

1 Climate and anthropogenic factors determine site occupancy  
2 in Scotland's Northern-range badger population: implications of  
3 context-dependent responses under environmental change

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5 André P. Silva<sup>\*1,2</sup>, Gonçalo Curveira-Santos<sup>\*1,2</sup>, Kerry Kilshaw<sup>3</sup>, Chris  
6 Newman<sup>3</sup>, David W. Macdonald<sup>3</sup>, Luciana Simões<sup>2</sup>, Luís M. Rosalino<sup>2,4</sup>

7 <sup>1</sup> Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University,  
8 Norbyvägen 18D, 752 36 Uppsala, Sweden

9 <sup>2</sup> Centre for Ecology, Evolution and Environmental Changes – cE3c, Faculdade de Ciências,  
10 Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal

11 <sup>3</sup> Wildlife Conservation Research Unit, Department of Zoology, University of Oxford,  
12 Recanti-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxfordshire OX13 5QL,  
13 UK

14 <sup>4</sup> Departamento de Biologia & CESAM, Universidade de Aveiro, Campus Universitário de  
15 Santiago, 3810-193 Aveiro, Portugal

16  
17 \* These authors contributed equally to this work

18 Correspondence: André P. Silva (pintodasilva.a@gmail.com) and Gonçalo Curveira-Santos  
19 (goncalo-cs@hotmail.com), tel. +46 18 4712930, Department of Animal Ecology,  
20 Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, 752 36 Uppsala,  
21 Sweden.

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## Abstract (A)

### Aim (B)

In the light of human-induced rapid environmental change (HIREC) populations are exposed to ever-greater bioclimatic stress at the edge of a species' historic range. The distribution dynamics of European badgers (*Meles meles*) at their southern-edge are linked tightly to climatic variability. We contribute critical data on how climatic context and local factors determine site occupancy in a northern-range population.

### Location (B)

11 study areas (averaging  $\sim 21.3 \text{ km}^2$ ) spread over  $\sim 50,000 \text{ km}^2$  in Northern Scotland.

### Methods (B)

While accounting for heterogeneous detectability, we applied single-season occupancy models to broad-scale camera-trapping data (168 stations) to evaluate how Autumn-Winter weather conditions interact with land cover type (including agricultural land) and human disturbance to determine badger occupancy.

### Results (B)

Mean minimum daily winter temperature and elevation influenced inter-site occupancy. When clustering study areas into two distinct topo-climatic types, badger occupancy was associated with agricultural sites in areas with lower mean minimum winter temperatures ( $< 0.3^\circ\text{C}$ ) at higher elevation ( $> 246\text{m}$ ). In areas with higher mean minimum winter temperature ( $> 1.2^\circ\text{C}$ ) at lower elevation ( $< 133\text{m}$ ) badgers selected sites further away from human infrastructures (settlements and main roads). Climatic factors and human disturbance interact in intricate, context-dependent patterns to determine badger site occupancy.

### Main conclusions (B)

The UKCP09 Medium Emissions Scenario projects a winter mean minimum temperature increase of between  $1\text{-}3^\circ\text{C}$  (central estimate) for Northern Scotland by the 2050s. Although

warmer weather should benefit badger occupancy, this may be counteracted by up to a predicted 5% human population increase in the Scottish highlands, by 2037, which is likely to disturb badgers. We show that, even in instances where species' regional responses to climate change are positive, these effects can be neutralised by other anthropogenic pressures. Our findings add to the growing body of evidence advocating that interactive effects should be taken into account when planning conservation management.

**Key-words** Agriculture, behavioural plasticity, carnivore, global warming, hierarchical modelling, habitat use, human settlements and infrastructures

