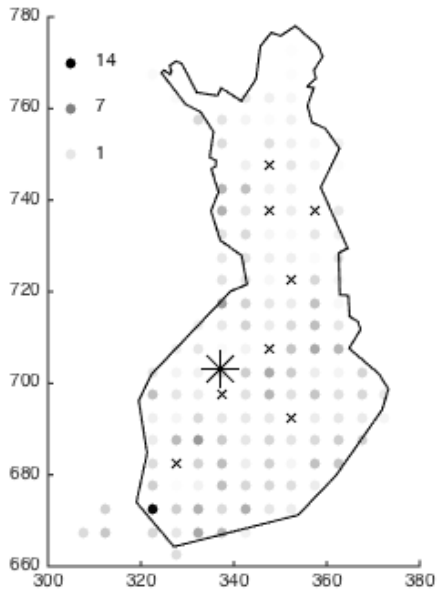
Supplementary fig. 88. *Regulus regulus*



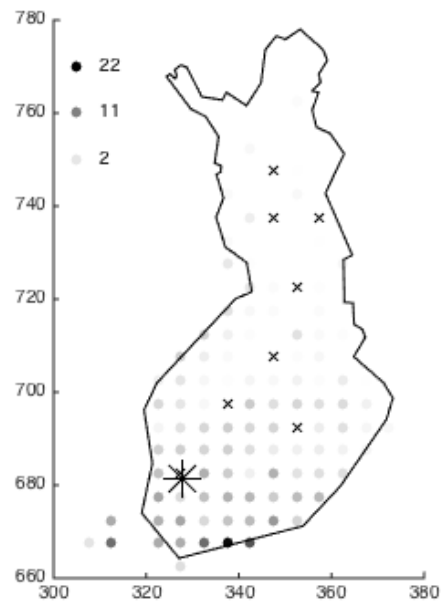
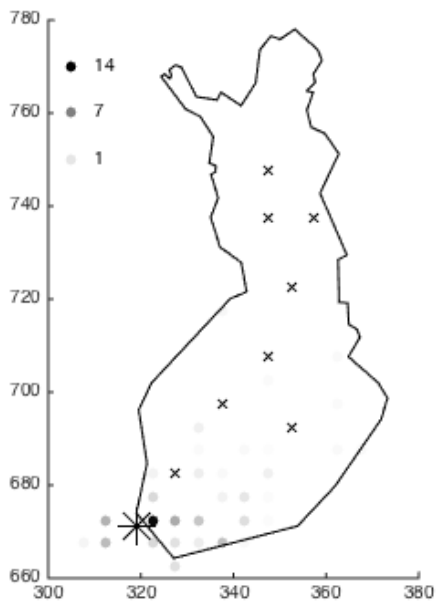
Supplementary fig. 89. *Muscicapa striata*



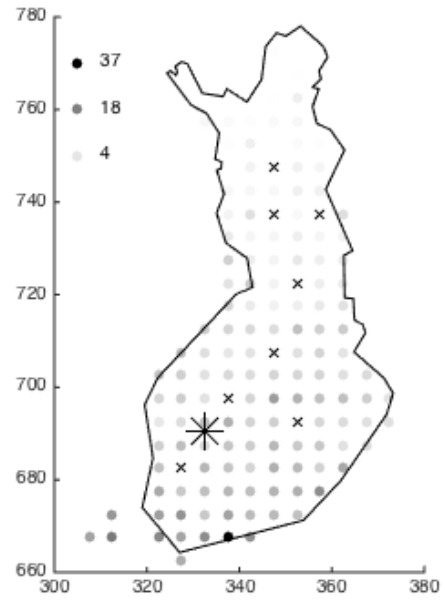
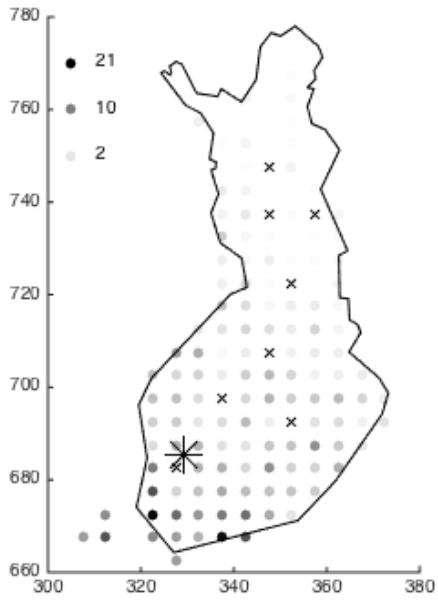
Supplementary fig. 90. *Ficedula parva*



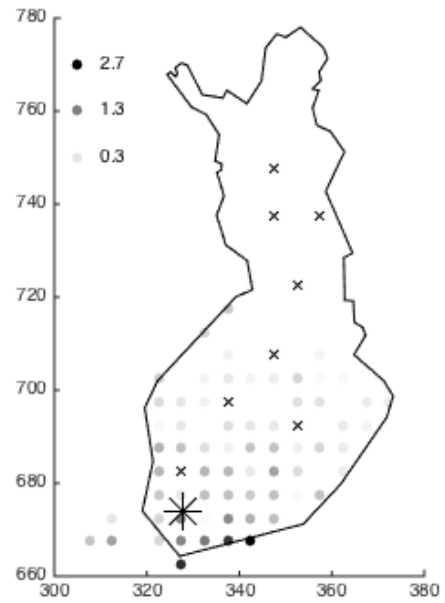
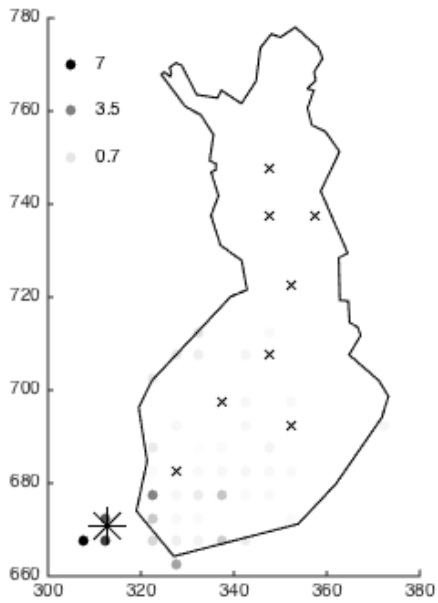
Supplementary fig. 91. *Ficedula hypoleuca*



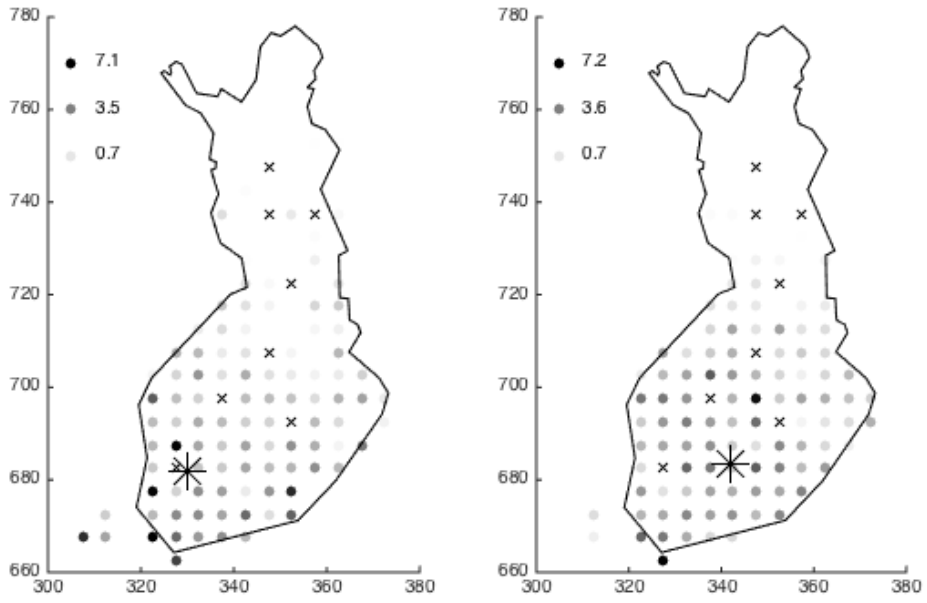
Supplementary fig. 92. *Cyanistes caeruleus*



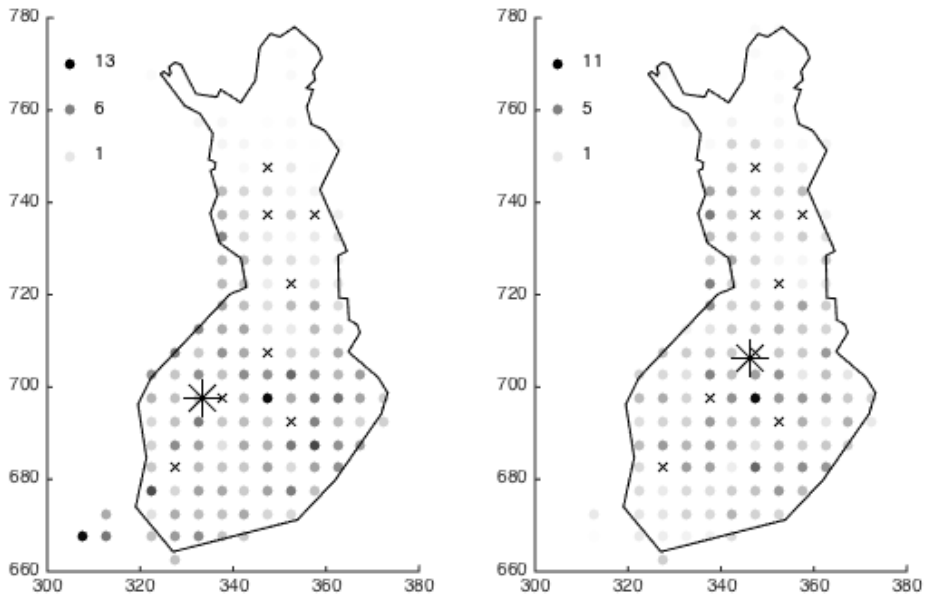
Supplementary fig. 93. *Parus major*



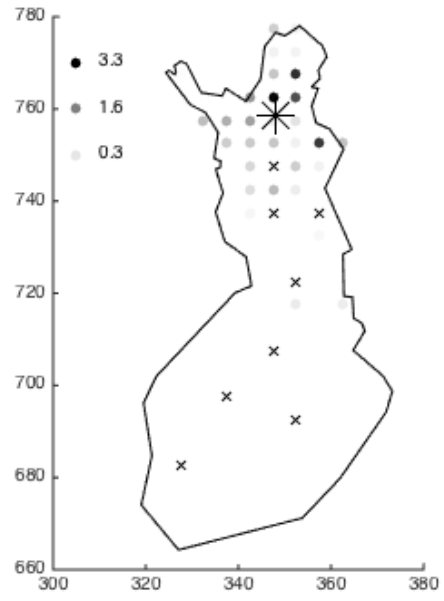
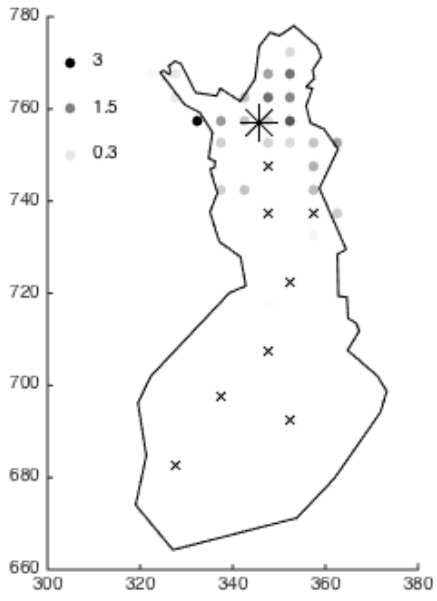
Supplementary fig. 94. *Periparus ater*



