

1 **Co-occurrence patterns and habitat selection of the mountain hare, European hare, and**
2 **European rabbit in urban areas of Sweden**

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13

14 **Abstract**

15 Assessing the underlying mechanisms of co-occurrence patterns can be challenging as biotic and

16 abiotic causations are hard to disentangle. To date, few studies have investigated co-occurrence

17 patterns within urban areas that constitute novel habitat to numerous wildlife species. Moreover, as

18 urban areas expand and are increasingly used as habitat by wildlife, there is a need for a better

19 understanding of urban ecology to facilitate human-wildlife coexistence. Here, we investigated co-

20 occurrence patterns and habitat selection of the European hare (*Lepus europaeus*), mountain hare

21 (*L. timidus*), and European rabbit (*Oryctolagus cuniculus*) inside urban areas of Sweden, using joint

22 species distribution models and generalized linear mixed models based on citizen science

23 observations. All three species were observed within urban areas, but European hares and rabbits

24 appear to be more successful urban colonizers compared to mountain hares. Overall, our findings

25 suggested that urban occurrence by all three lagomorphs was related to suitable conditions within
26 the distribution of each species (e.g. climate and elevation), rather than by the presence of other
27 lagomorph species or specific land cover types within urban areas. On a finer spatial scale, our
28 findings suggested facilitation of European hares by rabbits, though the mechanism for this remains
29 unclear. European hares and rabbits generally selected for green urban areas and mountain hares for
30 residential gardens, which likely constitute suitable foraging sites. Our findings contribute to the
31 understanding of urban ecology and provide valuable insight for management measures of the three
32 lagomorphs in urban areas of Sweden.

33

34 **Keywords:** citizen science, competition, facilitation, joint species distribution model, *Lepus*
35 *europaeus*, *Lepus timidus*, *Oryctolagus cuniculus*, urban ecology

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38 **1. Introduction**

39 Studying the underlying mechanisms of species co-occurrence and interactions can be challenging,
40 because disentangling abiotic and biotic factors affecting the occurrence and abundance of species
41 is difficult, especially in heterogeneous environments. However, studies on co-occurrence and new
42 methods, which can untwine abiotic and biotic factors, have received more attention in recent years.
43 Niche differences, distinct habitat preferences, competitive exclusion, environmental filtering, or a
44 combination of these factors were proposed as ecological explanations for species segregation or
45 co-occurrence (Pollock *et al.* 2014; Bar-Massada 2015; Estevo, Nagy-Reis & Nichols 2017; Kohli,
46 Terry & Rowe 2018; Ulrich *et al.* 2018).

47

48 Urban areas are highly human-modified, which might lead to altered co-occurrence and interactions
49 of the species that are able to persist in these areas. Urbanization increases globally and is a major
50 driver of environmental change, negatively affecting ecosystems globally (Brown 2001; Grimm *et*
51 *al.* 2008). Both the expansion of urban areas into animal habitats as well as active urban
52 colonization leads to the increasing occurrence of wildlife in these novel habitats (Luniak 2004).
53 The causes of urban colonization are often not well understood. For example, urban colonization
54 might be driven by poorer habitat conditions or increased hunting pressure outside urban areas
55 (Rutz 2008; Mayer & Sunde 2020). Thus, urban areas can constitute an advantageous habitat, e.g.
56 due to relaxed predation (Møller 2012) or increased resource availability (Contesse *et al.* 2004).
57 While some species proliferate in urban areas, others are not able to adapt and become locally
58 extinct (McKinney 2006; Shochat *et al.* 2006). Consequently, an increased understanding of habitat
59 preferences by urban wildlife can be a valuable tool to aid conservation actions, ensuring suitable
60 habitats for urban colonizers. At the same time, it is important to consider biotic interactions, as
61 competition between species might cause exclusion from otherwise suitable habitats (Thulin
62 2003). While habitat selection within urban areas has been previously addressed in numerous
63 species (Chambers & Dickman 2002; Bozek, Prange & Gehrt 2007; Duduś *et al.* 2014; Mayer &
64 Sunde 2020), research on urban community ecology and species interactions are scarce (Carrete *et*
65 *al.* 2010; Magle *et al.* 2012; Ramírez-Cruz *et al.* 2019).

66
67 Citizen science observations provide large quantities of data from broad geographical scales and
68 restricted areas (e.g. private property), which would otherwise be nigh impossible to obtain for
69 researchers (Dickinson, Zuckerberg & Bonter 2010). However, such data also has limitations. Point
70 occurrence data collected by volunteers is prone to pseudo-absences, temporal and spatial biases,
71 and varying observer quality (Crall *et al.* 2011; Geldmann *et al.* 2016). Nevertheless, high human

72 population densities within urban areas yield good coverage and increased sampling efforts
73 (Dickinson, Zuckerberg & Bonter 2010; Mair & Ruete 2016).

74

75 Using citizen science observations, we investigated co-occurrence patterns and habitat selection of
76 the European hare (*Lepus europaeus*), mountain hare (*L. timidus*), and European rabbit
77 (*Oryctolagus cuniculus*, hereafter rabbit) in urban areas of Sweden to assess how occurrence and
78 habitat selection was affected by land cover and the presence of other lagomorphs. Sweden was
79 selected as a case study due to its high quantity of citizen science data, and for harboring three
80 lagomorph species of similar ecology, providing an optimal model to investigate species
81 interactions (Leach, Montgomery & Reid 2015).

82

83 Mountain hares are native to Sweden, typically associated with tundra, open forest, and heathland in
84 upland areas (Flux & Angermann 1990; Thulin 2003). Moreover, mountain hare occurrence is
85 positively associated with deep and lasting snow cover, and negatively with human influence
86 (Jansson & Pehrson 2007; Leach, Montgomery & Reid 2016). They are declining and categorized
87 as near threatened in Sweden (Artdatabanken 2020), with milder winters and competitive exclusion
88 by European hares expanding their distribution northwards proposed to be responsible for this
89 decline (Thulin 2003; Jansson & Pehrson 2007). Both European hares and rabbits were introduced
90 to Sweden (Artdatabanken 2020). European hares are associated with agricultural lowland, and their
91 densities have been found to be positively correlated with higher temperatures and lower
92 precipitation (Smith, Jennings & Harris 2005; Leach, Montgomery & Reid 2016). While European
93 hare populations have been declining in large parts of Europe since 1960 due to agricultural
94 intensification (Smith, Jennings & Harris 2005), they might still be expanding their distribution in
95 Sweden (Jansson & Pehrson 2007). The rabbit is categorized as ‘near threatened’ in its native range

96 in the Iberian peninsula, but appears to proliferate in areas where it was introduced (Lees & Bell
97 2008). Although flexible in their habitat preferences, rabbits are predominantly found in grassland,
98 pastures or arable land bordering scrubland, providing cover from predators (Calvete *et al.* 2004;
99 Tapia *et al.* 2014). They prefer sandy soil that allows them to dig burrows, and their distribution is
100 positively correlated with temperature and negatively with precipitation and mean slope (Calvete *et*
101 *al.* 2004; Leach, Montgomery & Reid 2016). All three species are game species in Sweden, with
102 European hares and rabbits being regulated in areas where they might cause damage
103 (<https://jagareforbundet.se/>).

104

105 Previous studies are not in compliance on European hare and rabbit interactions. Most studies have
106 found no or limited evidence for competition between the two species (Stott 2003; Katona *et al.*
107 2004; Flux 2008), with one study suggesting facilitation (Leach, Montgomery & Reid 2017).
108 However, an assessment of the effectiveness of different measures to eradicate rabbits from islands
109 showed that European hares were markedly more effective than both cats and myxomatosis in
110 removing rabbits due to competitive exclusion (Flux 1993). The distribution of the mountain hare,
111 apart from being affected by abiotic factors (Leach, Montgomery & Reid 2016), might be limited
112 via competitive exclusion by the European hares' northward expansion (Thulin 2003).

113

114 Both European hares and rabbits now occur in urban areas (Mayer & Sunde 2020; Ziege *et al.*
115 2020) that, under certain conditions, appear to constitute advantageous habitat. For example, rabbits
116 became more diurnal, spent less energy on anti-predator behaviors, and reduced their home range
117 size, possibly due to increased resource availability (Ziege *et al.* 2016; Ziege *et al.* 2020). There is
118 little information regarding urban colonization by mountain hares, although some urban and
119 suburban observations exist (Haigh & Lawton 2007; Levänen, Pohjoismäki & Kunnasranta 2019).

120

121 Here, we first described patterns of urban occurrence by the three lagomorphs, and then used joint
122 distribution models to investigate the underlying mechanisms (i.e. environmental filtering or biotic
123 interactions) of the three species' co-occurrence patterns on urban area and 1×1 km urban grid cell
124 level. Moreover, we investigated species occurrence and habitat selection within urban areas,
125 assessing the role of urban area size, climate, elevation (occurrence analysis only), urban land cover
126 types and observations of the other lagomorph species. We predicted that urbanization might
127 increase competition for resources between European hares and rabbits, which should lead to
128 segregation of the two species within urban areas. We further predicted that mountain hares
129 segregate from both European hares and rabbits, due to environmental filtering, given the mountain
130 hares' distinct habitat preferences, and potentially due to competitive exclusion. Regarding habitat
131 selection, we predicted that the lagomorphs selected land covers that resemble those of their
132 preferred habitats outside urban areas, i.e. European hares and rabbits selecting open herbaceous
133 vegetated areas, e.g. green urban areas and residential lawns (and rabbits additionally for sandy
134 soils), and mountain hares selecting forested areas.