## **Introduction (A)**

Human-Induced Rapid Environmental Change (HIREC; Sih *et al.* , 2011; 2013), particularly climate change, presents a major conservation challenge. Many species are increasingly exposed to novel conditions, with the potential to alter regional population dynamics and distributions (e.g., Parmesan & Yohe, 2003). Effects are most evident at species distribution margins (Kirkpatrick & Barton, 1997; Hampe & Petit, 2005), where population densities tend to be lower (Vucetich & Waite, 2003); margins often include much of the species' genetic plasticity and evolutionary potential (i.e., ability to adapt to new or changing environments) (Lesica & Allendorf, 1995; Remy & Petit, 2003; Hewitt, 2004). As bio-climatic niches shift, population declines are generally anticipated along their trailing (low latitude) distribution edge (Woodroffe *et al.* , 1990; Lawton, 1993). Important, however, is to better understand how climatic factors govern species ecology and demographics along a populations' leading (high latitude) margin (VanDerWal *et al.* , 2012). If conditions become more suitable along leading edge ecotones, this can push species pole-ward (Neilson, 1993). Conversely, cold-

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3 74 adapted species may rely on critical high-latitude refugia (Lomolino & Channell, 1995) where  
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5 75 climate change risks the loss of these sites.  
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7 76 Altered conditions also create scope for emerging human-wildlife interactions, which can lead  
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9 77 to anthropogenic impacts on populations (White & Ward, 2011). Furthermore, it is crucial to  
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11 78 establish how other HIREC factors, such as habitat change/loss and landscape management  
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13 79 (e.g. farming practices, urbanisation, fragmentation, etc.; see Dale, 1997; Opdam & Wascher,  
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15 80 2004; Mawdsley *et al.*, 2009), could interact with climate-driven changes to influence species  
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17 81 distributions and population dynamics (e.g. Macdonald *et al.*, 2010)  
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19 82 Consequently, detailed data (Morin & Lechowicz, 2008; Angert *et al.*, 2011) are needed to  
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21 83 underpin conservation policies specific to these particular risk factors. Nevertheless, few  
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23 84 studies have explicitly acknowledged and accounted for interactive effects of land use and  
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25 85 climate change on species biogeographic distributions (Oliver and Morecroft, 2014), resulting  
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27 86 in predictions that are generally limited to climate-occupancy interactions (Schwalm *et al.*  
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29 87 2016).  
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33 88 Generally, species with a broader intrinsic bio-climatic niche (Pearson & Dawson, 2003) are  
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35 89 more tolerant to climate change (Fisher-Reid *et al.*, 2012), and thus provide more informative  
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37 90 study models than do range-restricted, or rare species (Pimm *et al.*, 1988; McNamara *et al.*,  
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39 91 2001; Sih *et al.*, 2011). Also, vagile, migratory species tend to respond to climate change by  
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41 92 simply moving to maintain continuity with a suitable ecotope (Parmesan, 2006). In contrast,  
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43 93 the responses of less mobile species, especially central place foragers that are tied to a den or  
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45 94 territory, are less well understood (Pearson & Dawson, 2003; Jump & Peñuelas, 2005), but  
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47 95 tend not to arise through immigration or emigration, but from changes to intrinsic  
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49 96 demographic rates.  
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53 97 Here we look at how climatic factors, human modification of the landscape and land cover  
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55 98 shape occupancy (or site use) by the European badger, *Meles meles* (henceforth ‘badger’), in  
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the Scottish Highlands. This is the north-western margin of the species' distribution, which extends from the Mediterranean to the Arctic (Johnson *et al.*., 2002). Badgers are territorial and central-place foragers, not prone to moving in response to tracking food supply (Byrne *et al.*., 2015). Furthermore, climatic conditions have proven influential on badger population dynamics (Macdonald & Newman, 2002; Macdonald *et al.*., 2010; Nouvellet *et al.*., 2013; see also Newman *et al.*., *in press*) and regional population densities (Johnson *et al.*., 2002; Byrne *et al.*., 2015). Long, unproductive winter conditions (see Macdonald & Newman, 2002), associated with less suitable high-latitude and high-elevation weather and habitats, generally limit badgers' northern distribution (Bevanger & Lindström, 1995). Kauhala (1995) noted how warming trends led to badger distribution extending northwards in Finland through the second half of the 20<sup>th</sup> Century (see also Kowalczyk *et al.*., 2003). Similarly, Balestrieri *et al.*., (2009) reported how food resources, related to climatic conditions, limit badger distribution at high elevation in the Italian Alps. In parallel, Long (1972) speculated that the northern distribution limit of the North American badger, *Taxidea taxus*, may be limited by the availability of un-frozen diggable soil (Long & Killingley, 1983) and of grassland colonial rodents, the main food of *T. taxus* (see Weir *et al.*., *in press*). Concomitant constraints are also experienced by badgers at their southern limits, such as in Spain, where Virgós & Casanovas (1999) reported that climate is a more limiting factor than habitat type.