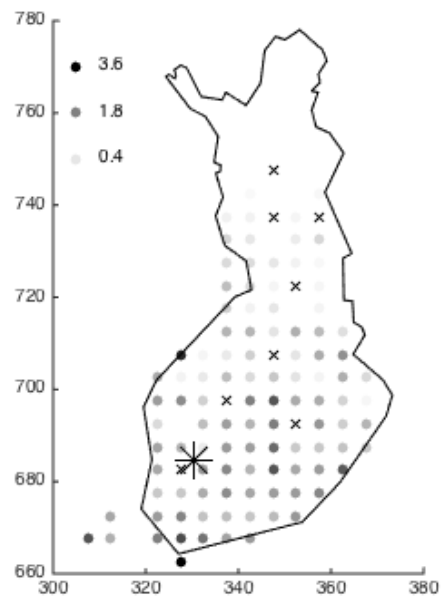
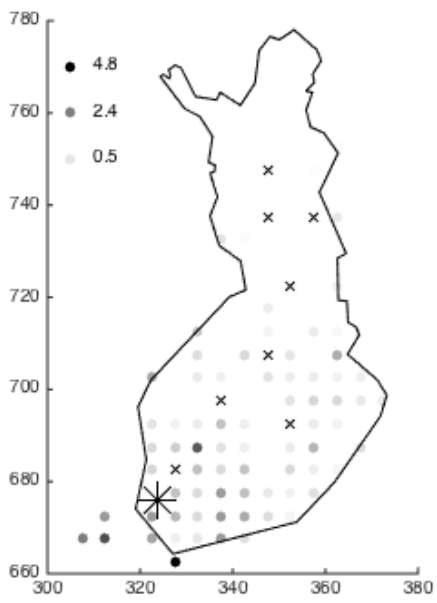
Supplementary fig. 95. *Lophophanes cristatus*



Supplementary fig. 96. *Poecile montanus*

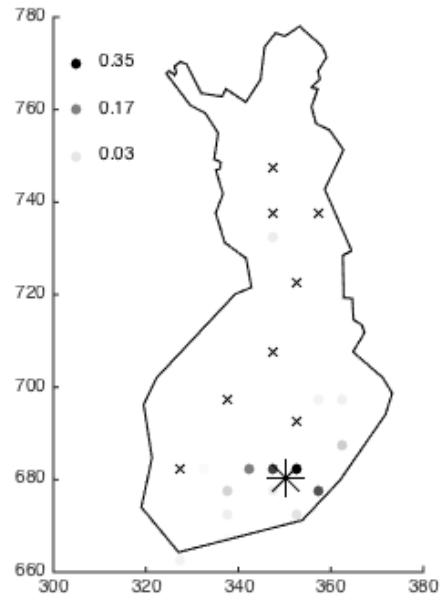
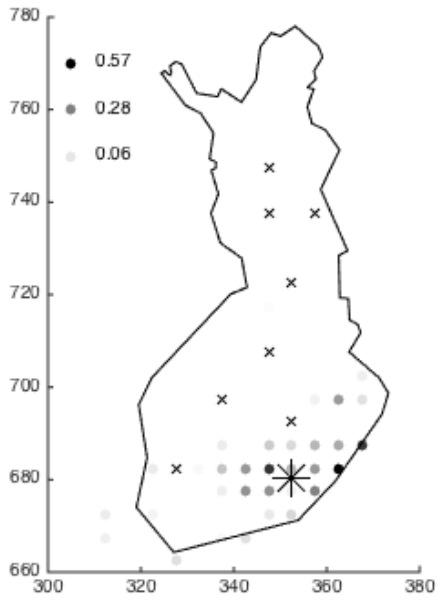


Supplementary fig. 97. *Poecile cinctus*

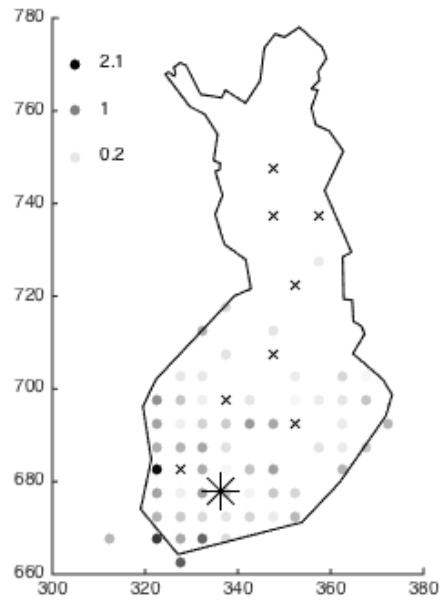
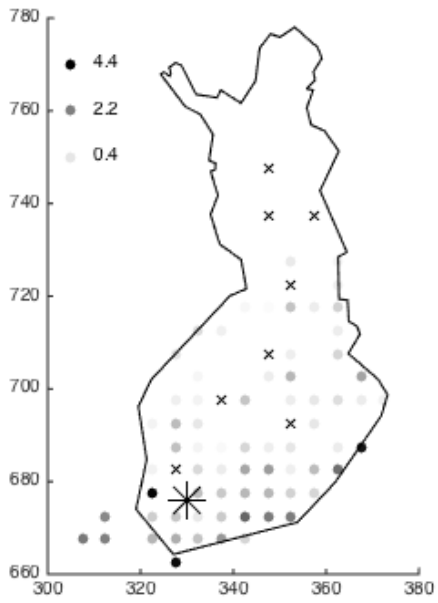


Supplementary fig. 98. *Certhia familiaris*

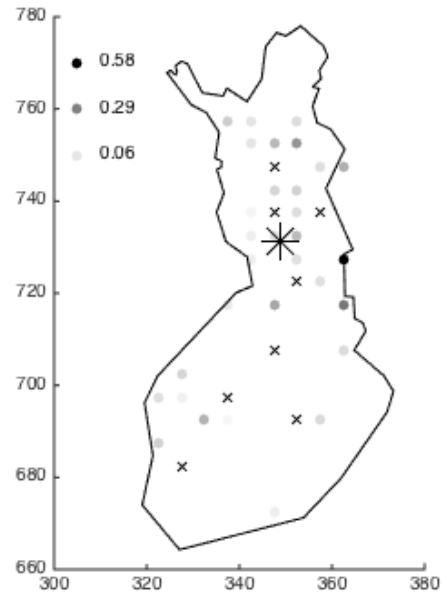
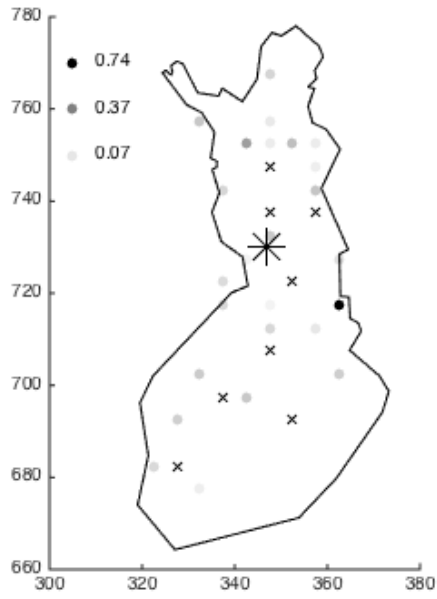




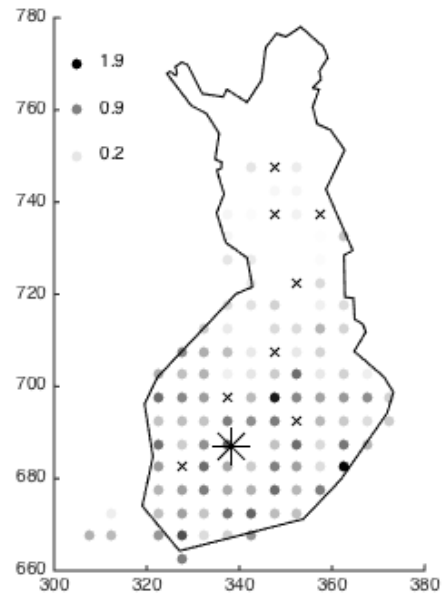
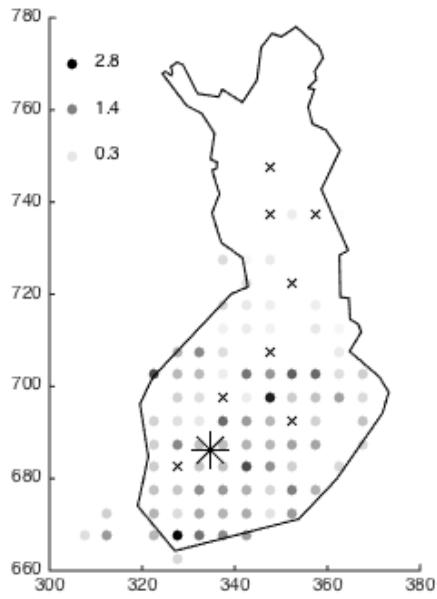
Supplementary fig. 99. *Oriolus oriolus*



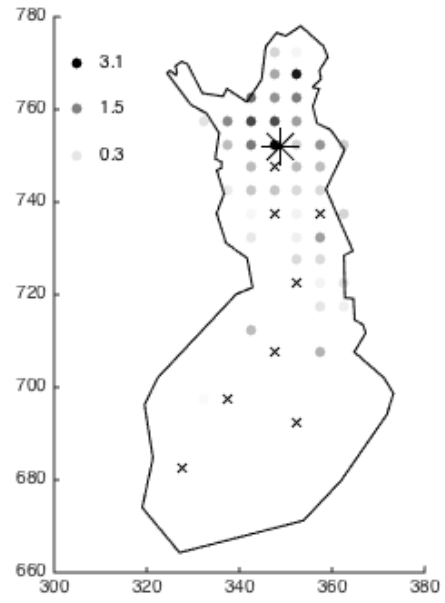
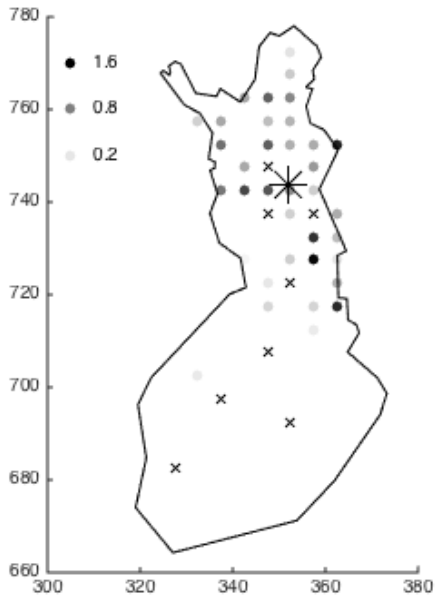
Supplementary fig. 100. *Lanius collurio*



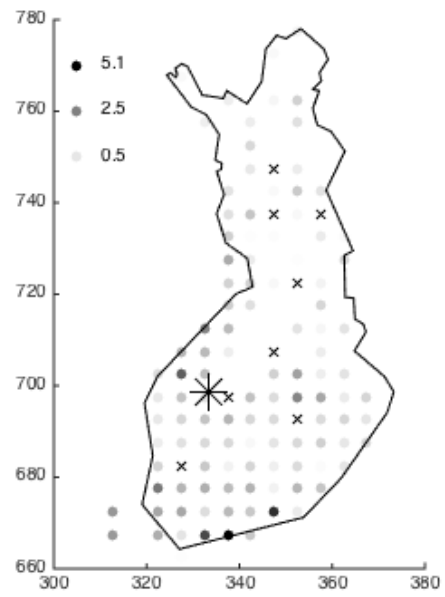
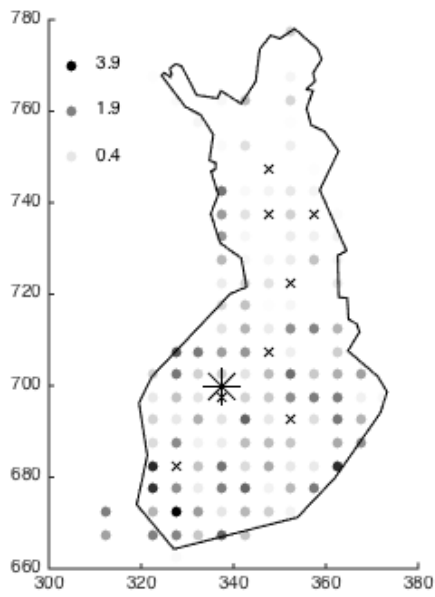
Supplementary fig. 101. *Lanius excubitor*