135

136 **2. Methods**

137 *Study areas and preparation of spatial data*

138 Our study area comprised Urban Morphological Zones (UMZ) of the CORINE Land Cover 2000
139 version 16, defined as areas within 200 meters of each other considered to contribute to the urban
140 tissue and function ([https://www.eea.europa.eu/data-and-maps/data/urban-morphological-zones-](https://www.eea.europa.eu/data-and-maps/data/urban-morphological-zones-2000-2)
141 [2000-2](https://www.eea.europa.eu/data-and-maps/data/urban-morphological-zones-2000-2)), within Sweden, obtained from The European Environment Agency (EEA)
142 (<http://ftp.eea.europa.eu/www/umz/v4f0/UMZ2000.zip>). Because higher human population
143 densities increase sampling effort, thereby reducing the number of pseudo-absences and the effect

144 of spatially biased sampling effort in point occurrence data (Geldmann *et al.* 2016; Mair & Ruete
145 2016), we only considered UMZ's > 10 km² (hereafter urban areas) for our analysis, leaving 97
146 urban areas (Fig. 1A). Moreover, we created 1×1 km grid cells within urban areas using ArcGISPro
147 2.8.3 (Esri Inc. 2020), resulting in 4,915 grid cells, to analyze species associations on a finer spatial
148 scale (see below).

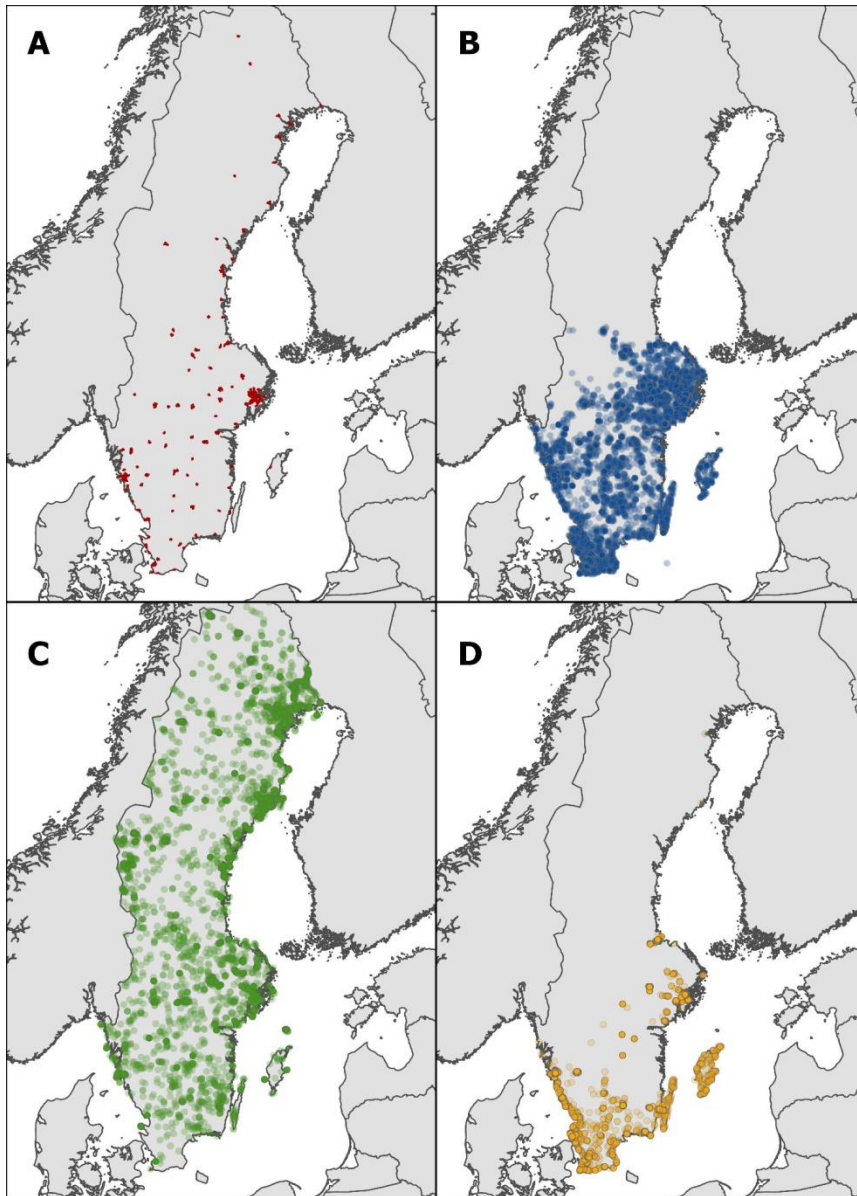
149

150 *Citizen science observations and hunting bag data*

151 Point occurrence data for the three lagomorph species within Sweden were derived from the Global
152 Biodiversity Information Faculty (GBIF) (GBIF.org (21 March 2022) GBIF Occurrence Download
153 <https://doi.org/10.15468/dl.du6h5m>) for the years 2007-2021 (Fig. 1B-D). There were very few
154 observations before 2007, which is why we used this year as cut-off. GBIF is a database providing
155 institutions from all over the world with common standards and open-source tools for sharing
156 information on when and where species have been recorded (<https://www.gbif.org/what-is-gbif>).
157 The bulk of data in this study (98.5%) came from Artportalen
158 (<https://www.artportalen.se/Home/About>), a website for reporting species in Sweden. To reduce
159 variation in data quality and ensure a certain degree of location precision, observations with a
160 spatial uncertainty of >1000 m were excluded. We intersected all observations with urban areas and
161 grid cells to assign them to environmental variables (see below), using the R package 'raster'
162 (Hijmans *et al.* 2015).

163

164



165

166 **Fig. 1:** Depicting (A) the urban areas (dark red) of Sweden, and all reported citizen observations of
167 (B) European hares (blue dots), (C) mountain hares (green dots), and (D) European rabbits (orange
168 dots) within Sweden from 2007-2021.

169

170

171 Moreover, we used hunting bag data, derived from the Swedish Hunters Associations databank
172 Viltdata (<https://rapport.viltdata.se/statistik/>), as a relative measure of non-urban population trends
173 for the three species. We compared hunting bag data with the proportion of urban observations

174 (compared to all observations) for each species separately for each year, to assess concurrence and
175 temporal patterns in urban colonization. Changes in human urban population were obtained from
176 the World Bank database

177 (<https://data.worldbank.org/indicator/SP.URB.TOTL.IN.ZS?locations=SE>).

178

179 *Environmental data*

180 We obtained environmental data known to and/or suspected to affect the occurrence of the three
181 species. We obtained climate data (i.e. annual mean temperature, mean temperature of the coldest
182 quarter, and annual precipitation) from 1970-2000 at 2.5 arc-minute resolution from WorldClim
183 version 2.1. (<https://www.worldclim.org>), and mean soil sand content and bulk density at 250
184 meters resolution from the International Soil Reference and Information Centre version 2.0.1.
185 (<https://maps.isric.org/>). We selected a depth of 15-30 cm, because rabbit burrow depth is 20 cm on
186 average (Serrano & Hidalgo de Trucios 2011). Elevation data at 90 m resolution were obtained
187 from the Shuttle Radar Topography Mission (<http://srtm.csi.cgiar.org/>). To extract climate, soil and
188 elevation information for the urban areas, we created 100 random points per urban area using
189 ArcGIS Pro2.8.3. We extracted the environmental values from each raster layer using the R
190 package ‘raster’ (Hijmans *et al.* 2015) and values were averaged for each urban area. Land cover
191 data at Minimum Mapping Unit 25 ha were downloaded from CORINE Land Cover 2018 version
192 of the Copernicus Land Monitoring Service ([https://land.copernicus.eu/pan-european/corine-land-](https://land.copernicus.eu/pan-european/corine-land-cover/clc2018?tab=download)
193 [cover/clc2018?tab=download](https://land.copernicus.eu/pan-european/corine-land-cover/clc2018?tab=download)). We intersected the land cover vector with urban areas and urban
194 grid cells and calculated the area of each land cover patch. Moreover, to describe the land cover
195 surrounding urban areas, we buffered each urban area by 1000 m, and then intersected this buffer
196 with the land cover vector. We re-classified the CORINE land cover classes into 8 categories within
197 urban areas: (1) continuous urban fabric (e.g. city centers, >80% of the ground covered by artificial

198 surfaces, i.e. soil sealed), (2) discontinuous urban fabric (e.g. suburbs, >30% scattered urban fabric
199 without sealed soil), (3) industry (including airports, railways, etc.), (4) green urban areas (e.g.
200 parks), (5) agriculture, (6) forest (including other (semi)natural areas including heathland), (7)
201 water, and (8) other areas (water, beaches, bare rock, etc.) (Table S1). The land covers surrounding
202 urban areas were categorized into (1) agriculture, (2) forest, (3) urban areas (merging the above-
203 mentioned urban categories due to little urban land cover surrounding urban areas), and (4) other
204 areas. We then calculated the proportion of each land cover category per urban area, grid cell, and
205 surrounding urban areas.

206

207 *Defining species occurrence*

208 We categorized a species occurring in an urban area when there were ≥ 7 observations within the
209 urban area, i.e. at least one observation per year when most observations were recorded (from 2015-
210 2021; see results). We chose this categorization to minimize defining species occurrence based on
211 misidentifications, observations of escaped/released pet hares and rabbits, or dispersing individuals
212 that had not established in the area. Defining occurrence based on a single observation did not
213 markedly change the results (not shown). On grid cell level, we defined species presence in grid
214 cells with ≥ 1 observation, because on this fine scale, point occurrence data likely was more prone to
215 false-negatives rather than false-positives (Crall *et al.* 2011).