European badgers achieve some of their highest densities in Ireland (Byrne *et al.*., 2014) and in the south of the United Kingdom. Macdonald *et al.*., (2015) report over 50 badgers km<sup>2</sup>, in a study site in Central England, with similarly high densities elsewhere in the south-western UK (e.g., Thornton, 1988; Rogers *et al.*., 1997). These high densities are linked to suitable weather and habitats that, along with land-management practices, promote earthworm abundance (a favoured badger food source - Kruuk & Parish, 1981), thus leading to greater badger success. In these regions, recent climate change has tended to enhance habitat

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3 124 suitability (see Newman *et al.*, in press). In contrast, badger distribution and abundance in  
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5 125 Scotland is much sparser, with densities < 0.1 badger km<sup>2</sup> in the Highlands (Wilson *et al.* ,  
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7 126 (1997). Furthermore, although Wilson *et al.* , (1997) described a 77% estimated increase in  
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9 127 badger numbers across the entire UK for the period 1988 - 1997, they reported no change in  
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11 128 Scotland. Given this gradation toward fewer badgers in the north of the UK, the majority of  
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13 129 studies have taken place in the south, with only Rainey *et al.* , (2009) conducting a census of  
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15 130 Scottish badger density, and reporting an apparent increase in the number of badger main  
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17 131 setts, since Wilson *et al.*'s study, although both studies used different methodology. It is thus  
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19 132 crucial to gather data on Scottish badger populations and here we aim to fill this information  
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21 133 gap by utilising extensive ancillary camera trap data collected while documenting Scottish  
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23 134 wildcat (*Felis silvestris silvestris*) distribution (Kilshaw *et al.* , 2016).  
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27 135 When using site occupancy to assess species distribution and abundance it is imperative to  
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29 136 take imperfect detection into account (MacKenzie *et al.* , 2003; Royle *et al.* , 2005; Edwards  
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31 137 *et al.* , 2011; Lahoz-Monfort *et al.* , 2014). This is essential when weather conditions  
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33 138 influence activity rates and thus the ability to survey the species in question. Noonan *et al.* ,  
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35 139 (2015) established that badgers tend to stay below ground in their burrows (termed setts)  
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37 140 during poor weather (Noonan *et al.* , 2014). We addressed this potential problem using  
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39 141 hierarchical occupancy modelling (MacKenzie *et al.* , 2006). This approach integrates  
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41 142 detectability and occupancy metrics that are estimated separately to disentangle the effect of  
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43 143 detection error and reduce biases in occupancy estimates resulting from imperfect detection  
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45 144 (i.e. false-absences). Occupancy is derived from the overall presence/absence at each site. At  
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47 145 known occupied sites, the temporal replication of detection/non-detection histories enabled us  
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49 146 to estimate badger detection likelihood (i.e. detectability) (MacKenzie *et al.* , 2002).  
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53 147 Within this framework, we used Autumn-Winter occupancy data, i.e. covering a critical phase  
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55 148 of the badger life-cycle, when food availability and environmental conditions are likely to be  
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3 149 limiting (Nouvellet *et al.*., 2013; Noonan *et al.*., 2014), to test how badger occupancy is  
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5 150 influenced by: (i) climatic conditions (and associated elevation effects), which define the  
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7 151 species' climatic niche and thus directly affect its survival and recruitment patterns (Thornton,  
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9 152 1988; Macdonald *et al.*., 2010; Nouvellet *et al.*., 2013; Noonan *et al.*., 2015; Byrne *et al.*.,  
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11 153 2015); (ii) development of human infrastructures, as measures of anthropogenic disturbance  
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13 154 (Grilo *et al.*., 2009; Elliott *et al.*., 2015; Hipólito *et al.*., 2016); (iii) forested vs un-forested  
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15 155 habitats, because these relate to food availability and suitable sett sites (Virgós, 2001, 2002);  
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17 156 and (iv) structural complexity of the landscape matrix, -as a surrogate for resource richness  
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19 157 and diversity (Santos *et al.*., 2016; Virgós, 2001). We then investigated how distinct topo-  
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21 158 climatic contexts (i.e. temperature and elevation) interact with habitat type, human  
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23 159 infrastructural development and modification of the landscape for agriculture. Finally, we  
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25 160 considered what our findings might imply for future Scottish badger demographics in the  
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27 161 context of UKCP09 climate projections (Medium Emissions Scenario, 2050s) (Murphy *et al.*.,  
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29 162 2009) and human population projections (Population Projections for Scottish areas, 2014) for  
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## 165 **Methods (A)**