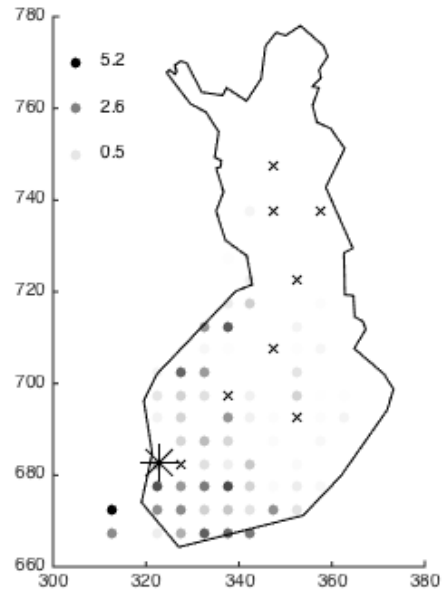
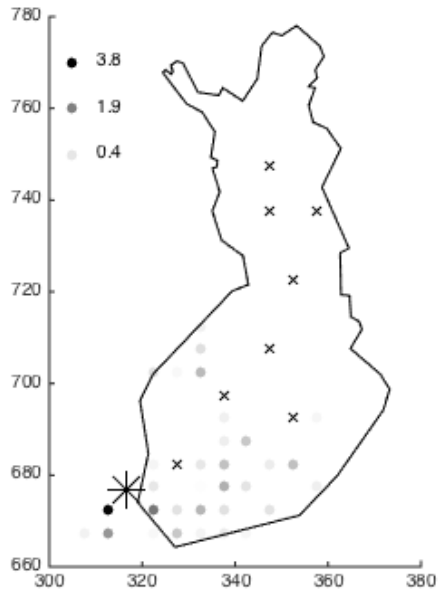
Supplementary fig. 102. *Garrulus glandarius*



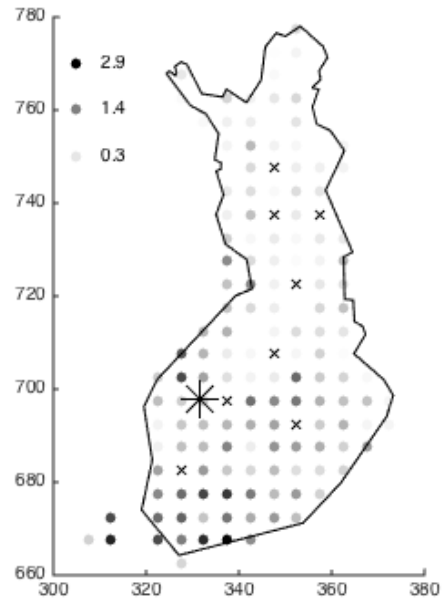
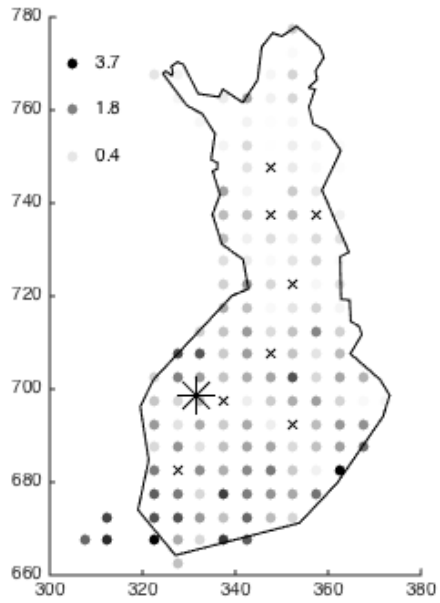
Supplementary fig. 103. *Perisoreus infaustus*



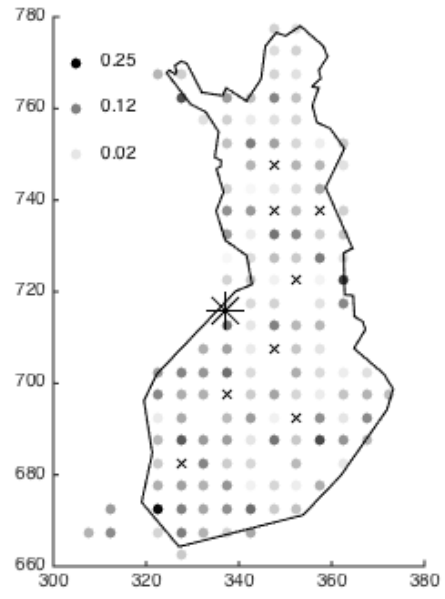
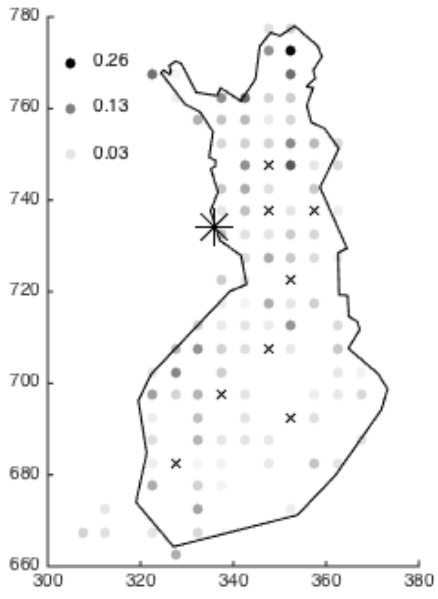
Supplementary fig. 104. *Pica pica*



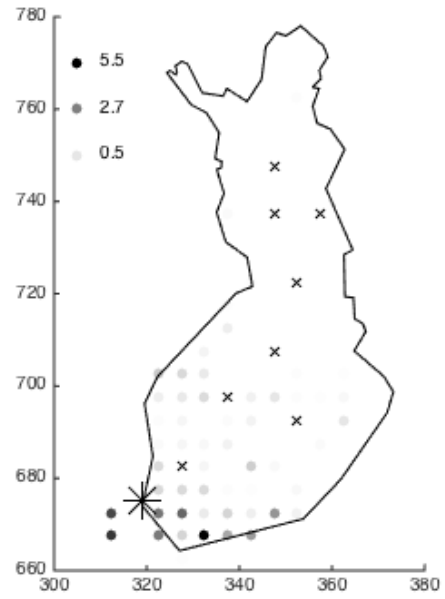
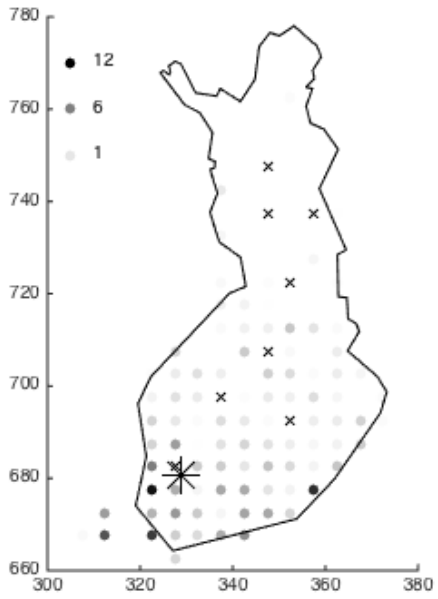
Supplementary fig. 105. *Corvus monedula*



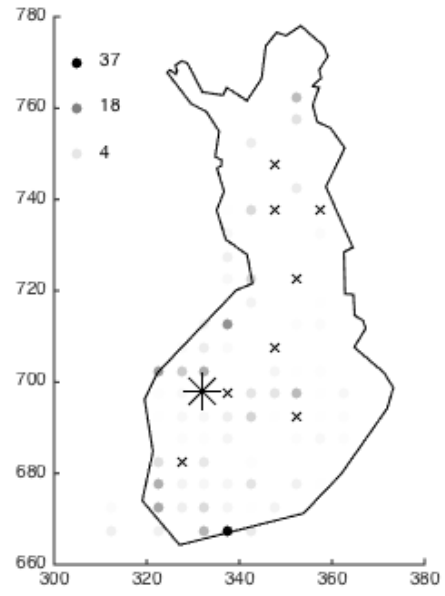
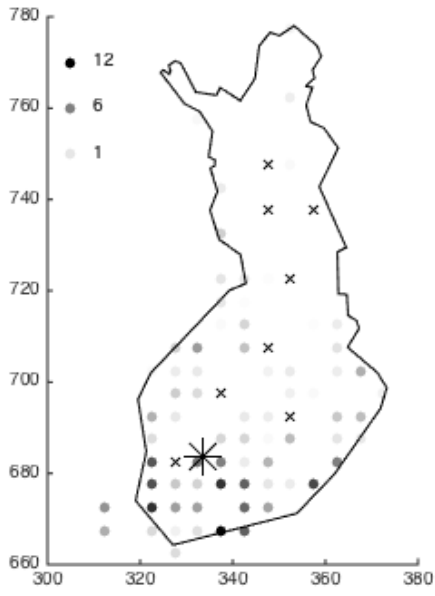
Supplementary fig. 106. *Corvus corone*



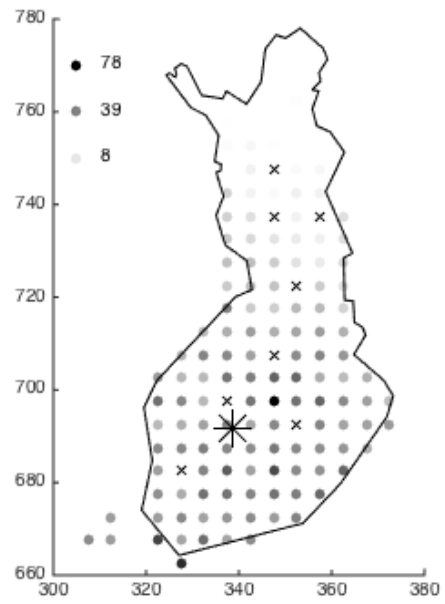
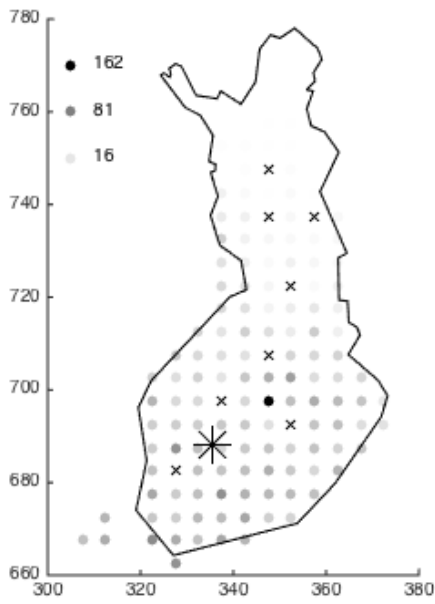
Supplementary fig. 107. *Corvus corax*



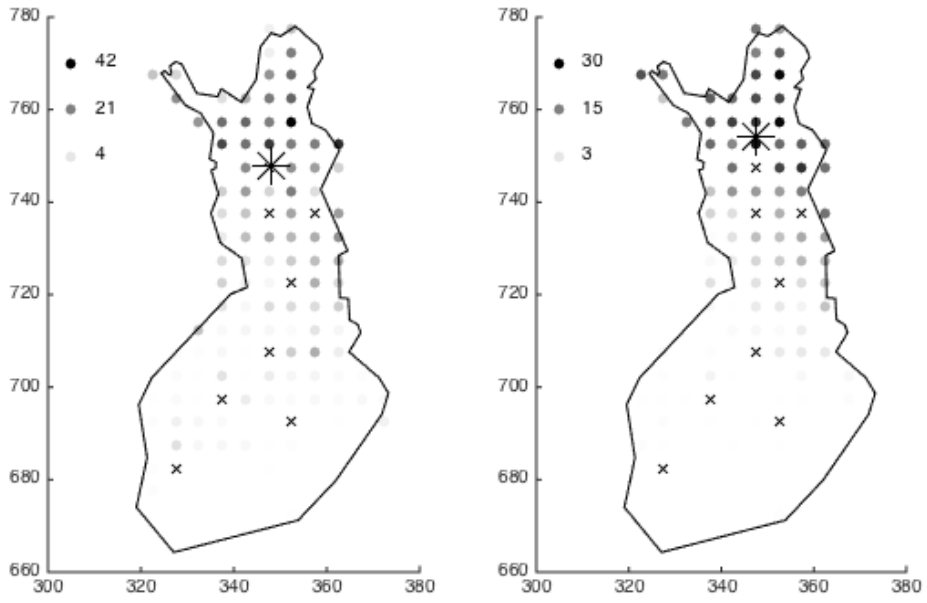
Supplementary fig. 108. *Sturnus vulgaris*