216

217 *Data analyses*

218 First, to assess whether there was evidence of biotic interactions between the three species and
219 whether the three species shared or had distinct environmental affiliations, we used the joint species
220 distribution model (JSDM) provided by Pollock *et al.* (2014), which accounts for co-occurrence
221 patterns of multiple species. We modeled predicted probabilities of occurrences, using a binary

222 response variable (i.e. presence/absence), using a multivariate probit regression model (Pollock *et*
223 *al.* 2014). The model provides environmental correlations for species pairs indicating shared or
224 differing environmental responses, whilst residual correlations suggest biotic interactions, such as
225 competition or facilitation (Pollock *et al.* 2014). We did two model runs, one on an urban area level
226 and one on a grid cell level, as environmental effects and competitive interactions are known to
227 appear at different scales (Leach, Montgomery & Reid 2017). For the JSDMs, collinearity among
228 environmental variables was assessed building a correlation matrix, defining correlation as
229 Pearson's coefficient > 0.6 (Zuur, Ieno & Elphick 2010). Consequently, we removed mean annual
230 temperature (positively correlated with temperature of coldest quarter), soil bulk density (positively
231 correlated with soil sand content) and surrounding forest (negatively correlated with surrounding
232 agriculture). Moreover, we removed the proportion of forest (positively correlated with surrounding
233 forest and negatively with surrounding agriculture) for the urban area level analysis and the
234 discontinuous urban fabric (negatively correlated with industry) for the analysis on grid cell level.
235 Consequently, we included temperature of coldest quarter, soil sand content, precipitation,
236 elevation, the proportion of continuous urban fabric, discontinuous urban fabric (for the urban area
237 level analysis only), forest (for the grid cell level analysis only), industry, green urban areas,
238 agriculture, surrounding agriculture and surrounding urban fabric. We centered and scaled
239 covariates prior to analyses (Grueber *et al.* 2011).

240

241 Second, we investigated the factors affecting species occurrence within urban areas, separately for
242 the three lagomorphs within their distribution, using generalized linear models with a log link and a
243 binomial response distribution (present = 1 versus absent = 0). To estimate the European hares' and
244 rabbits' distribution in Sweden (the mountain hares' range covers the whole of Sweden), we created
245 100% minimum convex polygons based on citizen science observations (excluding obvious

246 outliers). We initially built 4 candidate models based on biological hypotheses: (1) land covers
247 within urban areas affect the presence of a species, including the proportion of continuous urban
248 fabric, discontinuous urban fabric, green urban areas, industry, forest, and agriculture; (2) land
249 covers surrounding urban areas affect species occurrence, including the proportion of surrounding
250 agriculture, forest, and urban areas; (3) climate and the size of an urban area (as proxy for the
251 number of observers) affect occurrence, including mean temperature of coldest quarter, mean
252 annual precipitation, elevation, soil sand content (for rabbits only), and urban area size; (4)
253 competition with or facilitation by other lagomorphs affects occurrence, including the presence of
254 other lagomorph species (estimated as above). The proportion of surrounding forest and agriculture
255 were highly correlated (Pearson's correlation coefficient > 0.6 and variance inflation factor > 3
256 (Zuur, Ieno & Elphick 2010)) so we only included agriculture (European hares and rabbits) or forest
257 (mountain hares) in our analysis. Additionally, as measure of relative abundance, we analyzed the
258 number of observations per urban area separately for each species (again including all urban areas
259 within the species' distribution), using generalized linear models of the R package 'glmmTMB'
260 (Magnusson *et al.* 2017) with a log link function and negative binomial distribution to account for
261 overdispersion and zero-inflation (O'hara & Kotze 2010). We again built the same candidate
262 models as for the species presence analyses. We scaled all numeric variables (mean = 0; standard
263 deviation = 1) to obtain comparable estimates. We initially compared the 4 models based on
264 biological hypotheses for both the analyses of species presence and relative abundance using
265 Akaike's Information Criterion (AIC). To obtain the most parsimonious (hereafter best) model, we
266 performed a stepwise backward selection, starting from the full model including all variables, and
267 removed variables that lead to an increase in AIC, selecting the model with the lowest AIC
268 (Wagenmakers & Farrell 2004). This approach resulted in the same best model compared to model

269 selection based on creating all possible combinations of candidate models using the ‘dredge’
270 function of the R package ‘MuMIn’ (Barton 2020).
271
272 Third, to analyze habitat selection within urban areas, we selected urban areas that had at least 10
273 observations of a given species. For this analysis, we excluded observations with spatial uncertainty
274 of >500 m, because this analysis was conducted at a finer spatial scale. To get a measure of
275 resource availability, we created 5× the number of random positions than we had obtained from
276 citizen observations within each urban area. We then assigned each random and used (observed)
277 position to the land cover type (as defined above) and the soil sand content (for rabbits only). To
278 analyze habitat selection (observed location = 1 versus random location = 0, dependent variable),
279 we used generalized linear mixed models with a binomial distribution and a logit link, using the R
280 package ‘lme4’ (Bates *et al.* 2015). We included the land cover type (excluding ‘other’ land cover),
281 soil sand content (for rabbits only), the presence of other lagomorph species, and the interaction of
282 land cover type with lagomorph presence (to investigate if habitat selection differs in the presence
283 of other lagomorphs) as fixed effects, and urban ID as random intercept to control for non-
284 independence of the data. We again performed a stepwise backward selection, starting from the full
285 model including all variables, selecting the model with the lowest AIC. Parameters that included
286 zero within their 95% confidence interval were considered uninformative (Arnold 2010). All
287 analyses were carried out in R4.0.3.

288

289 **3. Results**

290 *Patterns of urban occurrence*

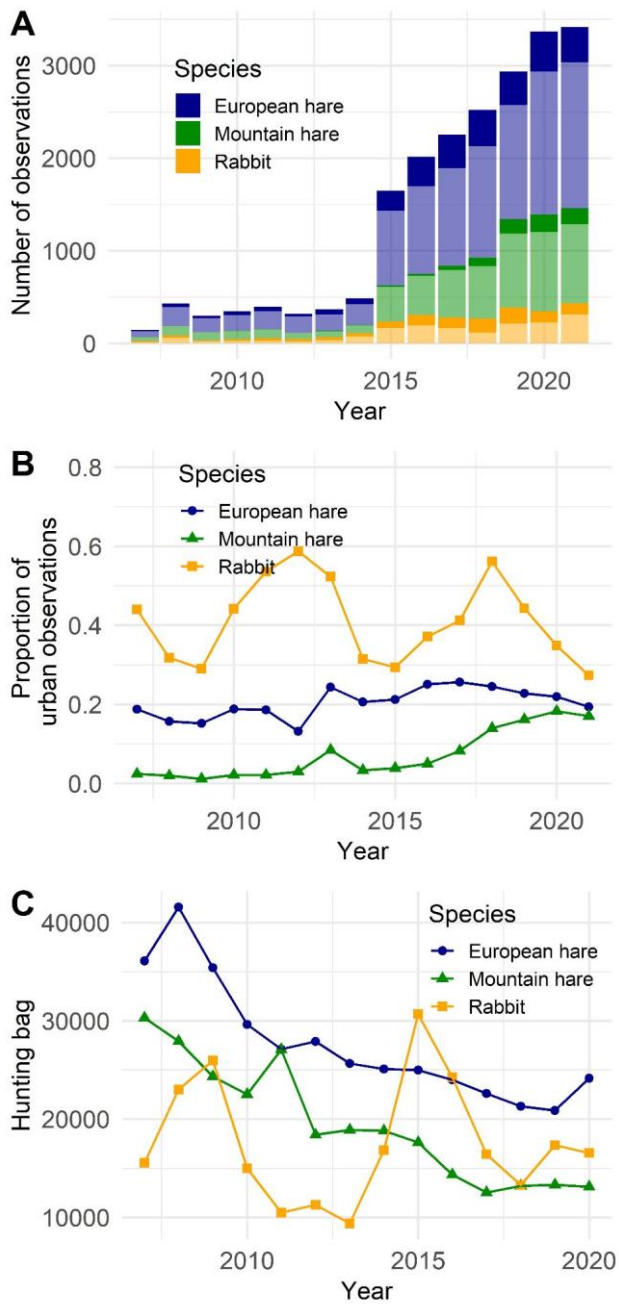
291 Out of a total of 20,931 observations (both within and outside urban areas), European hares
292 constituted 12,492 observations (60%), mountain hares 5,727 observations (27%), and rabbits 2,712

293 observations (13%). The number of observations increased over time, with few observations before
294 2015, when Artportalen was initiated (Fig. 2A). Of the three species, rabbits had the highest
295 proportion of urban observations, accounting for 39% (1,049 observations) of all rabbit
296 observations. The proportion of urban rabbit observations fluctuated between years, with noticeable
297 decreases in 2008-2009, 2014-2015 and 2020 (Fig. 2B). For European hares, 22% (2,769) were
298 urban observations, with the proportion of urban observations being relatively stable over time (Fig.
299 2B). For mountain hares, urban observations accounted for 12% (714 observations), and the
300 proportion of urban observations increased over the years, being 2.4% in 2007 and 21% in 2021
301 (Fig. 2B). Hunting bag numbers decreased for European hares and mountain hares, and fluctuated
302 for rabbits, with pronounced increases in 2009 and 2015 (Fig. 2C). The percentage of people living
303 in urban areas increased from 85% in 2007 to 88% in 2020.

304

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306



307

308 **Fig. 2:** (A) The number of all reported observations for each year (2007-2021) and species, and
309 shown for urban observations (dark colors) and observations outside urban areas (bright colors). (B)
310 The proportion of urban observations out of total observations for the three species, and (C) hunting
311 bag numbers from 2007 to 2020 (numbers from 2021 were not available yet).

312

313

314 *Environmental and residual correlations*

315 European hares and rabbits shared environmental responses (i.e. concerning mean temperature of
 316 the coldest quarter, annual precipitation, soil sand content, elevation, and land cover proportions),
 317 while mountain hares had distinct environmental responses from the other two species (Table 1,
 318 Fig. 3). These responses were more pronounced on a grid cell level. All three species pairs had
 319 positive residual correlations (especially European and mountain hares, and rabbits and mountain
 320 hares), suggesting that all species pairs co-occurred more than expected, due to unmodelled factors
 321 (Table 1, Fig. 3). For European and mountain hares, and rabbits and mountain hares, this pattern
 322 was more pronounced on urban level compared to grid cell level, but for European hares and rabbits
 323 residual correlation was stronger on grid cell level (Table 1).