### 166 *Study region (B)*

167 This study was carried out across ~50,000 km<sup>2</sup> of the Scottish Highlands, north of the  
168 industrialised and urbanised Central Belt, between Glasgow and Edinburgh (see Fig. 1).  
169 Topography, climate and habitat across this region vary from east to west and from north to  
170 south (see Table 1), with large bodies of water (Lochs) breaking up the landscape (~0.5% of  
171 landscape). Climate is cooler to the north, and milder but wetter to the west, and temperature  
172 lapses predictably with elevation (c. 0.7 °C for every 100m increase in elevation) (ICAO  
173 1993), thus heavy snowfall (> 30 cm depth) is common across higher ground (>400 m),

174 particularly to the east and north (MET, 2012) (Table 1). Human population density is lowest  
175 in the northern Highlands (~8 people/km<sup>2</sup>) and the highest in the southern Central Uplands  
176 (~58.2 people/km<sup>2</sup>) (SCROL, 2011) (Table 1).

#### 178 *Badger data (B)*

179 From October 2010 to March 2013, a total of 168 camera-trap stations were deployed at 11  
180 study areas of on average 21.3km<sup>2</sup> (SD=3.6; min=14.3; max=26.0) Study areas were selected  
181 to survey a range of different habitats across Northern Scotland (Fig. 1). At each site we  
182 deployed a grid of 10-20 camera-trap-stations (average = 15.3) typically spaced 0.85-1.5 km  
183 apart.

184 The mean home range size for badgers in Scotland (121 ± 56 ha, Kruuk & Parish, 1987) is  
185 similar to that of wildcats (approx. 169 ± 25 ha; Corbett, 1979), and therefore this camera  
186 spacing design was adequate for the effective detection of both species. Because badgers  
187 could not be identified individually from their pelage patterns, we only considered captures  
188 separated by more than a 1h interval as independent detections.

189 At each station we deployed two camera-traps, either; a pair of Cuddeback Capture 3.0  
190 (Cuddeback IR Cuddeback Digital, Green Bay, Wisconsin, USA) or a pair of Reconyx  
191 HC500 IR (Reconyx, Inc., Holmen, Wisconsin, USA). Both camera types were set to take  
192 photos with minimum delay between photos (Cuddeback interval time = 30s; Reconyx = 1s  
193 with 3 frames per photo). Prior to the study, we trialled both camera types and established  
194 that they achieved similar (c.95%) capture success. Camera-traps were positioned 10-40cm  
195 above ground level, facing each other across obvious animal trails, but slightly staggered to  
196 avoid flashes interfering with photos from opposing cameras. Each camera station was baited  
197 with dead pheasant (*Phasianus colchicus*), or red-legged partridge (*Alectoris rufa*), and a  
198 scent lure (Hawbakers Wildcat lure #1 and #2; F & T Fur Harvesters Trading Post Inc) to help



199 attract carnivore species. Bait was tied to the top of a 1m wooden stake driven into the ground  
200 between the two camera-traps and lure spread on the lower section of the stake. Camera-traps  
201 were active for 60-80 days/sampling session (see Table S1 in Supporting Information) and  
202 were checked every 10-14 days to replace bait and lure, check batteries and download  
203 photographs (Kilshaw *et al.* , 2016).