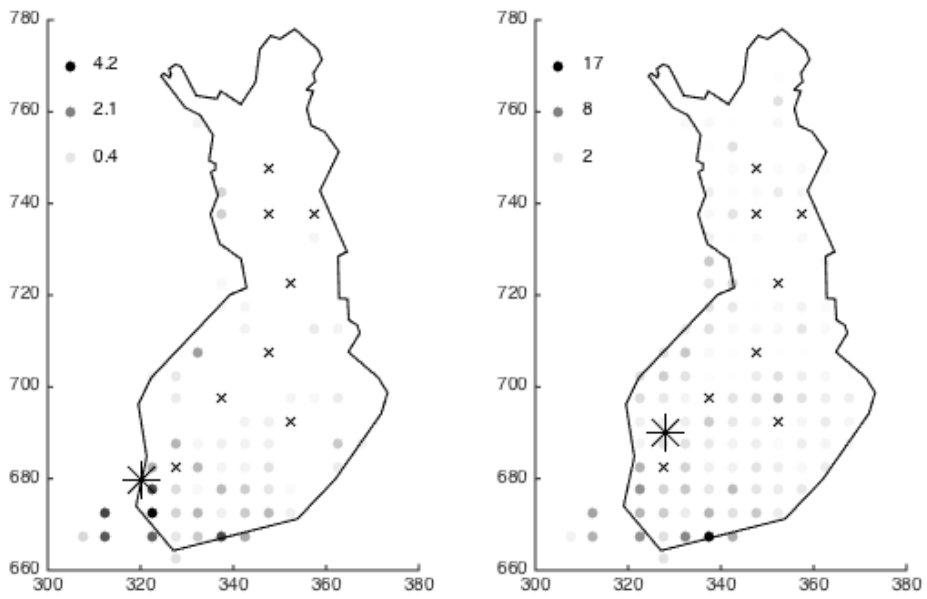
Supplementary fig. 109. *Passer domesticus*



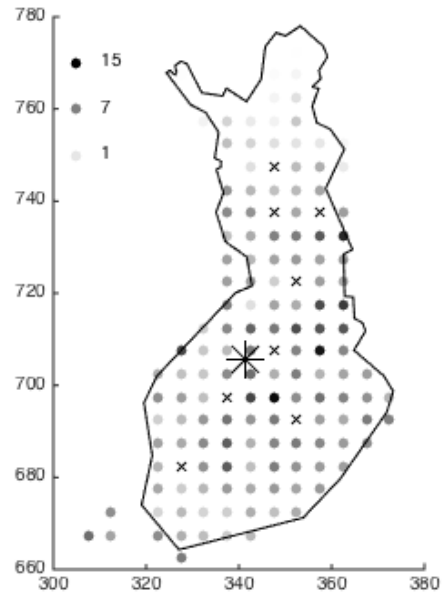
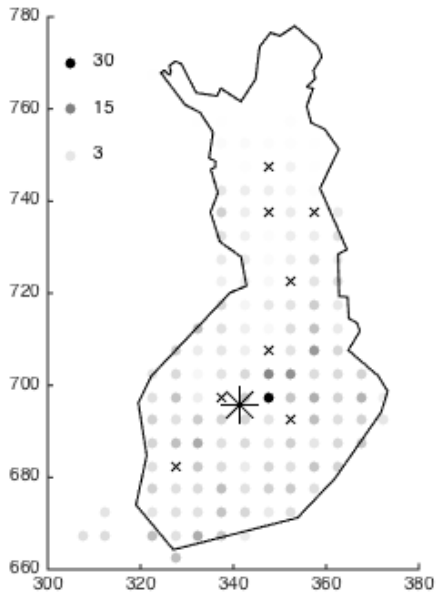
Supplementary fig. 110. *Fringilla coelebs*



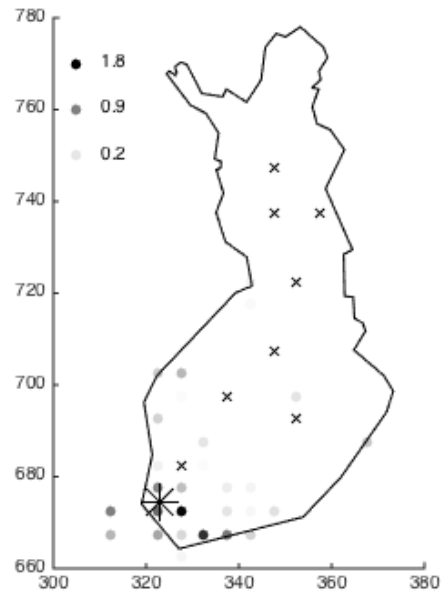
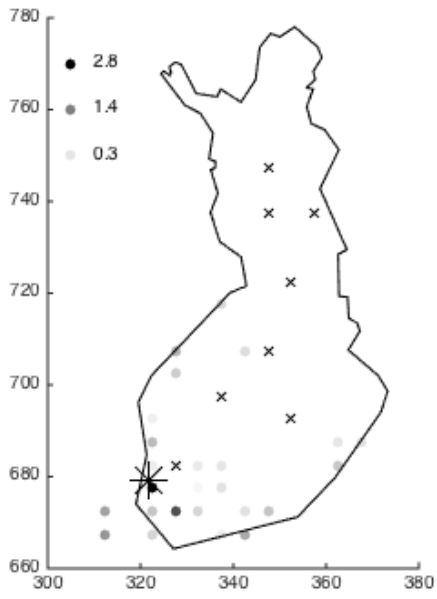
Supplementary fig. 111. *Fringilla montifringilla*



Supplementary fig. 112. *Carduelis chloris*

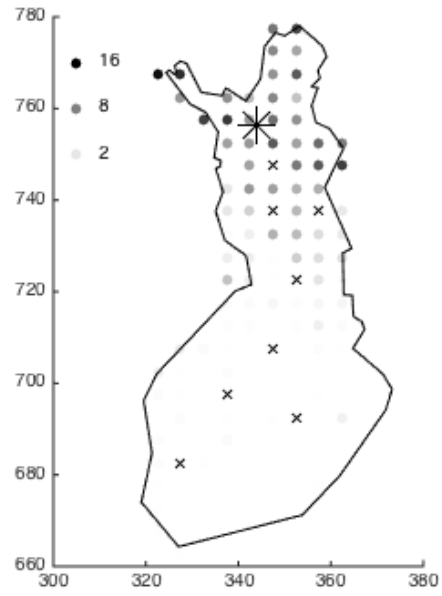
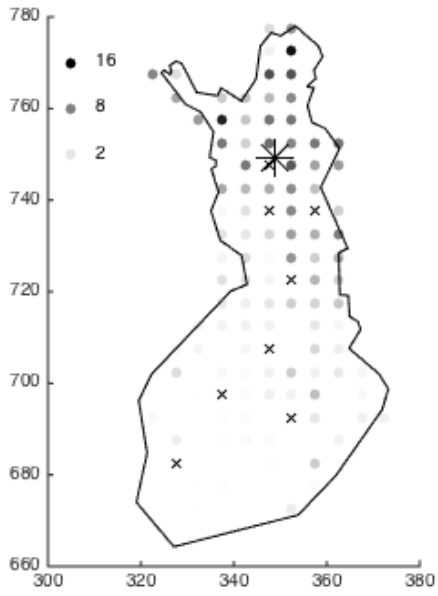


Supplementary fig. 113. *Carduelis spinus*

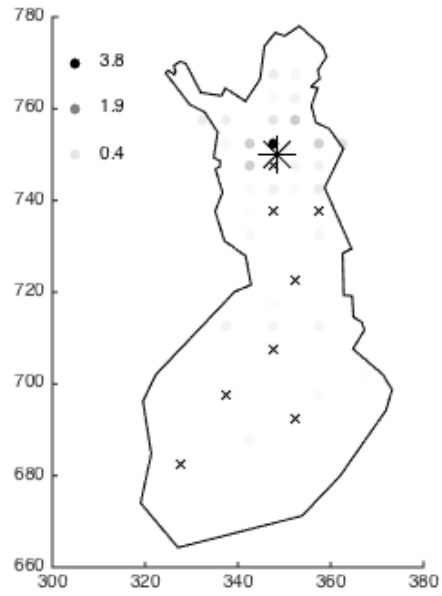
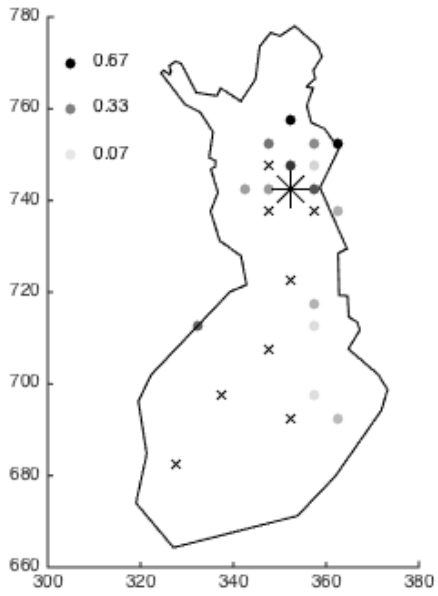


Supplementary fig. 114. *Carduelis cannabina*

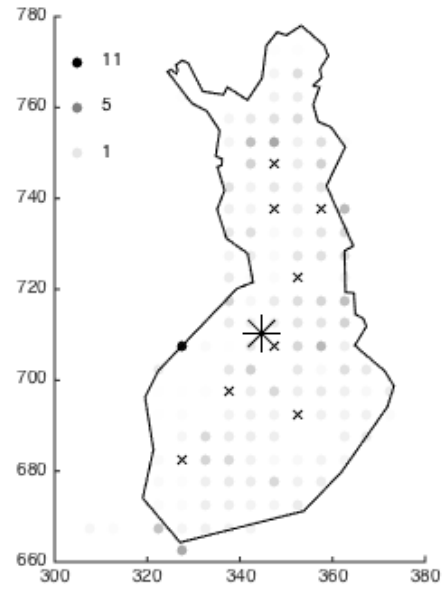
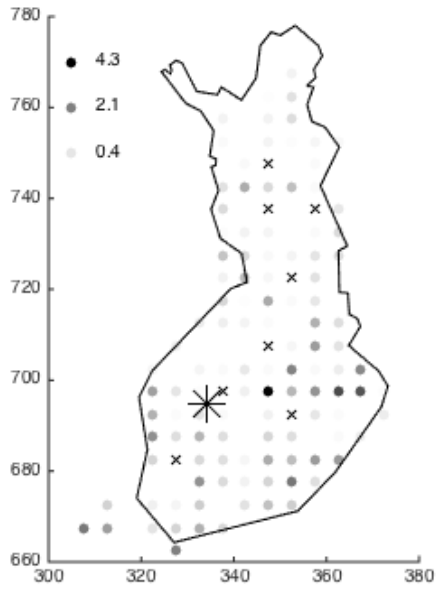




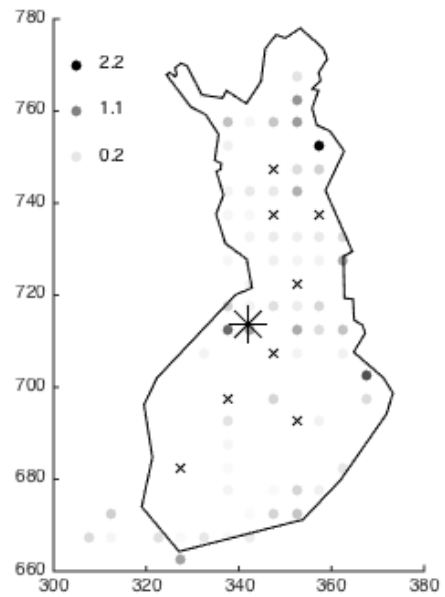
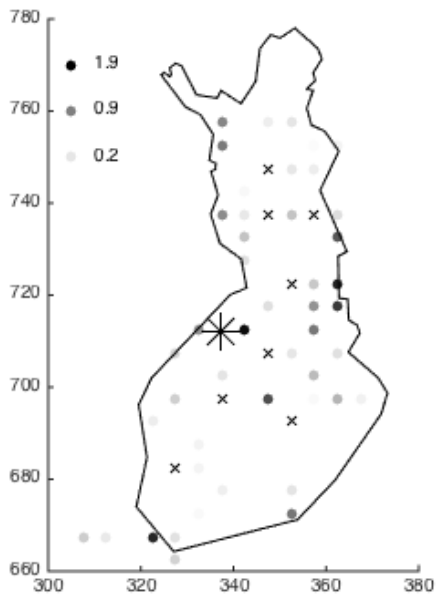
Supplementary fig. 115. *Carduelis flammea*