324

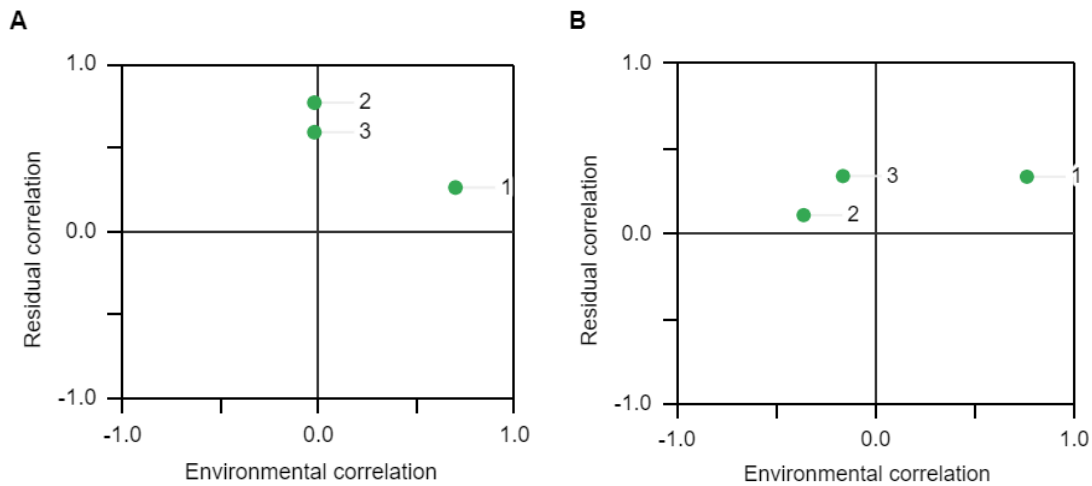
325

326 **Table 1:** Mean (\pm SD) environmental and residual correlations between the three species pairs
 327 separately for urban and grid cell level.

Species 1	Species 2	Environmental correlation		Residual correlation	
		Urban area level	Grid cell level	Urban area level	Grid cell level
European hare	European rabbit	0.7 ± 0.13	0.76 ± 0.04	0.26 ± 0.22	0.33 ± 0.04
European rabbit	Mountain hare	-0.02 ± 0.21	-0.36 ± 0.08	0.77 ± 0.26	0.11 ± 0.09
Mountain hare	European hare	-0.02 ± 0.18	-0.16 ± 0.08	0.59 ± 0.34	0.34 ± 0.07

328

329



330

331 **Fig. 3:** Environmental and residual correlations between European hare and European rabbit (1),
332 European rabbit and mountain hare (2), and mountain hare and European hare (3), on urban area
333 level (A), and grid cell level (B).

334

335

336 *Species occurrence and observations per urban area*

337 Within their respective ranges (Fig. 1), 63 of 77 urban areas (82%) contained European hare
338 observations, 38 of 97 urban areas (39%) contained mountain hare observations, and 40 of 69 urban
339 areas (58%) contained rabbit observations. When defining species presence as at least 7
340 observations within an urban area, European hares occurred in 45% of urban areas within their
341 distribution, mountain hares in 10%, and rabbits in 26% of urban areas.

342

343 For all three species, the probability of occurrence within an urban area was best explained by the
344 model including climate variables, elevation, and the size of the urban area, followed by the model
345 including the surrounding land cover (European and mountain hare analysis) or other species (rabbit
346 analysis), and finally the model including land cover within urban areas (Table 2). After model

347 selection, the best model explaining the probability of urban European hare occurrence included
 348 urban area size (positive correlation), elevation (positive correlation; Fig. 4A), mean annual
 349 precipitation (negative correlation; Fig. 4B), and temperature of the coldest quarter (uninformative
 350 positive correlation; Table 3). The probability of urban mountain hare occurrence also increased
 351 with urban area size, and declined with increased temperature of the coldest quarter (Fig. 4C, Table
 352 3). Elevation was included in the best model, but was uninformative (positive correlation). The
 353 probability of urban rabbit occurrence also increased with urban area size, and with the proportion
 354 of green urban areas (Fig. 4D), though this effect was uninformative (Table 3).

355

356

357 **Table 2:** Overview of the candidate models based on biological hypothesis for the analysis of urban
 358 occurrence by European hares, mountain hares, and European rabbits. Models were ranked based on
 359 AIC.

Model	Parameters	Model rank (delta AIC)		
		European hare	Mountain hare	Rabbit
Climate and size of urban area	Temperature + Precipitation + Size of urban area + Sand content	1 (0)	1 (0)	1 (0)
Surrounding land cover	Proportion agriculture/forest + Proportion urban	2 (15.1)	2 (36.9)	3 (1.8)
Co-occurrence of other leporids	European hare presence/Mountain hare presence/Rabbit presence	3 (16.3)	3 (38.4)	2 (0.9)
Urban land cover	Proportion agriculture + Proportion forest + Proportion continuous urban + Proportion discontinuous urban + Proportion green urban + Proportion industry	4 (18.9)	4 (40.3)	4 (2.5)

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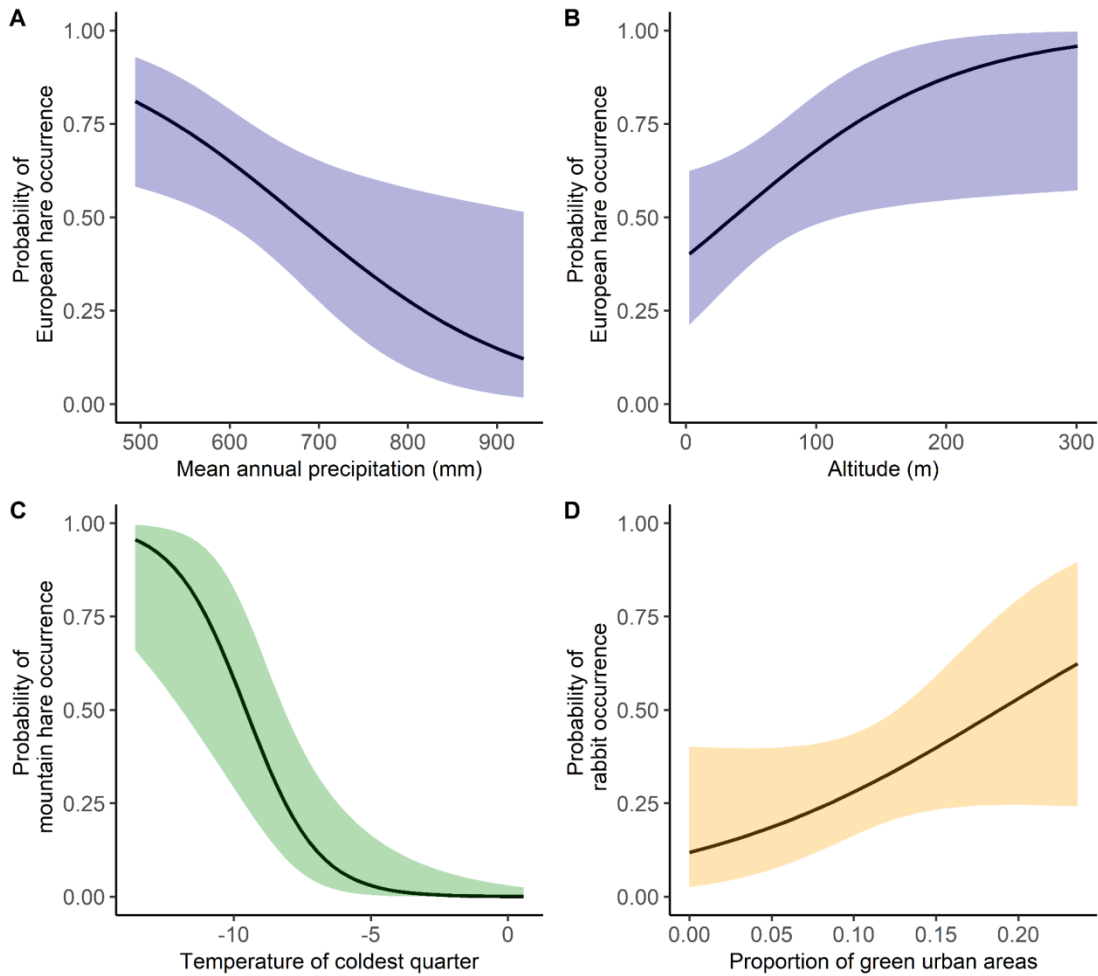
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363 **Table 3:** Estimate, standard error (SE), lower 95% confidence interval (LCI) and upper 95%
 364 confidence interval (UCI) of explanatory variables for the analyses of urban occurrence separately
 365 for European hares, mountain hares, and European rabbits. Informative parameters are in bold.

Parameter	Estimate	SE	LCI	UCI
<i>European hare occurrence</i>				
Intercept	0.31	0.34	-0.34	1.03
Mean annual precipitation	-0.75	0.32	-1.42	-0.17
Size of the urban area	4.06	1.33	1.68	6.94
Altitude	0.74	0.36	0.07	1.51
Temperature of the coldest quarter	0.58	0.35	-0.08	1.30
<i>Mountain hare occurrence</i>				
Intercept	-4.97	1.45	-9.05	-2.90
Temperature of the coldest quarter	-2.78	0.92	-5.21	-1.37
Size of the urban area	4.19	2.86	1.44	11.24
Altitude	0.95	0.61	-0.04	2.65
<i>Rabbit occurrence</i>				
Intercept	-0.93	0.35	-1.65	-0.26
Proportion of green urban areas	0.57	0.35	-0.08	1.30
Size of the urban area	2.71	1.19	0.68	5.23

366

367



368

369 **Fig. 4:** The predicted probability of urban occurrence by (A) European hares in relation to mean
370 annual precipitation and (B) elevation, and (C) by mountain hares in relation to the temperature of
371 the coldest quarter, and (D) by rabbits in relation to green urban areas. 95% confidence intervals are
372 shown as shading.