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#### 205 *Explanatory variables (B)*

206 We selected predictor variables categories, *a priori*, based on factors known to be important  
207 to badger's ecology and distribution (e.g. *Climate*: Nouvellet *et al.* , 2013; *Land cover*:  
208 Remonti *et al.* , 2006; *Disturbance*: Hipólito *et al.* , 2016; *Competition*: Soto & Palomares,  
209 2015; *Elevation*: Prigioni & Deflorian, 2005). We used QGIS 1.8.0. Lisboa (Quantum GIS  
210 Development Team, 2012) to develop a multi-source GIS database, from which we measured  
211 topography [i.e. elevation (m)], climate variables, land-cover and disturbance covariate values  
212 (see Table 2 and S2 for a full description). Elevation was derived from the OS Terrain 50 free  
213 digital terrain model from the OS OpenData Supply (50m resolution) platform  
214 (<https://www.ordnancesurvey.co.uk/opendatadownload/products.html>). Climate data (2007-  
215 2011) was sourced from the Met Office UKCP09 5 x 5 km gridded data archive  
216 ([http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/download/access\\_gd](http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/download/access_gd/index.html)  
217 [/index.html](http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/download/access_gd/index.html)), averaged for the period November – April, corresponding with the months for  
218 which badger data was collected. Land-cover metrics were obtained from the Land Cover  
219 Map 2007 (LCM2007 - 25 m resolution; Morton *et al.* , 2011)  
220 (<http://www.ceh.ac.uk/landcovermap2007.html>) and human disturbance factors were assessed  
221 using the Ordnance Survey Strategi digital map (1:250,000)  
222 (<https://www.ordnancesurvey.co.uk/opendatadownload/products.html> accessed on June  
223 2011). These predictor variable metrics were then extracted for circular 500m radius buffer

224 zones around each camera-trap station (according, approximately, to badger minimum mean  
225 home range size, above).

226 Additionally, camera-trap records of human presence were used as an anthropogenic  
227 disturbance measurement. Likewise, we used the sum of camera-trap captures of the most  
228 common sympatric carnivore species (e.g. red fox *Vulpes vulpes*) to quantify potential inter-  
229 specific competition derived from co-occurrence at the site level.

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### 231 *Statistical analyses (B)*

232 We used likelihood-based single-season occupancy models (MacKenzie *et al.* , 2006) to  
233 evaluate the effect of site environmental covariates (see Table 2) on the probability of badger  
234 occupancy ( $\Psi$ ), while explicitly accounting for variations in detectability ( $p$ ), i.e. the  
235 probability of detecting the species when truly present (MacKenzie *et al.* , 2002). The single-  
236 season occupancy model (MacKenzie *et al.* , 2006) uses spatio-temporal replicated data – i.e.  
237 repeated sampling events over several sites (i.e. camera-trap stations) – to construct a  
238 likelihood estimate using a series of probabilistic arguments that account for the possibility of  
239 false-absences. By simultaneously modelling occurrence and detection as a function of site  
240 specific variables, this occupancy-likelihood framework identifies species-habitat  
241 relationships while correcting for imperfect detection. This approach is particularly useful  
242 when individual identification is not possible and detection probability cannot be extracted  
243 from Mark-Recapture methods. Since badgers can have home ranges that encompass more  
244 than one camera-trap site (e.g. Scottish badgers' home-ranges may reach 324ha; Kruuk &  
245 Parish 1987), we assumed we were looking at the probability of site use rather than  
246 probability of absolute occupancy (i.e. the presence/absence at the home range area).  
247 Nevertheless, for simplicity we termed this measure 'occupancy'.