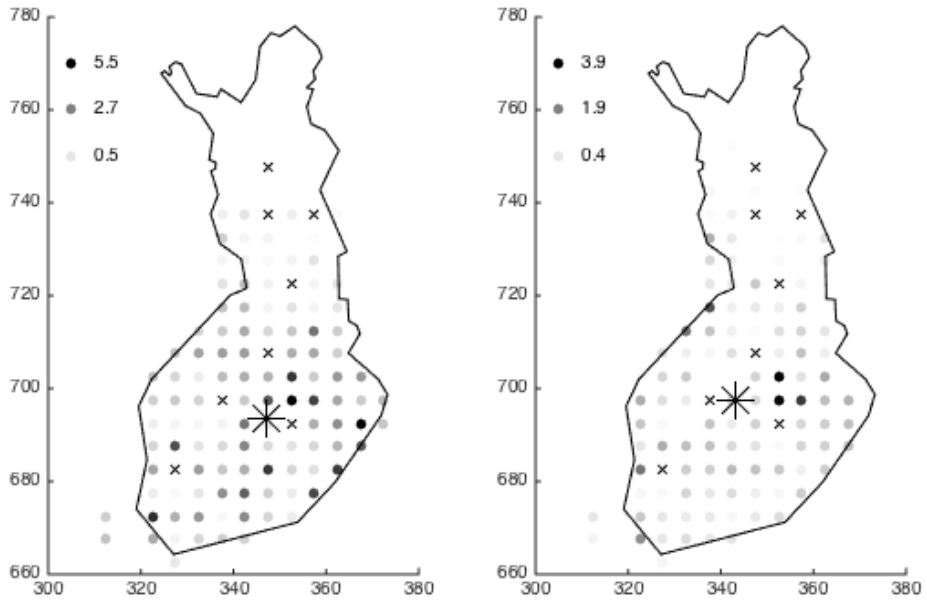
Supplementary fig. 116. *Loxia leucoptera*



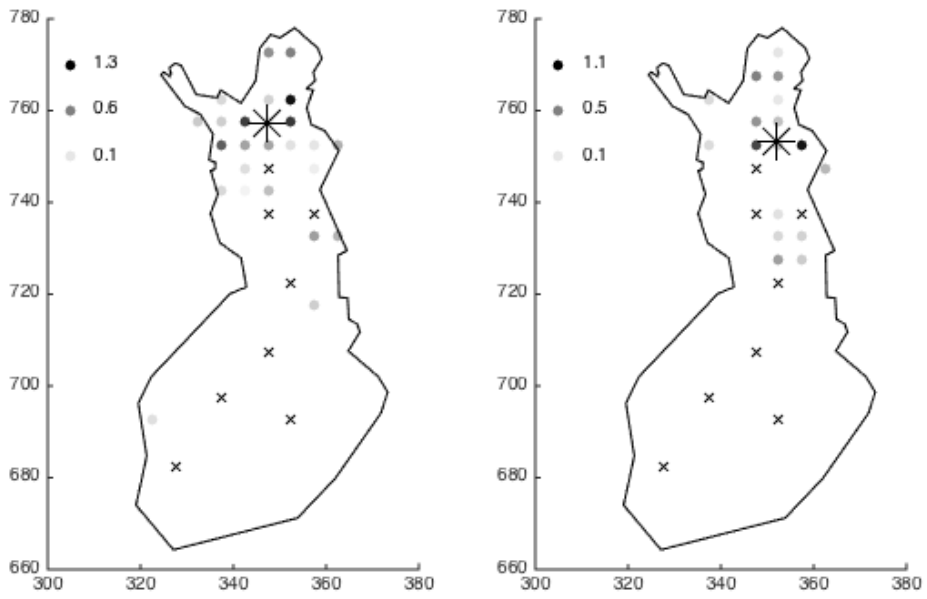
Supplementary fig. 117. *Loxia curvirostra*



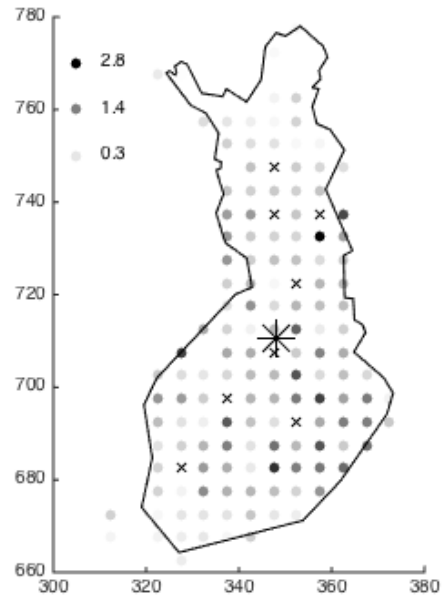
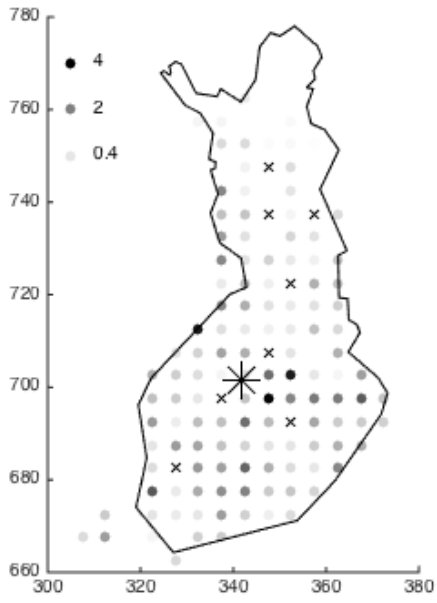
Supplementary fig. 118. *Loxia pytyopsittacus*



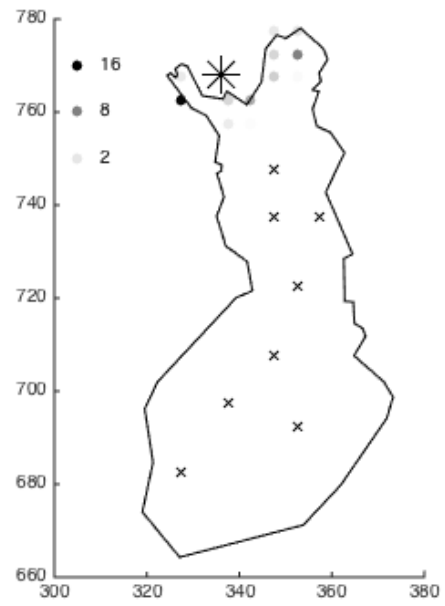
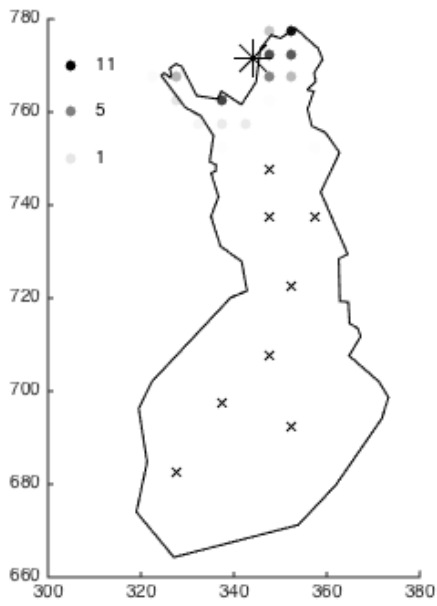
Supplementary fig. 119. *Carpodacus erythrinus*



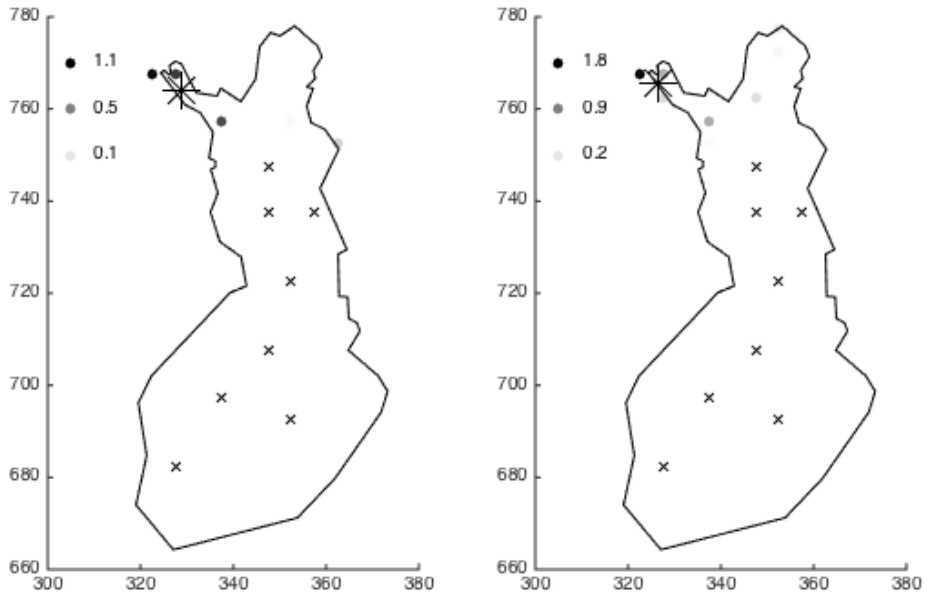
Supplementary fig. 120. *Pinicola enucleator*



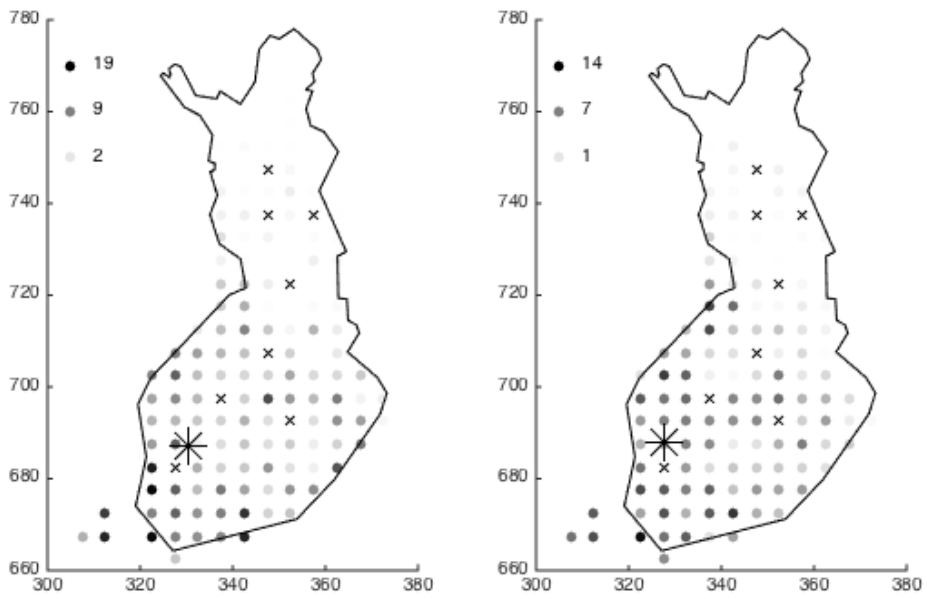
Supplementary fig. 121. *Pyrrhula pyrrhula*



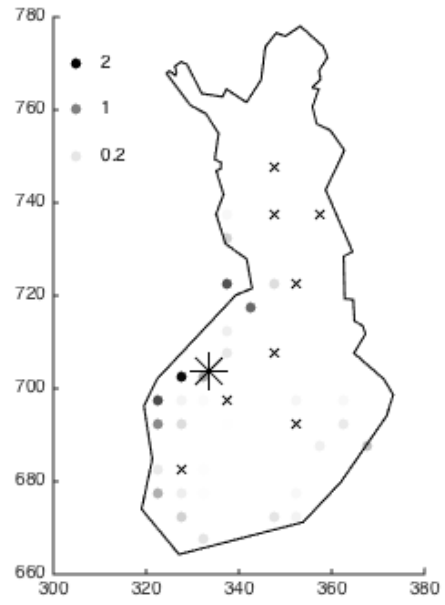
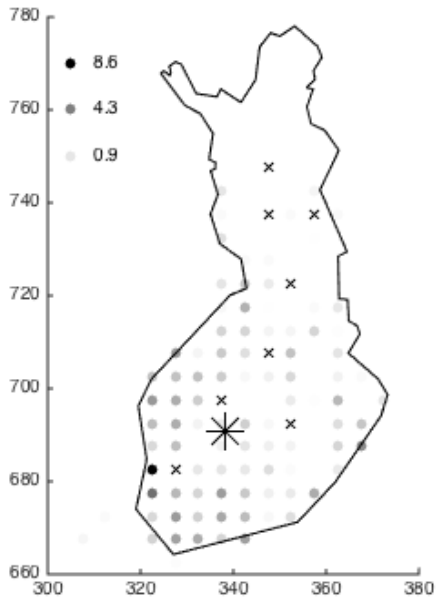
Supplementary fig. 122. *Calcarius lapponicus*