373

374

375 The number of observations per urban area ranged from 0 to 846 (mean \pm SD = 36 ± 116 , median =
376 5) for European hares, from 0 to 461 (mean \pm SD; 8 ± 48 , median = 0) for mountain hares, and from
377 0 to 226 (mean \pm SD; 15 ± 40 , median = 1) for rabbits. The number of European hare observations
378 per urban area was positively correlated with the size of the urban area, the proportion of forest,

379 continuous urban fabric, surrounding agriculture, and rabbit presence, and negatively correlated
380 with increasing precipitation and temperature of the coldest quarter (Table S2, Table S3, Fig. S1).
381 Urban mountain hare observations were positively correlated with urban area size, the proportion of
382 surrounding urban areas, and European hare presence, and negatively with the proportion of
383 discontinuous urban fabric and temperature of the coldest quarter (Table S2, Table S3, Fig. S2).
384 Proportion of agriculture was included in the best model (positive correlation), but was
385 uninformative. Urban rabbit observations were positively correlated with increasing urban area size,
386 soil sand content, proportion of discontinuous urban fabric, green urban areas, industry, and the
387 proportion of surrounding urban areas, and negatively with increasing elevation and proportion of
388 urban forest (Table S2, Table S3, Fig. S3).

389

390 *Habitat use and selection within urban areas*

391 Based on random positions (located within urban areas where lagomorphs were present), urban
392 areas were dominated by discontinuous urban fabric (61%), followed by industrial areas (20%),
393 green urban areas (13%), forest (3%), continuous urban fabric (<2%), and agriculture (<2%). All
394 three species were mostly observed in discontinuous urban fabric (especially mountain hares),
395 followed by green urban and industrial areas (Fig. 5A). For any species, <5% of observations came
396 from continuous urban fabric, forest, and agriculture combined. Further, there were more European
397 hare and rabbit observations in discontinuous urban fabric when they occurred in absence of the
398 other lagomorph species (Fig. 5A). The opposite was the case in green urban and industrial areas,
399 i.e. more European hares were observed in green urban areas when rabbits were present, and more
400 rabbits were observed in industrial areas when European hares were present (Fig. 5A).

401

402 Habitat selection by European hares differed between urban areas where rabbits were absent versus
403 present (Table 4). European hares selected for green urban areas and avoided discontinuous urban
404 fabric when rabbits were present, but avoided green areas and selected for discontinuous urban
405 fabric when rabbits were absent (Fig. 5B). Moreover, they showed no clear selection or avoidance
406 of continuous urban fabric and agriculture when rabbits were present, but avoided these land covers
407 when rabbits were absent (Table 4). They consistently avoided industrial areas and forests
408 independent of rabbit presence (Fig. 5B). Only 6 urban areas had at least 10 mountain hare
409 observations, all located outside the distribution of European hares and rabbits. Mountain hares
410 selected for discontinuous urban fabric, and avoided green urban and industrial areas, and forests
411 (Fig. 5C, Table 4). We removed the continuous urban fabric and agriculture from this analysis,
412 because there were no mountain hare observations in these areas and they constituted a negligible
413 portion of the area (<1%). Habitat selection by rabbits was not affected by European hare presence.
414 Rabbits selected for green urban areas, showed no clear selection or avoidance of continuous urban
415 fabric, and avoided discontinuous urban fabric, industrial areas, forests and agriculture within urban
416 areas (Fig. 5D, Table 4).

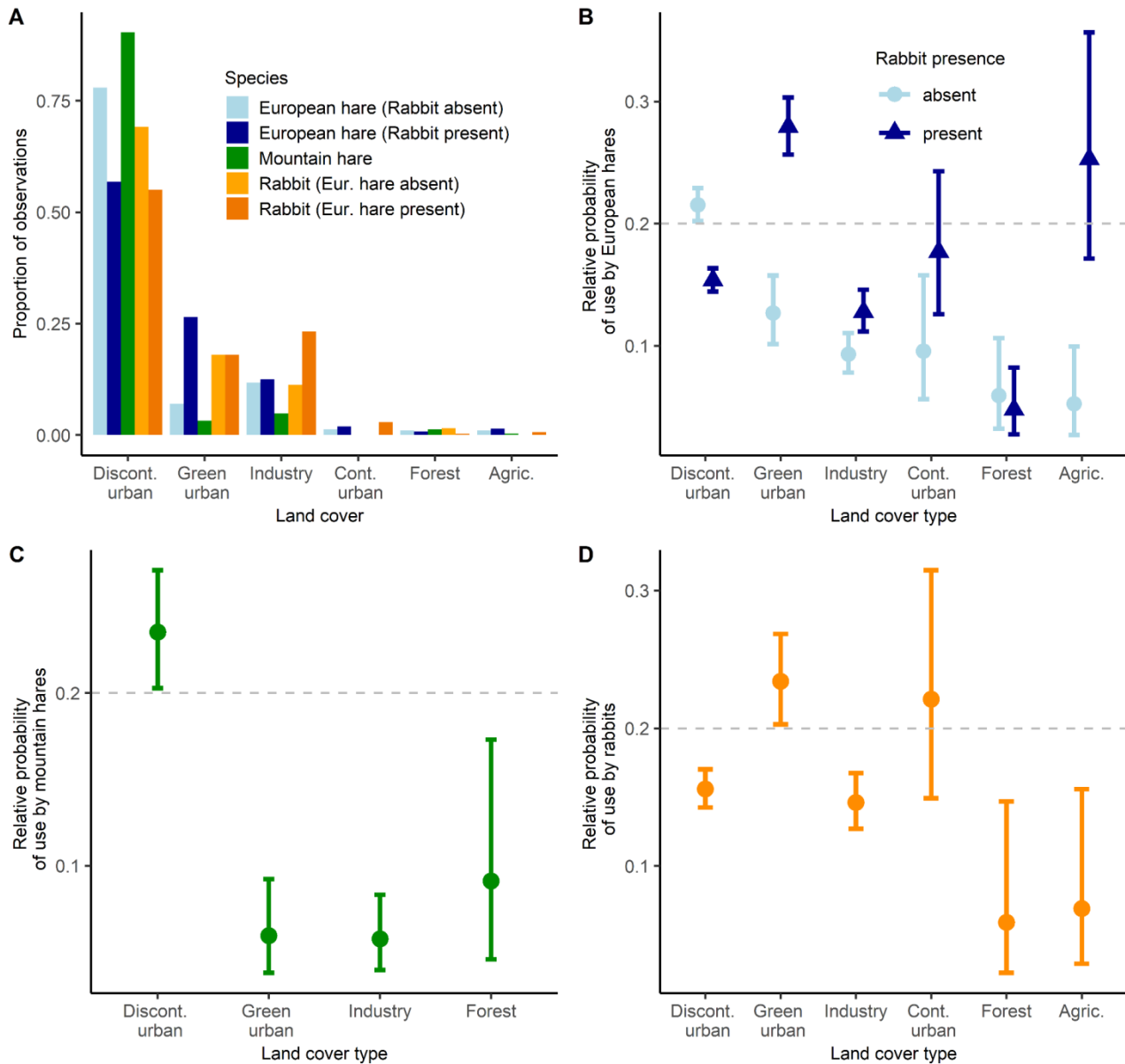
417

418

419 **Table 4:** Estimate, standard error (SE), lower 95% confidence interval (LCI) and upper 95%
420 confidence interval (UCI) of explanatory variables for the analyses of urban habitat selection
421 separately for European hares, mountain hares and rabbits. Informative parameters are in bold. The
422 land cover ‘discontinuous urban fabric’ was used as reference category, with positive estimates
423 indicating a higher relative probability of use (selection) and negative values indicating a lower
424 relative probability of use (avoidance) in comparison to this land cover.

Parameter	Estimate	SE	LCI	UCI
<i>European hare</i>				

Intercept	-1.29	0.04	-1.37	-1.21
Green urban areas	-0.64	0.14	-0.90	-0.37
Industry	-0.98	0.11	-1.19	-0.78
Continuous urban	-0.95	0.29	-1.53	-0.38
Forest	-1.47	0.33	-2.12	-0.83
Agriculture	-1.60	0.33	-2.24	-0.96
Rabbit presence present	-0.41	0.06	-0.52	-0.30
Green urban areas × Rabbit presence present	1.39	0.15	1.10	1.69
Industry × Rabbit presence present	0.77	0.14	0.50	1.04
Continuous urban × Rabbit presence present	1.12	0.36	0.42	1.83
Forest × Rabbit presence present	0.19	0.44	-0.68	1.06
Agriculture × Rabbit presence present	2.23	0.41	1.42	3.03
<i>Mountain hare</i>				
Intercept	-1.18	0.10	-1.37	-0.99
Green urban areas	-1.58	0.24	-2.04	-1.12
Industry	-1.62	0.19	-2.00	-1.24
Forest	-1.12	0.38	-1.86	-0.38
<i>European rabbit</i>				
Intercept	-1.43	0.06	-1.54	-1.32
Soil sand content	-0.39	0.05	-0.48	-0.30
Green urban areas	0.50	0.10	0.30	0.71
Industry	-0.08	0.09	-0.26	0.10
Continuous urban	0.43	0.25	-0.06	0.92
Forest	-1.08	0.52	-2.09	-0.07
Agriculture	-0.91	0.47	-1.82	0.00



426

427 **Fig. 5:** (A) The proportion of urban observations in the different land cover categories separately
 428 for the three species. For European hares and rabbits, observations are further separated by the
 429 presence or absence of rabbits/European hares (mountain hares were only observed in urban areas
 430 without the other two species). Moreover, the relative probability of use by European hares (B),
 431 mountain hares (C), and rabbits (D). For European hares, rabbit presence affected habitat selection,
 432 but not for mountain hares and rabbits. Values >0.2 indicate selection, whereas values <0.2 indicate
 433 avoidance. The 95% confidence intervals are given as bars.