248 Capture histories at each site (camera-trap location) were pooled into consecutive 7-day  
 249 sampling events to generate a presence-absence matrix. For each 7-day period, and for each  
 250 trap site, if at least a single badger photograph was obtained we denoted this as '1' (present);  
 251 otherwise a '0' (absent) was registered. Probability of detection and occupancy were  
 252 integrated hierarchically following a two-step methodology (Richmond *et al.* , 2010). First we  
 253 modelled detection probability as a function of separate environmental covariates that may  
 254 affect badger activity, and thus detectability (see Table 2), while fixing occupancy as  
 255 constant, i.e.  $\psi(\cdot), p(\text{covariate})$ . Then, we combined the best fitting model for detectability with  
 256 candidate models representing plausible biological hypothesis explaining badger occupancy  
 257 probabilities (Burnham & Anderson, 2002). The set of covariates and combinations used to  
 258 build the candidate models varied according to the objectives of each stage of analysis, as  
 259 described below (see also Table 2). Prior to the analysis, we assessed pairwise covariate  
 260 relationships using Spearman's correlation coefficients, to ensure that no highly correlated  
 261 variables ( $r \geq 0.7$ ) were incorporated in the models, to avoid multi-collinearity. Continuous  
 262 environmental covariates were standardised to z-scores to facilitate the interpretation of  
 263 coefficients (Cooch & White, 2006). Model fit was assessed using a goodness-of-fit test on  
 264 the most parameterised (global) model using the Pearson chi-square statistic, followed by a  
 265 parametric bootstrap procedure (1000 samples) to estimate an over-dispersion factor ( $\hat{c}$ ), as  
 266 recommended by Mackenzie & Bailey (2004). Provided models exhibited good-fit ( $p\text{-value} \geq$   
 267 0.05), candidate models were ranked using the Akaike Information Criterion corrected for  
 268 small sample sizes (AICc) (Burnham & Anderson, 2002). Models with  $\Delta\text{AICc}$  values  $\leq 2$ ,  
 269 compared to the most parsimonious model in the set, were considered to have strong support,  
 270 and a model averaging approach was adopted when drawing inferences (Burnham &  
 271 Anderson, 2002). The effect of individual covariates included in top-ranked models was  
 272 considered to be well-supported when 90% unconditional CI's of averaged beta coefficient

estimates did not overlap zero (MacKenzie *et al.* , 2006). Occupancy models were implemented using the ‘unmarked’ package in R statistical software V. 2.15.1 (Fiske & Chandler, 2011; R Development Core Team, 2011).

With sampling areas distributed throughout a wide geographical area, in a non-uniform pattern (see Fig. 1), it was important to disentangle the effects originating from inter-area heterogeneity from the influence of intra-area factors on badger occupancy probabilities. Inter-area heterogeneity mostly reflected dissimilar regional environmental contexts (for instance, badgers in the North are more likely to be exposed to colder conditions and inhabit dwarf shrub heath habitat compared to badgers in the South), while possibly masking species responses to local ecological factors (e.g., habitat preferences at the patch level) and context dependent patterns (e.g. Dussault *et al.* , 2005; Gaillard *et al.* , 2010). To address this, we conducted a two-stage analysis. In stage one, we explored the effect of covariates driving inter-area environmental heterogeneity (see “*Inter-area variability in occupancy probability across Northern Scotland*” section). In stage two, we used knowledge from the first analytical stage to reduce inter-area variability, and assessed how different local factors (i.e. intra-area) influence badger occupancy under more similar ecological contexts (see “*Context-specific responses to local environmental conditions*” section).

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Stage 1: *Inter-area variability in occupancy probability across Northern Scotland (C)*

Due to the spatially clustered nature of these data, we did not attempt to develop explicit predictive models of badger occupancy across the Northern Scottish landscape. Instead, we built candidate models to investigate how inter-area environmental heterogeneity (climate, topography, disturbance and landscape structure) affected the probability of badger occupancy, based on 168 camera-trapping sites across all 11 study areas (see Table 3).

We tested the extent to which badger occupancy was influenced by:

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3 298 i) Climate [rainfall (mm), minimum daily winter temperature, temperature variation (°C),  
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5 299 snow-lying and ground-frost days) and topography (elevation(m));  
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7 300 ii) Human infrastructural development – specifically whether badgers avoid or are  
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9 301 attracted to human settlements and roads;  
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11 302 iii) Habitat structure and composition [where ‘Conif’(forest) and ‘Dwarf Shrub Heather’  
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13 303 (non-forest) explain most of land-cover heterogeneity across study areas];  
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15 304 iv) Structural complexity of the landscape matrix, using habitat richness (“[HRich](#)”) as a  
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17 305 surrogate.  
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23 307 *Stage 2: Context-specific responses to local environmental conditions (C)*  
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25 308 To investigate the context-specific effect of local factors, we divided study areas into two  
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27 309 topo-climatic types, based on the average values of minimum temperature (WTemp) and  
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29 310 elevation (Elev): “Warmer and lower elevation” context (WLE) (average temperature >  
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31 311 1.2°C; average elevation < 133m) and “Colder and higher elevation” context (CHE) (average  
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33 312 temperature < 0.3°C; average elevation > 247m). The statistical significance of temperature  
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35 313 and elevation variation in both topo-climatic types was tested using Mann-Whitney U-tests  
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37 314 (See results and Table S4). Although there was substantial variation in temperature and  
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39 315 elevation within each topo-climatic type, this was significantly less than between types [see  
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41 316 Fig. S1; two areas (Inchnadamph and Spinningdale) did not fit these topo-climate  
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43 317 classification (sites; n = 32) and were excluded from further analysis]. By modelling reduced  
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45 318 inter-area environmental variability, this approach allowed us to test for context-dependent  
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47 319 responses to local factors.  
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51 320 For each topo-climatic type, we modelled occupancy as the dependent variable in univariate  
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53 321 candidate models (i.e., predicted by land-cover, disturbance and interspecific competition  
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55 322 covariates; Table 2) to explicitly assess and compare the influence of each predictor on  $\Psi$  (as  
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3 323 established by, e.g. Tuytens *et al.*, 2000; Byrne *et al.*, 2012; Barrull *et al.*, 2014). We also  
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5 324 ran univariate models with climate and topography variables to establish if these factors had  
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7 325 less influence at the local scale.  
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## 11 327 **Results (A)**

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14 328 A total of 527 badger photos were collected over 8610 effective trap-days, with a global  
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16 329 average trapping rate of 6.12 captures/100 trap days, i.e. 1 badger capture every 16.34 trap  
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18 330 days. The average naïve occupancy rate, i.e. the proportion of sites with badger recordings,  
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20 331 across areas was 0.41 (SD=0.23; min=0.14; max=0.82) with badgers detected in all study  
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22 332 areas. “Days of snow lying” was highly correlated with both “Winter minimum daily  
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24 333 temperature” ( $r=-0.83$ ) and “Elevation” ( $r=0.70$ ) and was therefore excluded from further  
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26 334 analyses.  
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### 31 32 336 *Heterogeneity in detection probability (B)*

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34 337 The best-fitting detection models for both the inter- and intra- area stages of analyses revealed  
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36 338 a consistent, well-supported, positive influence of minimum daily winter temperature on  
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38 339 badger’s detectability (Table S3). Over all sites, the detection probability estimate was 0.396  
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40 340 ( $\pm 0.024$ ). Detectability was higher with the WLE topo-climate type ( $0.518 \pm 0.035$ ), than  
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42 341 with the CHE topo-climate type ( $0.261 \pm 0.041$ ).  
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### 46 47 343 *Stage 1: Inter-area variability in occupancy probability across Northern Scotland (B)*

48  
49 344 The primary global model had a significant goodness-of-fit (p-value = 0.105) permitting us to  
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51 345 use AICc for model selection (Burnham & Anderson, 2002). The most parsimonious models  
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53 346 within the candidate set included the influence of climate and topography covariates on  $\Psi$   
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55 347 (Table 3). Model averaged estimates showed that badger occupancy was positively associated  
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with average minimum daily winter temperatures (WTemp), while being negatively associated with site elevation (Elev); both well-supported effects (Table 5). We detected a significant difference between WLE and CHE topo-climate types regarding temperature and elevation ( $U=229$ ,  $p<0.001$ ;  $U=4228.5$ ,  $p<0.001$ ; respectively; Fig. S1), providing statistical support to the discrimination of the two environmental contexts.

#### *Stage 2: Context-specific responses to local environmental conditions (B)*

Goodness-of-fit tests on the global model for both WLE (p-value = 0.968) and CHE (p-value = 0.155) topo-climate types indicated that the models fitted these data adequately. Thus, AICc was used for model ranking procedures.