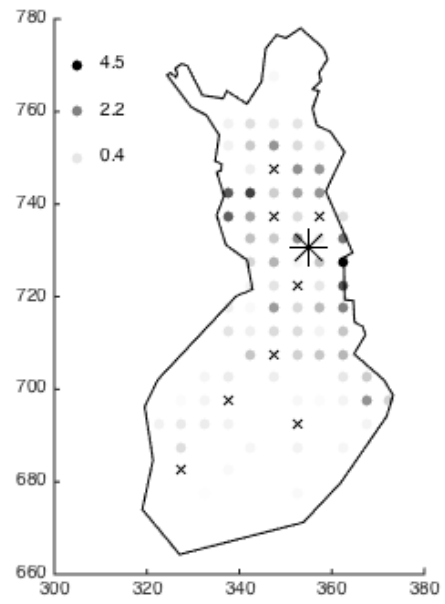
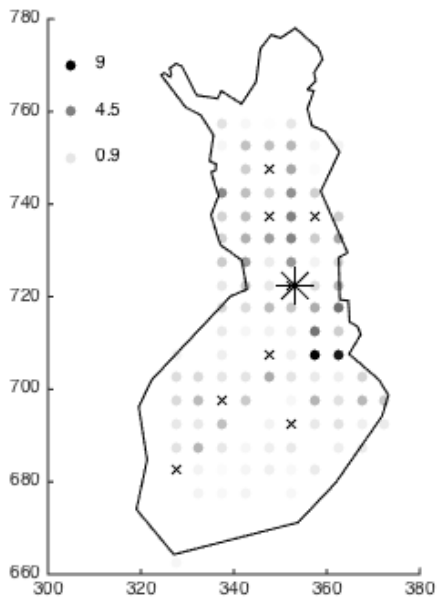
Supplementary fig. 123. *Plectrophenax nivalis*



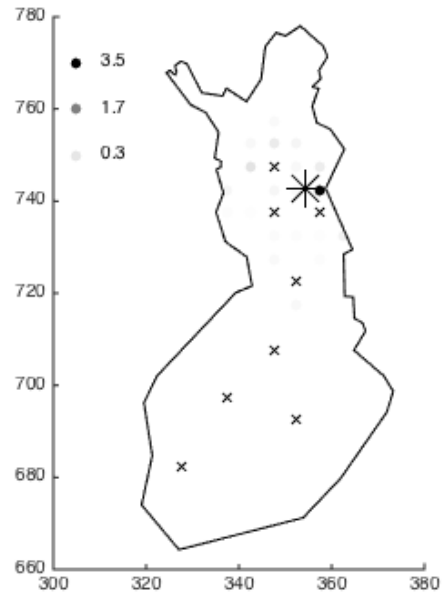
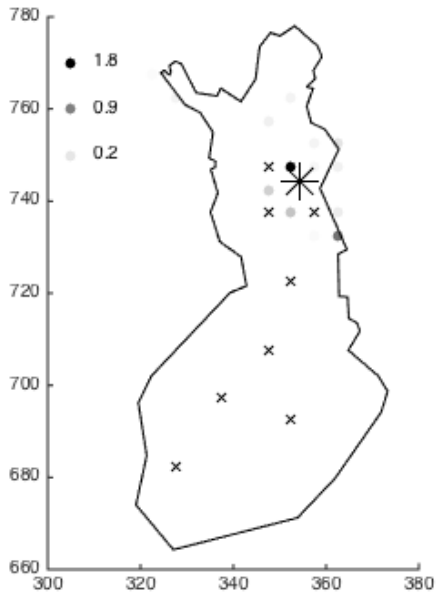
Supplementary fig. 124. *Emberiza citrinella*



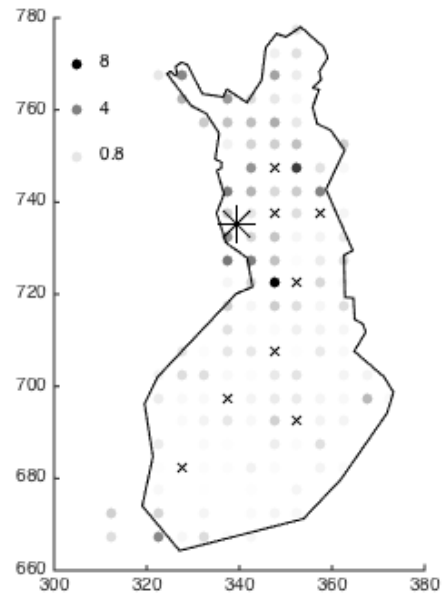
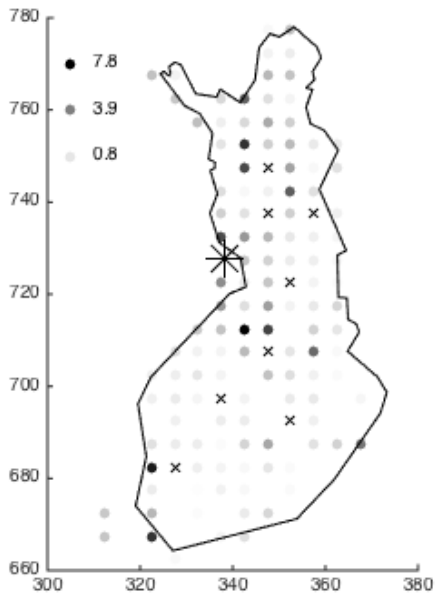
Supplementary fig. 125. *Emberiza hortulana*



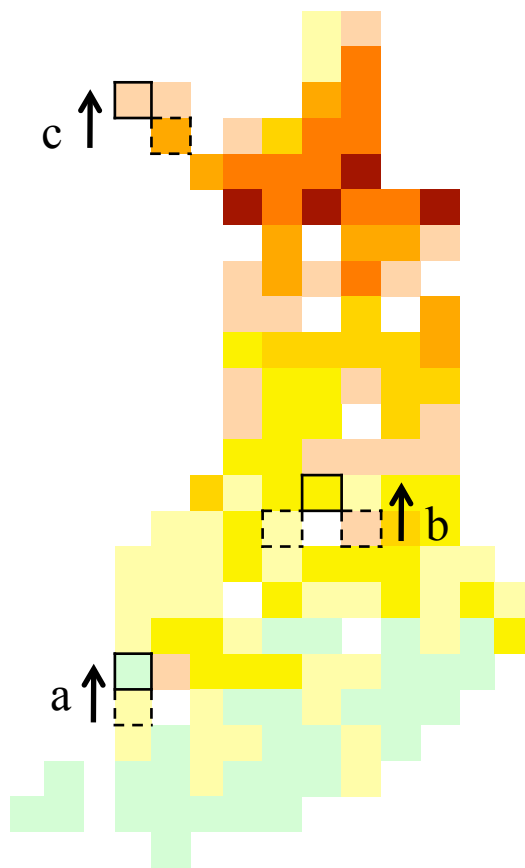
Supplementary fig. 126. *Emberiza rustica*



Supplementary fig. 127. *Emberiza pusilla*

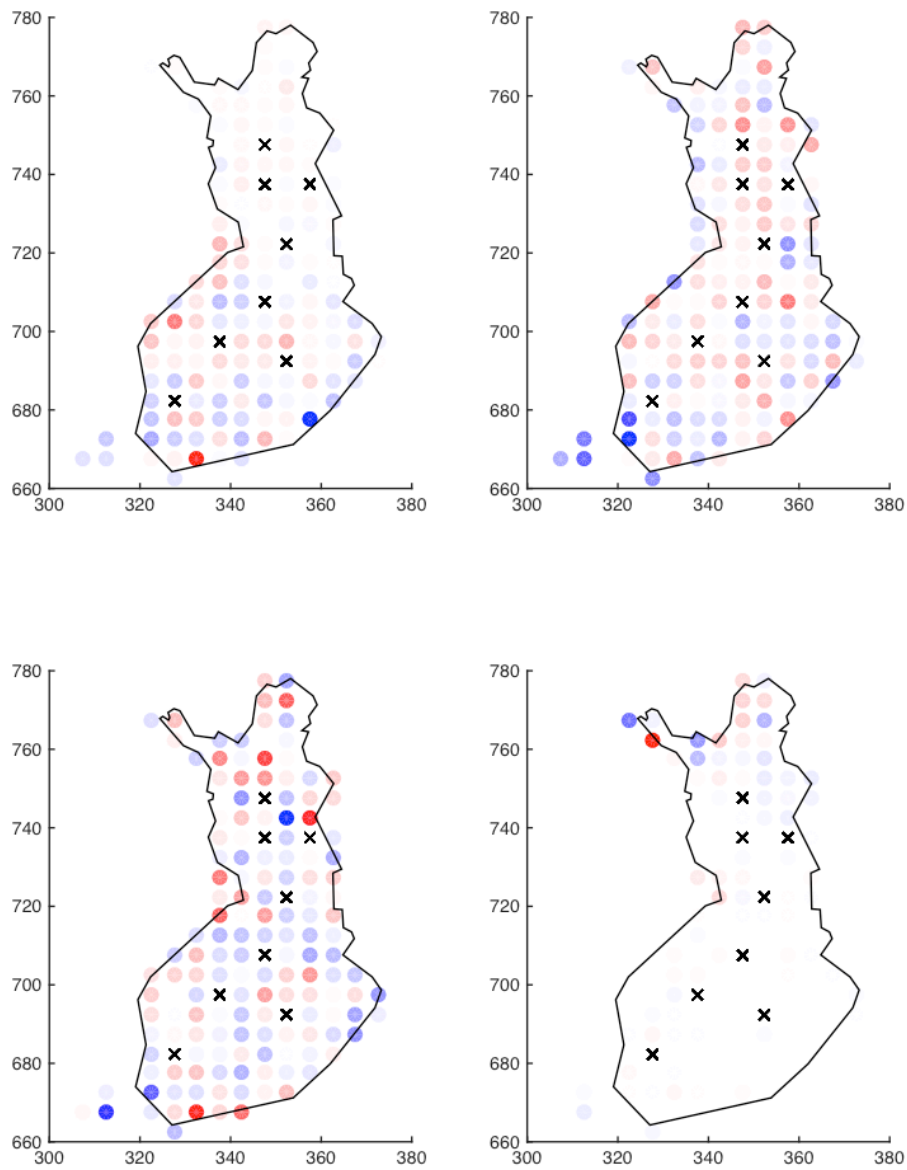


Supplementary fig. 128. *Emberiza schoeniclus*



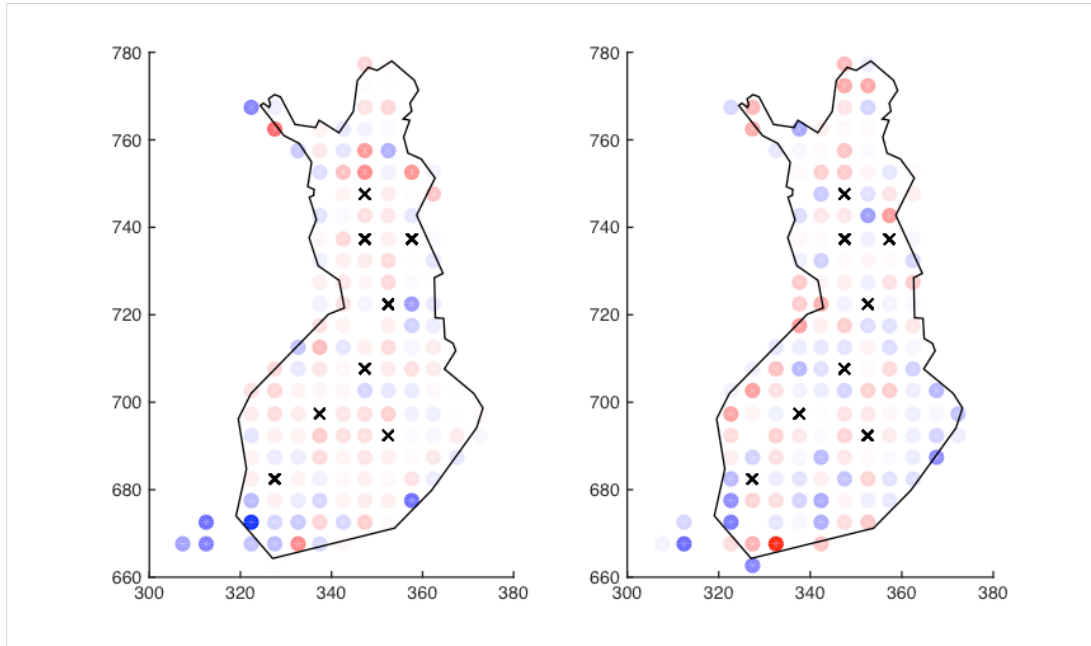
Supplementary Fig. 1. Illustration of how we moved densities of species one grid northwards to estimate the potential effect of shape of the country on the direction of density shifts. In a normal situation (a), the densities were moved one grid northwards. In situations, where the density value was missing from the southern side (b), we used mean of the nearest southwest and southeast grids, or only one of them (c) if both values were not available. The dashed line grids in the figure illustrate the former situation and the solid line grids represents the corresponding grids after the moved densities in Brambling *Fringilla montifringilla* (see also Supplementary Figs 1-129). In case of examples b and c, the densities in the dashed grids were also moved directly northwards like in case a.