434

435

436 **4. Discussion**

437 Citizen observations were useful in describing urban occurrence and habitat selection of the three
438 lagomorphs in Sweden. The data suggests that European hares and rabbits are successful urban
439 colonizers, and mountain hares also begin to establish populations in some urban areas in the
440 northern part of Sweden. Urban occurrence by all species was generally better explained by climatic
441 conditions, elevation, and urban area size, rather than by the proportion of land cover types within
442 urban areas or the presence of other lagomorph species. Thus, urban colonization was likely driven
443 by suitable conditions within the distribution of each species. In contrast to our prediction, the
444 JSDM and habitat selection analyses indicated no direct competition among the three species, but
445 actually indicated a facilitative relationship between European hares and rabbits.

446

447 *Trends in urban observations*

448 Both citizen observations and hunting bag data suggest that European hares were the most abundant
449 of the three lagomorphs in Sweden. However, hunting bag reports indicated that European hare
450 populations are declining, a trend seen throughout Europe (Smith, Jennings & Harris 2005). The
451 relatively stable proportion of urban European hare observations over time suggests that European
452 hare populations have established in urban areas of Sweden, similar to urban areas in Denmark
453 (Mayer & Sunde 2020). Like European hares, rabbits appeared to be strong urban colonizers, with
454 nearly 40% of all observations coming from urban areas, consistent with previous findings showing
455 that rabbits are successful urban colonizers (Ziege *et al.* 2015; Ziege *et al.* 2016; Ziege *et al.* 2020).
456 Assuming hunting bag data to be a measure of population trends, rabbit populations fluctuated over
457 the years. Hunting bag reports and the proportion of urban observations mirrored each other well,

458 i.e. increases in hunting bag were accompanied by decreases in the proportion of urban
459 observations. A potential explanation might be that rabbits were culled in urban areas to prevent
460 damage to city parks. For example, in Stockholm 6,000 rabbits were culled in 2008 and 3,000 in
461 2009 (<https://abcnews.go.com/International/rabbits-burned-fuel-sweden/story?id=8824540>), which
462 coincided with the decrease in proportion of urban rabbit observations. Additionally, fluctuations in
463 rabbit numbers could be related to fluctuations in climate conditions and/or disease outbreaks
464 (Calvete *et al.* 2002; Rödel & Dekker 2012). Based on hunting bag data, mountain hare numbers
465 were intermediate compared to European hares and rabbits, and were declining, consistent with the
466 species' red list status in Sweden (Artdatabanken 2020). This decline has been attributed to climate
467 warming and competitive exclusion by and hybridization with the European hare (Thulin 2003).
468 The proportion of urban mountain hare observations increased in recent years, indicating that urban
469 areas are increasingly colonized by mountain hares. However, this increase might also be partly
470 related to an increased proportion of humans living in urban areas. Overall, urban mountain hare
471 observations were less common compared to the other two species, consistent with findings
472 showing that mountain hares select for areas of low human influence (Leach, Montgomery & Reid
473 2016). Conversely, the proportion of urban observations for both European hares and rabbits might
474 be biased in relation to mountain hare observations, because their range covered the more densely
475 populated south of the country, potentially leading to a comparatively greater sampling effort inside
476 urban areas (Geldmann *et al.* 2016).

477

478 *Biotic interactions and environmental filtering*

479 European hares and rabbits shared environmental responses, while mountain hares had distinct
480 environmental responses, consistent with previous findings (Leach, Montgomery & Reid 2017).

481 This was likely related to the distribution of the three species, with the European hares and rabbits'

482 southern distribution characterized by higher temperatures and lower elevations compared to
483 northern Sweden, where only mountain hares occurred. Both European hares and rabbits are
484 generally associated with comparatively warm and dry climate, and lowland areas (Calvete *et al.*
485 2004; Smith, Jennings & Harris 2005; Tapia *et al.* 2014; Leach, Montgomery & Reid 2016),
486 whereas mountain hares typically occupy colder areas at higher elevations (Thulin 2003; Jansson &
487 Pehrson 2007). For all species pairs, environmental correlations were stronger on a grid cell level,
488 probably because this finer spatial scale captured more detailed environmental differences.

489

490 The positive residual correlations (both on urban area and grid cell level) between European hares
491 and rabbits suggest that the two species co-occurred more than expected from their shared
492 environmental responses, indicating a facilitative interaction consistent with previous studies
493 (Leach, Montgomery & Reid 2017). Although there is evidence that European hares and rabbits are
494 not in competition (Stott 2003; Katona *et al.* 2004), the study by Leach, Montgomery and Reid
495 (2017) and this study, to our knowledge, are the only implying a facilitative interaction between
496 European hares and rabbits. Co-existence between the two species have been proposed to be
497 mediated by the larger home range of the European hare, which enables local scale avoidance, and
498 diet partitioning with regards to grass species (Stott 2003; Lush, Ward & Wheeler 2017).

499 Alternatively, positive residual correlations, representing unmodelled correlations, could also
500 represent shared environmental preferences from environmental variables not included in the
501 models or biases in citizen observations (also see discussion of habitat selection below).

502 Observation biases were likely, considering the high residual correlation between mountain hares
503 and the other two species, despite the fact that the 6 urban areas with >10 mountain hare
504 observations were all located in areas outside the other species distribution.

505

506 *Species occurrence, relative abundance and habitat selection*

507 Urban area size was the most important factor explaining the occurrence of all three lagomorphs.
508 This might indicate that urban areas have to be large enough to allow a sufficient number of
509 individuals to adjust (either via selection of bold individuals or behavioral adaptations) to the novel
510 conditions (e.g. high level of human disturbance), and consequently establish a population.
511 Alternatively, there might not be sufficient observers in smaller urban areas to reliably detect the
512 presence of a species, cautioning against interpreting this finding too much in the absence of a true
513 measure of observation effort (Kelling *et al.* 2015). Apart from urban area size, the probability of
514 urban European hare occurrence decreased with higher precipitation and tended to increase with
515 higher temperatures, suggesting that warmer and drier areas generally favor European hare
516 occurrence (Smith, Jennings & Harris 2005; Leach, Montgomery & Reid 2016). Moreover, the
517 probability of European hare occurrence increased with elevation; a counterintuitive finding, as this
518 species is typically associated with lowland. However, the average elevation of urban areas within
519 the European hares' distribution was 62 m, and only a single urban area was located >210 m asl (at
520 300 m), i.e. all urban areas were located at comparatively low elevations. The probability of
521 mountain hare occurrence markedly decreased when temperatures were higher, in line with this
522 species' preference for colder climates (Jansson & Pehrson 2007). Rabbit occurrence, apart from
523 urban area size, tended to increase when more green urban areas were present, suggesting that parks
524 and other green areas constitute important habitat for this species. The general lack of urban land
525 cover in the best models explaining the probability of urban occurrence suggests that factors
526 explaining the general distribution of the species (climate and elevation) are better at predicting
527 urban occurrence, especially for European and mountain hares. We have no evidence that species
528 competition affected urban occurrence by any of the three species.

529

530 The analyses of the number of citizen observations per urban area yielded different results
531 compared to the urban occurrence and habitat selection analyses. For example, the number of
532 mountain hare observations decreased with the proportion of discontinuous urban fabric, whereas
533 the habitat selection analysis indicated that mountain hares selected for this land cover type. Similar
534 contrasting results were found for European hares in relation to forest and for rabbits concerning
535 discontinuous urban fabric. We deem the analyses of relative abundance less reliable, because the
536 number of observations was likely more biased (based on observer distribution) compared to a
537 presence/absence measure and compared to accounting for availability in the habitat selection
538 analysis, though the latter might have also resulted in biases due to creating random positions in
539 areas where no observers went. This highlights that using different analytical approaches can be
540 useful to test the generality of findings, especially when using heterogeneous citizen science data.
541
542 Inside urban areas, European hares selected for green areas (parks, sport facilities, cemeteries, etc.)
543 in the presence of rabbits, but avoided them when rabbits were absent. General selection of green
544 urban areas is consistent with previous findings of urban habitat selection by European hares in
545 Denmark (Mayer and Sunde 2020), likely because these areas resemble the hares' preferred habitat,
546 characterized by low vegetation height, providing high-quality forage (Lush, Ward & Wheeler
547 2017; Mayer *et al.* 2018). Similarly, hares selected for discontinuous urban fabric (often consisting
548 of residential areas) in the absence of rabbits, but avoided them when rabbits co-occurred.
549 Residential gardens, which have been found to constitute important habitats for other urban wildlife
550 (Van Helden *et al.* 2020), might also constitute foraging sites for European hares. It is harder to
551 explain the difference in habitat selection depending on the presence of rabbits that seemingly
552 facilitated the use of green urban areas by European hares (also selected for by rabbits) at the
553 expense of discontinuous urban fabric. One explanation could be that the presence of rabbits

554 increased overall grazing intensity and fertilization via defecation on lawns, leading to increased
555 grass growth, benefitting European hares. This facilitation of European hares by rabbits might be
556 mitigated by dietary differences between the two species (Lush, Ward & Wheeler 2017), allowing
557 their interaction to be rather facilitative than competitive. Similarly, it has been shown that
558 megaherbivore trampling and feeding stimulates high-quality grass regrowth, making it more
559 accessible for smaller ungulates (Wegge, Shrestha & Moe 2006).

560

561 We found no evidence that the presence of European hares affected habitat selection by rabbits,
562 indicating that rabbit space use and occurrence was unaffected by hares, as suggested in previous
563 studies (Stott 2003; Katona *et al.* 2004; Flux 2008; Leach, Montgomery & Reid 2017). Rabbits
564 generally selected for green urban areas that likely provided good forage opportunities (Bakker *et*
565 *al.* 2005). They showed no selection or avoidance for continuous urban fabric, and avoided the
566 other land cover types, including forest. An avoidance of areas that likely provided cover (such as
567 forest and discontinuous urban fabric via hedgerows) might indicate that urban rabbits experienced
568 relaxed predation pressure, as previously proposed, reducing the need for cover (Ziege *et al.* 2016),
569 in combination with these areas probably providing less forage (Lombardi *et al.* 2003). However, as
570 most observations likely came from active rabbits, our results might not apply to inactive rabbits
571 that might select for areas with more cover, leading to a reduced detection probability (Geldmann *et*
572 *al.* 2016; also see discussion below).

573

574 As all 6 urban areas where >10 mountain hare observations were made were located outside the
575 current distribution of the other two lagomorphs, we could not investigate habitat selection
576 depending on species co-occurrence. Mountain hares selected for discontinuous urban fabric,
577 potentially providing both forage and cover, and avoided green urban areas, industry and forest. The

578 apparent avoidance of forest might be related to observer biases (see below). The avoidance of
579 green areas might be related to the absence of cover, as mountain hares are typically associated with
580 habitats providing cover, typically forest (Flux & Angermann 1990; Thulin 2003).

581

582 *Study limitations, future considerations, and conclusions*

583 Citizen science data is susceptible to spatial biases with regards to infrastructure and human
584 population density (Geldmann *et al.* 2016). Consequently, citizen observations might have
585 measured human-lagomorph encounters rather than actual habitat preferences, e.g. shown for canids
586 (Mueller, Drake & Allen 2019). Urban areas, while generally having high levels of infrastructure
587 and human population densities, yielding a high sampling effort overall, might still be prone to
588 varying sampling efforts due to being highly heterogeneous (Dickinson, Zuckerberg & Bonter
589 2010; Crall *et al.* 2011). For example, it is plausible that citizens rather recorded animal
590 observations in their own gardens and in parks compared to city centers and industrial areas.
591 Moreover, detectability also differs between land cover types, accessibility, and depending on
592 animal activity (Mair & Ruete 2016; Pereira-Ribeiro *et al.* 2019). As most observations likely came
593 from active lagomorphs, our results probably represent occurrence and habitat selection of active
594 individuals and from areas that were easily accessible to observers. However, habitat selection by
595 active and inactive lagomorphs differs (Neumann *et al.* 2012; Mayer *et al.* 2018), implying that we
596 might have underestimated the importance of certain land cover types that are predominantly used
597 by resting individuals (e.g. forest patches). Avoiding such biases in citizen observations will be
598 hard. One potential solution would be to select larger spatial scales, as scaling up generally
599 decreases spatial bias and reduces pseudo-absences (Rondinini *et al.* 2006), and to define species
600 occurrence rather than relative abundance. Finally, species might have been misclassified in some
601 cases, resulting in false-positives (Dickinson, Zuckerberg & Bonter 2010). For example, pet rabbits

602 might have been mistaken for wild rabbits, and hybrids of European hares and mountain hares
603 might have been mistaken for either of these two. GPS tagging individuals would enable us to
604 obtain more detailed information on habitat selection and movements by lagomorphs in urban areas,
605 shedding more light on their adaptations to this novel environment. To quantify urban population
606 densities, transect counts could be used (Mayer & Sunde 2020), potentially conducted by citizen
607 scientists if incentivized correctly, like for example the Great Backyard Bird Count
608 (<https://www.birdcount.org/>).

609
610 Our study contributes to the understanding of species co-occurrence patterns and habitat preferences
611 within urban areas, while highlighting the benefits and challenges of citizen science data. We
612 generally found little evidence for competition between the three lagomorphs, though we cannot
613 exclude that urban mountain hare occurrence is inhibited interspecific competition. Future studies
614 should also investigate how the presence of predators, in this case predominantly red foxes (*Vulpes*
615 *vulpes*), affects the occurrence and habitat selection of lagomorphs within urban areas. Moreover, it
616 would be of interest to shed more light on the drivers of urban colonization by wildlife, to be able to
617 predict urban species occurrence. Insights into species habitat associations within urban areas and
618 depending on co-occurrence with other species can help in targeting urban management plans,
619 which will be useful to identify suitable habitats for desired species and efficient management of
620 pest species (Gaertner *et al.* 2017; Apfelbeck *et al.* 2020).

621

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625

626 **Conflict of interest statement**

627 The authors state no conflict of interest.

628

629 **References**

- 630 Apfelbeck, B., Snep, R.P., Hauck, T.E., Ferguson, J., Holy, M., Jakoby, C., MacIvor, J.S., Schär, L., Taylor, M. &
631 Weisser, W.W. (2020) Designing wildlife-inclusive cities that support human-animal co-existence.
632 *Landscape and urban planning*,**200**, 103817.
- 633 Arnold, T.W. (2010) Uninformative parameters and model selection using Akaike's Information Criterion.
634 *The Journal of Wildlife Management*,**74**, 1175-1178.
- 635 Artdatabanken, S. (2020) Rödlistade arter i Sverige 2020. *SLU, Uppsala*.
- 636 Bakker, E., Reiffers, R., Olff, H. & Gleichman, J. (2005) Experimental manipulation of predation risk and food
637 quality: effect on grazing behaviour in a central-place foraging herbivore. *Oecologia*,**146**, 157-167.
- 638 Bar-Massada, A. (2015) Complex relationships between species niches and environmental heterogeneity
639 affect species co-occurrence patterns in modelled and real communities. *Proceedings of the Royal
640 Society B: Biological Sciences*,**282**, 20150927.
- 641 Barton, K. (2020) Package 'MuMIn'.
- 642 Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Eigen, C. & Rcpp, L.
643 (2015) Package 'lme4'.
- 644 Bozek, C.K., Prange, S. & Gehrt, S.D. (2007) The influence of anthropogenic resources on multi-scale habitat
645 selection by raccoons. *Urban Ecosystems*,**10**, 413-425.
- 646 Brown, L. (2001) Building an Economy for the Earth. *Earth Policy Institute*.
- 647 Calvete, C., Estrada, R., Angulo, E. & Cabezas-Ruiz, S. (2004) Habitat factors related to wild rabbit
648 conservation in an agricultural landscape. *Landscape ecology*,**19**, 531-542.
- 649 Calvete, C., Estrada, R., Villafuerte, R., Osácar, J. & Lucientes, J. (2002) Epidemiology of viral haemorrhagic
650 disease and myxomatosis in a free-living population of wild rabbits. *Veterinary Record*,**150**, 776-
651 782.
- 652 Carrete, M., Lambertucci, S.A., Speziale, K., Ceballos, O., Travaini, A., Delibes, M., Hiraldo, F. & Donázar, J.A.
653 (2010) Winners and losers in human-made habitats: interspecific competition outcomes in two
654 Neotropical vultures. *Animal Conservation*,**13**, 390-398.
- 655 Chambers, L.K. & Dickman, C.R. (2002) Habitat selection of the long-nosed bandicoot, *Perameles nasuta*
656 (Mammalia, Peramelidae), in a patchy urban environment. *Austral Ecology*,**27**, 334-342.
- 657 Contesse, P., Hegglin, D., Gloor, S., Bontadina, F. & Deplazes, P. (2004) The diet of urban foxes (*Vulpes
658 vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. *Mammalian
659 Biology-Zeitschrift für Säugetierkunde*,**69**, 81-95.
- 660 Crall, A.W., Newman, G.J., Stohlgren, T.J., Holfelder, K.A., Graham, J. & Waller, D.M. (2011) Assessing citizen
661 science data quality: an invasive species case study. *Conservation Letters*,**4**, 433-442.
- 662 Dickinson, J.L., Zuckerberg, B. & Bonter, D.N. (2010) Citizen science as an ecological research tool:
663 challenges and benefits. *Annual Review of Ecology, Evolution, and Systematics*,**41**, 149-172.
- 664 Duduś, L., Zalewski, A., Koziół, O., Jakubiec, Z. & Król, N. (2014) Habitat selection by two predators in an
665 urban area: The stone marten and red fox in Wrocław (SW Poland). *Mammalian Biology*,**79**, 71-76.
- 666 Estevo, C.A., Nagy-Reis, M.B. & Nichols, J.D. (2017) When habitat matters: Habitat preferences can
667 modulate co-occurrence patterns of similar sympatric species. *PLoS One*,**12**, e0179489.
- 668 Flux, J.E. (1993) Relative effect of cats, myxomatosis, traditional control, or competitors in removing rabbits
669 from islands. *New Zealand Journal of Zoology*,**20**, 13-18.