Supplementary Fig. 130. Grid specific changes of relative densities of groups of species classified based on their main habitat type: (a) farmland species, (b) forest species, (c) wetland species and (d) montane species. In graphs the species-specific relative densities have been scaled into the same unit in all species so that all species would have equal impact (in contrast to a situation where the most abundant species would dominate the change) corresponding direction analyses (Fig. 1). These grid specific relative densities of species in the first period were subtracted from the corresponding densities

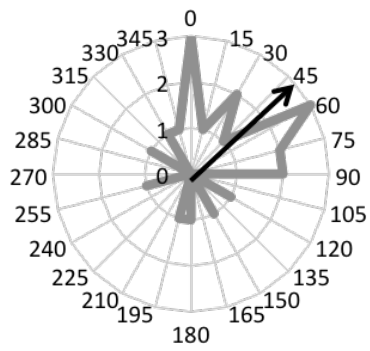
of the latter period. These density changes of the same habitat category were combined grid-specifically and are expressed in colours. Red colour means increasing relative densities and blue declining relative densities. The black crosses show grids without data.



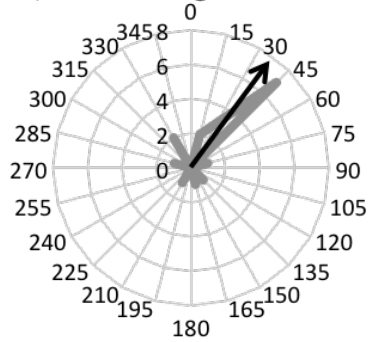
Supplementary Fig. 131. Grid specific changes of relative densities of groups of species classified based on their migration type: (a) residents and partial migrants and (b) short- and long-distance migrants. In graphs the species-specific relative densities have been scaled into the same unit in all species so that all species would have equal impact (in contrast to a situation where the most abundant species would dominate the change) corresponding direction analyses (Fig. 1). These grid-specific relative densities of species in the first period were subtracted from the corresponding densities of the latter period. These density changes of the same migration category were combined grid-specifically

and are expressed in colours. Red colour means increasing relative densities and blue declining relative densities. The black crosses show grids without data.

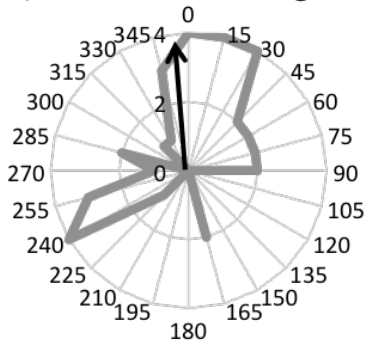
a) Residents



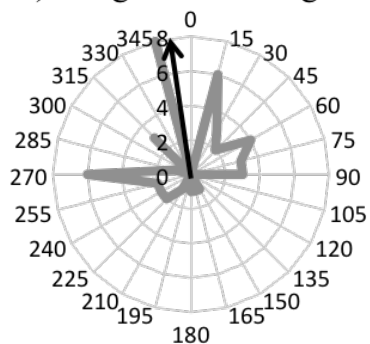
b) Partial migrants



c) Short-distance migrants



d) Long-distance migrants



Supplementary Fig. 132. Distribution of directions of changes in densities based on four migration groups (resident:  $\alpha = 43$ , partial:  $\alpha = 35$ , short-distance:  $\alpha = 359$ , and long-distance migrants:  $\alpha = 357$ ),

Supplementary Table 1. Species-specific sample sizes (N 70-80, N 2000), habitat (Hab), migration (Mig, Mdir) and distribution (Dist) classifications, central gravity of density expressed as latitudes (La70-80, La00) and longitudes (Lo70-80, La00) during both study periods, direction of the density shift (Dir in degrees), total distance of shift (Dist2), density shift along latitude (Ndist) and longitude (Edist) directions (negative values mean shifts towards south and west, respectively) and direction of the species-specific temperature shift. Bolded values in density shifts along latitude and longitude mean that separate Poisson regression analyses of the particular species revealed significant shift in latitude or longitude after Bonferroni correction (note that this is different than changes in the mean central gravity, see more accurately in the text).

Species	N 70-80	N 2000	Hab	Mig	Mdir	Dist	La70-80	La00	Lo70-80	Lo00	Dir (Deg)	Dist2	Ndist	Edist	Tdir (Deg)
Tetrastes bonasia	462	868	2	0	4	2	692.9	701.4	342.9	347.9	30.3	99.1	<b>85.6</b>	<b>50.1</b>	25.2
Lagopus lagopus	267	293	2	0	4	2	751.0	756.4	343.8	343.2	353.4	54.8	<b>54.4</b>	-6.3	350.1
Lagopus muta	43	41	4	0	4	3	766.2	763.5	324.9	326.1	155.6	29.7	-27.0	12.3	325.9
Tetrao tetris	1048	1916	2	0	4	2	699.0	708.9	334.2	344.1	45.3	139.8	98.4	99.4	21.3
Tetrao urogallus	228	418	2	0	4	2	714.6	714.9	347.9	352.1	85.9	42.3	3.0	42.2	14.1
Phasianus colchicus	384	515	1	0	4	2	671.6	683.5	330.3	330.2	359.4	119.5	119.5	-1.3	38.0
Pernis apivorus	22	36	2	1	2	2	689.9	690.8	351.4	340.9	274.6	105.9	8.6	-105.5	19.4
Circus cyaneus	45	44	3	1	1	2	725.5	713.7	350.2	341.2	217.6	148.0	-117.3	-90.3	9.5
Accipiter gentilis	60	59	2	0	4	2	699.1	702.2	334.9	335.6	11.5	31.4	30.8	6.3	30.3
Accipiter nisus	40	70	2	1	1	2	698.7	701.3	323.9	338.8	80.1	151.0	25.9	148.7	24.6
Buteo buteo	98	66	2	1	4	2	698.9	684.1	348.7	334.3	224.1	206.1	-148.1	-143.3	22.2
Buteo lagopus	96	66	2	0	3	3	763.0	767.0	341.4	346.5	51.9	64.8	<b>40.0</b>	51.0	309.6
Pandion haliaetus	41	54	2	1	2	2	685.8	704.2	333.3	347.2	37.0	230.3	183.9	138.7	18.3
Falco tinnunculus	39	121	1	1	1	2	701.3	728.1	338.7	343.5	10.0	271.9	267.7	47.4	22.8
Falco columbarius	21	32	2	1	1	2	745.3	763.9	333.1	339.2	18.2	195.5	<b>185.7</b>	61.2	333.2
Falco subbuteo	21	52	2	1	2	2	697.8	690.4	352.7	342.1	235.6	129.4	-73.1	-106.7	22.5
Grus grus	330	1696	3	1	2	2	710.2	708.4	344.0	333.7	260.3	105.2	-17.8	<b>-103.7</b>	20.8
Haematopus ostralegus	31	102	3	1	1	1	674.1	689.5	312.4	317.3	17.7	161.6	153.9	49.1	33.8
Charadrius hiaticula	34	69	4	1	1	2	754.8	758.8	330.2	337.5	61.1	82.9	<b>40.0</b>	72.6	310.7
Pluvialis apricaria	1139	1237	4	1	1	2	760.6	759.5	347.8	342.5	258.8	54.3	<b>-10.6</b>	-53.3	355.1
Vanellus vanellus	1308	2201	1	1	1	2	691.8	691.6	338.3	331.9	267.9	64.0	<b>-2.3</b>	-64.0	25.6
Calidris pugnax	407	156	3	1	1	3	746.3	750.2	344.5	345.6	15.6	40.2	<b>38.8</b>	10.8	351.0
Calidris falcinellus	114	206	3	1	3	3	751.1	752.1	339.4	343.4	76.3	41.4	<b>9.8</b>	40.2	328.1
Lymnocyptes minimus	205	172	3	0	1	3	754.1	752.6	346.5	345.7	207.8	17.0	<b>-15.0</b>	-7.9	334.4
Gallinago gallinago	1836	2146	3	1	1	2	723.7	729.8	338.2	342.2	33.3	72.5	<b>60.6</b>	39.7	12.6
Scolopax rusticola	158	440	2	1	1	2	690.7	691.5	327.3	334.1	83.4	67.6	<b>7.8</b>	67.2	28.9
Numenius phaeopus	1130	755	3	1	1	2	744.7	755.3	353.9	350.1	340.2	112.5	<b>105.9</b>	-38.2	352.0
Numenius arquata	1734	2744	1	1	1	2	703.5	705.6	341.4	341.5	4.1	21.1	21.0	1.5	26.5
Tringa erythropus	222	135	3	1	2	3	758.8	756.6	345.7	347.1	148.2	26.0	<b>-22.1</b>	13.7	332.2
Tringa totanus	313	342	3	1	1	2	701.5	712.6	316.0	320.9	23.5	121.3	111.3	48.4	35.6
Tringa nebularia	737	1284	3	1	2	2	733.1	730.1	355.1	352.8	217.3	38.8	-30.8	-23.5	4.0