- 670 Flux, J.E. (2008) A review of competition between rabbits (*Oryctolagus cuniculus*) and hares (*Lepus*
671 *europaeus*). *Lagomorph biology*, 241-249.
- 672 Flux, J.E. & Angermann, R. (1990) The hares and jackrabbits. *Rabbits, hares and pikas. Status survey and*
673 *conservation action plan*, **4**, 61-94.
- 674 Gaertner, M., Wilson, J.R., Cadotte, M.W., MacIvor, J.S., Zenni, R.D. & Richardson, D.M. (2017) Non-native
675 species in urban environments: patterns, processes, impacts and challenges. pp. 3461-
676 3469. Springer.
- 677 Geldmann, J., Heilmann-Clausen, J., Holm, T.E., Levinsky, I., Markussen, B., Olsen, K., Rahbek, C. & Tøttrup,
678 A.P. (2016) What determines spatial bias in citizen science? Exploring four recording schemes with
679 different proficiency requirements. *Diversity and Distributions*, **22**, 1139-1149.
- 680 Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X. & Briggs, J.M. (2008) Global change
681 and the ecology of cities. *Science*, **319**, 756-760.
- 682 Grueber, C., Nakagawa, S., Laws, R. & Jamieson, I. (2011) Multimodel inference in ecology and evolution:
683 challenges and solutions. *Journal of evolutionary biology*, **24**, 699-711.
- 684 Haigh, A. & Lawton, C. (2007) Wild mammals of an Irish urban forest. *The Irish Naturalists' Journal*, 395-403.
- 685 Hijmans, R.J., van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J.A., Lamigueiro, O.P., Bevan,
686 A., Racine, E.B. & Shortridge, A. (2015) Package 'raster'. *R package*.
- 687 Jansson, G. & Pehrson, Å. (2007) The recent expansion of the brown hare (*Lepus europaeus*) in Sweden
688 with possible implications to the mountain hare (*L. timidus*). *European Journal of Wildlife*
689 *Research*, **53**, 125-130.
- 690 Katona, K., Bíró, Z., Hahn, I., Kertész, M. & Altbacker, V. (2004) Competition between European hare and
691 European rabbit in a lowland area, Hungary: a long-term ecological study in the period of rabbit
692 extinction. *FOLIA ZOOLOGICA-PRAHA*, **53**, 255-268.
- 693 Kelling, S., Fink, D., La Sorte, F.A., Johnston, A., Bruns, N.E. & Hochachka, W.M. (2015) Taking a 'Big
694 Data' approach to data quality in a citizen science project. *Ambio*, **44**, 601-611.
- 695 Kohli, B.A., Terry, R.C. & Rowe, R.J. (2018) A trait-based framework for discerning drivers of species
696 co-occurrence across heterogeneous landscapes. *Ecography*, **41**, 1921-1933.
- 697 Leach, K., Montgomery, W.I. & Reid, N. (2015) Biogeography, macroecology and species' traits mediate
698 competitive interactions in the order Lagomorpha. *Mammal Review*, **45**, 88-102.
- 699 Leach, K., Montgomery, W.I. & Reid, N. (2016) Modelling the influence of biotic factors on species
700 distribution patterns. *Ecological modelling*, **337**, 96-106.
- 701 Leach, K., Montgomery, W.I. & Reid, N. (2017) Characterizing biotic interactions within the Order
702 Lagomorpha using Joint Species Distribution Models at 3 different spatial scales. *Journal of*
703 *Mammalogy*, **98**, 1434-1442.
- 704 Lees, A.C. & Bell, D.J. (2008) A conservation paradox for the 21st century: the European wild rabbit
705 *Oryctolagus cuniculus*, an invasive alien and an endangered native species. *Mammal Review*, **38**,
706 304-320.
- 707 Levänen, R., Pohjoismäki, J.L. & Kunasranta, M. (2019) Home ranges of semi-urban brown hares (*Lepus*
708 *europaeus*) and mountain hares (*Lepus timidus*) at northern latitudes. *Annales Zoologici Fennici*, pp.
709 107-120. BioOne.
- 710 Lombardi, L., Fernández, N., Moreno, S. & Villafuerte, R. (2003) Habitat-related differences in rabbit
711 (*Oryctolagus cuniculus*) abundance, distribution, and activity. *Journal of Mammalogy*, **84**, 26-36.
- 712 Luniak, M. (2004) Synurbization—adaptation of animal wildlife to urban development. *Proc. 4th Int.*
713 *Symposium Urban Wildl. Conserv. Tucson*, pp. 50-55. Citeseer.
- 714 Lush, L., Ward, A. & Wheeler, P. (2017) Dietary niche partitioning between sympatric brown hares and
715 rabbits. *Journal of Zoology*, **303**, 36-45.
- 716 Magle, S.B., Hunt, V.M., Vernon, M. & Crooks, K.R. (2012) Urban wildlife research: past, present, and future.
717 *Biological Conservation*, **155**, 23-32.
- 718 Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K., Bolker, B.,
719 Brooks, M. & Brooks, M.M. (2017) Package 'glmmTMB'. *R Package Version 0.2.0*.

- 720 Mair, L. & Ruete, A. (2016) Explaining spatial variation in the recording effort of citizen science data across
721 multiple taxa. *PLoS One*,**11**, e0147796.
- 722 Mayer, M. & Sunde, P. (2020) Colonization and habitat selection of a declining farmland species in urban
723 areas. *Urban Ecosystems*, **23**, 543–555.
- 724 Mayer, M., Ullmann, W., Sunde, P., Fischer, C. & Blaum, N. (2018) Habitat selection by the European hare in
725 arable landscapes: The importance of small-scale habitat structure for conservation. *Ecology and*
726 *Evolution*,**8**, 11619-11633.
- 727 McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological*
728 *Conservation*,**127**, 247-260.
- 729 Mueller, M.A., Drake, D. & Allen, M.L. (2019) Using citizen science to inform urban canid management.
730 *Landscape and urban planning*,**189**, 362-371.
- 731 Møller, A.P. (2012) Urban areas as refuges from predators and flight distance of prey. *Behavioral*
732 *Ecology*,**23**, 1030-1035.
- 733 Neumann, F., Schai-Braun, S., Weber, D. & Amrhein, V. (2012) European hares select resting places for
734 providing cover. *Hystrix, the Italian Journal of Mammalogy*,**22**.
- 735 O'hara, R.B. & Kotze, D.J. (2010) Do not log-transform count data. *Methods in Ecology and Evolution*,**1**, 118-
736 122.
- 737 Pereira-Ribeiro, J., Ferregueti, A.C., Bergallo, H.G. & Rocha, C.F.D. (2019) Good timing: evaluating anuran
738 activity and detectability patterns in the Brazilian Atlantic Forest. *Wildlife Research*,**46**, 566-572.
- 739 Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O'Hara, R.B., Parris, K.M., Vesk, P.A. & McCarthy, M.A.
740 (2014) Understanding co-occurrence by modelling species simultaneously with a Joint Species
741 Distribution Model (JSDM). *Methods in Ecology and Evolution*,**5**, 397-406.
- 742 Ramírez-Cruz, G.A., Solano-Zavaleta, I., Mendoza-Hernández, P.E., Méndez-Janovitz, M., Suárez-Rodríguez,
743 M. & Zúñiga-Vega, J.J. (2019) This town ain't big enough for both of us... or is it? Spatial co-
744 occurrence between exotic and native species in an urban reserve. *PLoS One*,**14**, e0211050.
- 745 Rondinini, C., Wilson, K.A., Boitani, L., Grantham, H. & Possingham, H.P. (2006) Tradeoffs of different types
746 of species occurrence data for use in systematic conservation planning. *Ecology Letters*,**9**, 1136-
747 1145.
- 748 Rutz, C. (2008) The establishment of an urban bird population. *Journal of Animal Ecology*,**77**, 1008-1019.
- 749 Rödel, H.G. & Dekker, J.J. (2012) Influence of weather factors on population dynamics of two lagomorph
750 species based on hunting bag records. *European Journal of Wildlife Research*,**58**, 923-932.
- 751 Serrano, S. & Hidalgo de Trucios, S. (2011) Burrow types of the European wild rabbit in southwestern Spain.
752 *Ethology Ecology & Evolution*,**23**, 81-90.
- 753 Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E. & Hope, D. (2006) From patterns to emerging
754 processes in mechanistic urban ecology. *Trends in Ecology & Evolution*,**21**, 186-191.
- 755 Smith, R.K., Jennings, N.V. & Harris, S. (2005) A quantitative analysis of the abundance and demography of
756 European hares *Lepus europaeus* in relation to habitat type, intensity of agriculture and climate.
757 *Mammal Review*,**35**, 1-24.
- 758 Stott, P. (2003) Use of space by sympatric European hares (*Lepus europaeus*) and European rabbits
759 (*Oryctolagus cuniculus*) in Australia. *Mammalian Biology*,**68**, 317-327.
- 760 Tapia, L., Domínguez, J., Regos, A. & Vidal, M. (2014) Using remote sensing data to model European wild
761 rabbit (*Oryctolagus cuniculus*) occurrence in a highly fragmented landscape in northwestern Spain.
762 *Acta Theriologica*,**59**, 289-298.
- 763 Thulin, C.G. (2003) The distribution of mountain hares *Lepus timidus* in Europe: a challenge from brown
764 hares *L. europaeus*? *Mammal Review*,**33**, 29-42.
- 765 Ulrich, W., Banks-Leite, C., De Coster, G., Habel, J.C., Matheve, H., Newmark, W.D., Tobias, J.A. & Lens, L.
766 (2018) Environmentally and behaviourally mediated co-occurrence of functional traits in bird
767 communities of tropical forest fragments. *Oikos*,**127**, 274-284.

- 768 Van Helden, B.E., Close, P.G., Stewart, B.A., Speldewinde, P.C. & Comer, S.J. (2020) An underrated habitat:
769 Residential gardens support similar mammal assemblages to urban remnant vegetation. *Biological*
770 *Conservation*,**250**, 108760.
- 771 Wagenmakers, E.-J. & Farrell, S. (2004) AIC model selection using Akaike weights. *Psychonomic bulletin &*
772 *review*,**11**, 192-196.
- 773 Wegge, P., Shrestha, A.K. & Moe, S.R. (2006) Dry season diets of sympatric ungulates in lowland Nepal:
774 competition and facilitation in alluvial tall grasslands. *Ecological research*,**21**, 698-706.
- 775 Ziege, M., Babitsch, D., Brix, M., Kriesten, S., Straskraba, S., Wenninger, S., Wronski, T. & Plath, M. (2016)
776 Extended diurnal activity patterns of European rabbits along a rural-to-urban gradient. *Mammalian*
777 *Biology*,**81**, 534-541.
- 778 Ziege, M., Brix, M., Schulze, M., Seidemann, A., Straskraba, S., Wenninger, S., Streit, B., Wronski, T. & Plath,
779 M. (2015) From multifamily residences to studio apartments: shifts in burrow structures of E
780 uropean rabbits along a rural-to-urban gradient. *Journal of Zoology*,**295**, 286-293.
- 781 Ziege, M., Hermann, B.T., Kriesten, S., Merker, S., Ullmann, W., Streit, B., Wenninger, S. & Plath, M. (2020)
782 Ranging behavior of European rabbits (*Oryctolagus cuniculus*) in urban and suburban landscapes.
783 *Mammal Research*,**65**, 607-614.
- 784 Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical
785 problems. *Methods in Ecology and Evolution*,**1**, 3-14.

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