Tringa ochropus	683	2394	2	1	1	2	689.6	697.4	345.6	338.5	317.9	105.6	<b>78.3</b>	-70.8	23.2
Tringa glareola	2970	3803	3	1	2	2	740.9	747.5	347.8	346.2	346.4	67.2	<b>65.3</b>	-15.8	7.0
Actitis hypoleucos	303	356	3	1	2	2	707.6	722.5	336.1	339.1	11.2	151.5	148.6	29.5	16.5
Phalaropus lobatus	85	34	3	1	3	3	758.9	762.1	341.0	338.1	317.1	43.3	<b>31.7</b>	-29.5	326.1
Stercorarius longicaudus	33	49	4	1	1	3	767.2	773.4	338.6	346.9	53.2	104.0	<b>62.3</b>	83.3	326.4
Columba livia	102	561	1	0	4	1	674.9	687.5	347.3	329.6	305.4	216.9	125.7	-176.8	20.9
Columba oenas	382	302	1	1	1	1	670.1	670.3	314.2	319.1	88.0	48.4	1.7	48.4	41.9
Columba palumbus	3682	8195	1	1	1	2	686.7	686.4	330.9	330.2	240.2	7.7	<b>-3.8</b>	<b>-6.7</b>	28.2
Cuculus canorus	4650	7760	2	1	2	2	710.5	711.0	339.5	345.2	85.5	57.5	<b>4.5</b>	<b>57.4</b>	14.0
Surnia ulula	27	25	2	0	4	3	740.5	744.3	345.9	349.9	46.8	55.6	38.1	40.5	327.5
Asio flammeus	66	69	3	1	1	2	740.4	753.8	343.5	340.6	347.5	137.2	<b>134.0</b>	-29.7	357.5
Apus apus	1231	2086	1	1	2	2	684.3	688.8	331.7	335.7	41.6	60.0	<b>44.9</b>	39.8	26.9
Jynx torquilla	376	206	2	1	1	2	696.7	707.1	337.7	334.1	340.9	110.2	104.1	-36.1	17.2
Picus canus	29	36	2	0	4	2	669.1	673.7	317.6	327.6	64.9	109.5	46.5	99.1	38.2
Dryocopus martius	270	1043	2	0	4	2	688.6	694.0	330.5	334.1	33.7	64.8	<b>53.9</b>	35.9	18.1
Dendrocopos major	1326	3648	2	0	4	2	694.8	702.4	341.8	338.3	335.3	83.5	<b>75.8</b>	-34.9	26.1
Dendrocopos minor	30	37	2	0	4	2	688.9	680.8	321.4	334.3	122.0	152.1	-80.5	129.0	27.8
Picoides tridactylus	74	148	2	0	4	2	735.7	730.6	351.5	349.9	197.2	53.4	-51.0	-15.8	337.5
Lullula arborea	31	101	2	1	1	1	668.1	666.3	325.4	316.1	259.2	95.2	-17.8	<b>-93.5</b>	34.6
Alauda arvensis	3912	3581	1	1	1	2	684.8	685.5	327.9	323.2	278.2	46.7	<b>6.7</b>	<b>-46.2</b>	25.7
Riparia riparia	341	532	3	1	2	2	714.5	713.3	353.7	348.5	256.9	52.5	-11.9	-51.2	16.2
Hirundo rustica	1552	1761	1	1	2	2	693.3	693.3	339.7	334.9	270.9	47.5	<b>0.7</b>	-47.5	26.9
Delichon urbicum	1031	758	1	1	2	2	687.2	697.1	338.1	336.0	347.8	101.6	99.4	-21.4	26.0
Anthus trivialis	15580	18958	2	1	2	2	700.5	701.3	340.2	342.6	71.0	25.9	<b>8.4</b>	24.4	16.4
Anthus prantensis	5147	4754	3	1	1	2	750.6	755.3	343.4	340.6	329.7	55.2	<b>47.7</b>	<b>-27.8</b>	8.7
Motacilla flava	4301	2805	3	1	1	2	735.2	748.7	349.0	345.5	345.6	139.4	<b>135.0</b>	-34.7	12.0
Motacilla alba	2283	3315	3	1	2	2	696.7	695.2	335.2	332.6	241.2	30.6	<b>-14.7</b>	<b>-26.8</b>	16.9
Bombycilla garrulus	73	611	2	0	4	2	737.8	741.9	353.6	355.0	18.8	43.3	<b>41.0</b>	14.0	326.3
Troglodytes troglodytes	289	1371	2	1	1	2	678.4	684.0	347.0	330.3	288.4	176.9	<b>55.9</b>	-167.8	22.5
Prunella modularis	2260	4949	2	1	1	2	686.7	693.0	340.3	343.3	25.5	69.8	<b>63.0</b>	<b>30.1</b>	23.2
Erithacus rubecula	5127	16046	2	1	1	2	688.4	695.8	338.7	336.7	344.9	77.2	<b>74.5</b>	-20.1	23.1
Luscinia luscinia	288	574	3	1	2	2	673.3	672.3	325.5	334.0	96.3	86.2	<b>-9.5</b>	85.7	31.5
Luscinia svecica	862	930	4	1	3	3	764.7	768.4	335.2	336.6	20.8	39.5	<b>36.9</b>	14.0	312.3
Phoenicurus phoenicurus	4109	7841	2	1	1	2	730.3	735.8	346.2	350.2	35.6	68.1	<b>55.4</b>	39.6	14.1
Saxicola rubetra	1687	1601	1	1	1	2	703.4	711.2	342.2	341.0	351.2	78.6	77.7	-12.1	16.8
Oenanthe oenanthe	1467	594	3	1	1	2	738.1	747.3	336.7	338.7	12.5	94.1	<b>91.9</b>	20.4	12.0
Turdus torquatus	25	35	4	1	1	3	769.9	768.5	326.1	326.4	169.0	14.0	-13.8	2.7	331.0

Turdus merula	2108	6764	2	0	1	2	672.8	677.8	319.0	324.9	49.4	77.5	<b>50.5</b>	<b>58.8</b>	32.2
Turdus pilaris	5173	13779	1	1	1	2	694.5	697.9	339.4	338.9	351.6	33.5	<b>33.1</b>	-4.9	16.1
Turdus philomelos	6892	13336	2	1	1	2	695.8	701.4	335.4	339.8	38.1	70.3	<b>55.3</b>	<b>43.3</b>	17.3
Turdus iliacus	12476	14609	2	1	1	2	713.8	724.3	341.4	342.7	7.1	106.2	105.4	13.2	13.7
Turdus viscivorus	448	1675	2	1	2	2	705.4	706.7	333.2	336.4	68.6	34.5	12.6	32.1	16.2
Locustella naevia	20	39	3	1	1	2	681.0	685.3	337.2	337.8	8.0	43.4	43.0	6.0	22.4
Acrocephalus schoenobaenus	1234	1691	3	1	2	2	701.6	701.9	339.9	332.8	273.0	71.1	3.8	-71.0	18.5
Acrocephalus dumetorum	51	176	3	1	3	2	686.6	682.4	363.6	352.0	249.8	124.2	<b>-42.9</b>	-116.6	17.1
Acrocephalus palustris	39	86	3	1	2	2	672.5	671.3	331.0	316.7	265.3	144.0	<b>-11.8</b>	-143.5	19.8
Acrocephalus scirpaceus	349	265	3	1	1	1	668.7	668.6	315.5	316.9	97.0	14.0	-1.7	13.9	33.7
Hippolais icterina	164	182	2	1	2	2	667.2	670.2	321.2	324.9	50.8	47.7	<b>30.1</b>	36.9	25.9
Sylvia curruca	1467	2885	2	1	2	2	689.0	689.9	338.7	334.7	283.3	41.7	<b>9.6</b>	-40.6	27.4
Sylvia communis	1939	3147	1	1	2	2	677.9	678.0	329.0	328.3	273.3	7.5	<b>0.4</b>	-7.5	30.1
Sylvia borin	6484	9260	2	1	2	2	685.9	687.4	337.2	340.5	66.6	35.5	<b>14.1</b>	32.6	26.9
Sylvia atricapilla	628	1334	2	1	2	2	672.3	671.9	317.4	316.8	229.1	7.3	<b>-4.8</b>	<b>-5.5</b>	31.6
Phylloscopus trochiloides	88	216	2	1	3	2	681.8	679.1	348.1	341.9	246.9	67.8	-26.6	-62.3	22.4
Phylloscopus sibilatrix	2475	1966	2	1	1	2	680.1	682.8	342.1	343.9	33.0	32.1	<b>26.9</b>	17.4	26.7
Phylloscopus collybita	2430	3336	2	1	2	2	685.7	687.8	330.9	332.3	34.2	25.4	<b>21.0</b>	14.3	29.3
Phylloscopus trochilus	58187	76890	2	1	2	2	711.8	716.5	343.2	342.3	349.0	47.9	47.0	-9.1	13.7
Regulus regulus	3122	5344	2	0	1	2	684.5	689.5	330.2	331.0	9.0	50.7	<b>50.1</b>	8.0	26.0
Muscicapa striata	4340	6815	2	1	2	2	700.1	701.5	337.3	340.4	65.8	33.6	<b>13.8</b>	30.6	16.9
Ficedula parva	43	125	2	1	3	2	669.0	680.5	330.2	353.8	64.0	262.6	<b>115.2</b>	235.9	31.4
Ficedula hypoleuca	3157	6607	2	1	1	2	702.9	698.2	337.1	338.2	166.7	48.6	<b>-47.3</b>	11.2	16.7
Poecile montanus	2744	3700	2	0	4	2	697.4	706.2	333.4	346.2	55.7	155.0	<b>87.4</b>	128.0	18.7
Poecile cinctus	223	152	2	0	4	3	757.1	758.6	345.6	348.1	59.4	28.7	<b>14.6</b>	24.7	316.0
Lophophanes cristatus	1071	2169	2	0	4	2	681.8	683.4	329.8	342.0	82.8	122.6	<b>15.3</b>	121.6	28.8
Periparus ater	398	690	2	0	1	2	670.9	673.8	312.6	327.7	79.1	154.1	<b>29.0</b>	151.3	34.5
Cyanistes caeruleus	442	4257	2	0	1	2	671.0	681.3	319.1	327.7	39.7	134.6	<b>103.6</b>	85.9	25.6
Parus major	3815	13145	2	0	1	2	685.4	690.5	329.0	332.6	34.5	62.2	<b>51.2</b>	35.2	21.1
Certhia familiaris	523	1245	2	0	1	2	676.0	684.5	323.7	330.5	39.0	109.2	<b>84.8</b>	68.8	25.9
Oriolus oriolus	98	37	2	1	2	1	680.1	680.3	352.3	350.1	274.2	22.1	1.6	-22.0	25.3
Lanius collurio	352	335	1	1	2	2	676.0	677.8	329.9	336.3	74.6	67.0	<b>17.8</b>	<b>64.6</b>	27.9
Lanius excubitor	38	51	2	1	1	2	729.9	731.1	346.8	348.9	60.4	23.7	11.7	20.6	359.3
Garrulus glandarius	534	936	2	0	4	2	686.1	687.1	334.6	338.1	74.0	36.5	<b>10.1</b>	35.1	31.3
Perisoreus infaustus	264	339	2	0	4	2	743.7	752.0	351.8	348.8	340.0	88.3	<b>83.0</b>	-30.1	334.6
Pica pica	1397	2978	1	0	4	2	700.0	698.6	337.4	333.2	252.1	43.6	<b>-13.4</b>	-41.5	19.6
Corvus monedula	452	2663	1	0	1	2	676.9	682.9	316.8	322.7	44.8	84.8	<b>60.2</b>	<b>59.7</b>	36.6



Corvus corone	4179	5956	1	0	1	2	698.8	697.8	331.4	331.6	166.5	10.0	<b>-9.7</b>	<b>2.3</b>	15.6
Corvus corax	448	1129	2	0	4	2	734.2	715.8	336.1	336.9	177.3	184.5	-184.3	8.8	11.4
Sturnus vulgaris	2120	1165	1	1	1	2	680.7	675.2	328.9	319.2	240.3	111.2	<b>-55.0</b>	<b>-96.6</b>	29.2
Passer domesticus	1291	3970	1	0	4	2	683.6	697.8	333.4	331.8	353.7	142.4	141.5	-15.7	25.2
Fringilla coelebs	40860	72779	2	1	1	2	688.0	691.5	335.4	338.5	42.1	46.6	<b>34.5</b>	31.2	20.3
Fringilla montifringilla	17398	13105	2	1	1	2	747.8	754.1	348.1	347.4	353.7	64.0	<b>63.6</b>	-7.0	8.2
Carduelis chloris	575	5110	1	0	1	2	679.7	689.9	320.2	328.2	37.8	129.8	<b>102.5</b>	<b>79.6</b>	27.5
Carduelis spinus	7562	20079	2	1	1	2	695.7	705.7	341.2	341.2	359.9	100.4	<b>100.4</b>	<b>-0.2</b>	19.7
Carduelis cannabina	101	180	1	1	1	1	679.0	674.5	321.9	323.0	166.7	47.1	-45.8	<b>10.8</b>	33.6
Carduelis flammea	6215	5976	2	0	3	2	749.3	756.5	348.8	343.9	325.5	87.0	<b>71.7</b>	-49.2	4.4
Loxia leucoptera	123	113	2	0	4	3	742.5	749.8	352.5	348.5	331.8	82.8	73.0	-39.2	338.5
Loxia curvirostra	1868	4196	2	0	4	2	694.9	710.3	334.2	344.8	34.3	186.7	154.2	105.2	17.8
Loxia pytyopsittacus	213	295	2	0	4	2	712.2	713.6	337.4	342.0	72.7	47.9	14.2	45.7	13.2
Carpodacus erythrinus	2177	1952	3	1	3	2	693.6	697.4	347.0	343.0	313.5	54.8	<b>14.2</b>	45.7	28.9
Pinicola enucleator	107	62	2	0	4	3	757.1	753.1	347.3	351.8	131.5	60.8	<b>37.7</b>	-39.7	319.5
Pyrrhula pyrrhula	1169	2121	2	0	4	2	701.7	710.7	341.9	348.1	34.8	109.4	<b>-40.3</b>	45.5	21.0
Calcarius lapponicus	337	497	4	1	3	3	771.5	768.2	343.9	336.0	247.0	86.4	<b>89.8</b>	<b>62.4</b>	307.2
Plectrophenax nivalis	92	97	4	1	3	3	763.8	765.6	328.8	326.6	308.9	28.5	<b>-33.8</b>	-79.5	325.9
Emberiza citrinella	6044	9415	1	0	1	2	687.0	687.9	330.4	327.6	286.8	30.2	<b>17.9</b>	<b>-22.2</b>	21.9
Emberiza hortulana	1119	182	1	1	1	2	690.8	703.6	338.3	333.7	340.1	135.6	8.7	-28.9	29.2
Emberiza rustica	916	554	3	1	3	2	722.3	730.5	353.1	354.9	12.2	84.3	127.5	-46.2	12.2
Emberiza pusilla	77	106	3	1	3	3	744.2	742.6	354.4	354.4	180.5	16.5	82.4	17.8	319.6
Emberiza schoeniclus	1907	2490	3	1	1	2	727.8	735.2	338.2	339.5	9.6	74.8	<b>-16.5</b>	-0.1	10.3