In areas within WLE type, badgers avoided sites close to Human settlements (DistSet) and main roads (DistMR) (Table 5), i.e. occupancy probability decreased with proximity to these structures. This was evidenced by best-fitting models in the candidate set, both composed by disturbance variables (Table 4). In contrast, in areas within the CHE type, badgers made most use of Agricultural (Agric) habitat, which was the only well-supported predictor of badger site occupancy (Table 4). Specifically, site occupancy likelihood was positively related to the percentage of agricultural fields within the site buffer area (Table 5).

#### **Discussion (A)**

Overall, variation in badger occupancy (or site use) was best explained by minimum winter temperature and elevation, which had a stronger influence than human development or land cover characteristics. When sites were divided up according to their different topo-climatic conditions, however, subtler but intricate patterns became apparent. Badger occupancy under CHE contexts was strongly influenced by the availability of agricultural land. In contrast, in WLE contexts badgers tended to occupy predominantly areas further away from human

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3 373 infrastructures (i.e. settlements and roads) (Fig. 2). These findings exemplify how species can  
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5 374 exhibit different environmental preferences (or avoidances) between optimal and sub-optimal  
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7 375 climate areas. This behavioural plasticity in the light of topo-climatic circumstances (Wong &  
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9 376 Candolin, 2015) highlights how HIREC factors potentially interact with each other and with  
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11 377 other environmental factors (Sih *et al.* , 2011) to affect future Scottish badger occurrence.  
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13 378 Based on these findings, we emphasise that species climatic vulnerability assessments must  
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15 379 take environmental interactions and context-dependent responses into account (see Oliver &  
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17 380 Morecroft, 2014; Schwalm *et al.* , 2016) since the same co-factors may cause different  
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19 381 responses according to the climate-type a species occupies, even within the same meta-  
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21 382 population (see Füssel & Klein, 2006).  
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#### 27 384 *Heterogeneity in detection probability (B)*

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29 385 We considered two potential sources of detection heterogeneity, based on camera trapping  
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31 386 surveys: variation in local badger abundance, and fluctuation in badger activity rate. Badgers  
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33 387 do not exhibit any specific annual pulse in mortality, or migration (Macdonald *et al.* , 2009),  
34  
35 388 thus outside of the cub rearing season (Fell *et al.* , 2006) it is unlikely that demographic  
36  
37 389 changes could account for heterogeneity in detectability. Badgers are strongly influenced by  
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39 390 temperature and rainfall patterns (Macdonald & Newman, 2002, Macdonald et al. 2010;  
40  
41 391 Nouvellet et al. 2013; Byrne *et al.* , 2015), therefore variation in their above-ground activity  
42  
43 392 regimes (Noonan *et al.* , 2014) provides the most likely source of variation in detection rates.  
44  
45 393 Noonan *et al.* , (2015) caution that if weather conditions affect badger activity, and thus  
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47 394 detectability, this can obscure actual population demographic responses to climate change;  
48  
49 395 which we addressed here by using hierarchical occupancy modelling (as recommended by  
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51 396 Noonan *et al.* , 2015).  
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398 *Badger occupancy in Northern Scotland: the influence of topo-climatic contexts and local*  
399 *anthropogenic factors (B)*

400 Temperature and elevation are intrinsically related through the adiabatic lapse rate. This  
401 physical law is, however, modified by topography, air moisture content, aspect and prevailing  
402 wind direction (Still *et al.* , 1999).

403 Combining temperature and elevation ( $r=0.65$ ) to define distinct topo-climatic contexts, we  
404 found that CHE study areas were closer to the tree line (500m - Usher *et al.* , 2000) and likely  
405 to provide less suitable habitat for badgers due to winter wind, snow and colder temperatures  
406 leading to lower earthworm (badger's' main food type) availability (Lucherini & Crema,  
407 1995; Curry, 2004). This could potentially increase the energetic costs of thermoregulation,  
408 known to cause a decrease in badger body weight and, consequently, survival and  
409 abundance/density (Macdonald & Newman, 2002; Macdonald *et al.* , 2010; Nouvellet *et al.* ,  
410 2013). Thus, it is plausible that badgers inhabiting CHE and WLE are subject to different  
411 environmental conditions that may translate into distinct local ecological responses.

412 We also identified context-dependent responses in badger occupancy to local anthropogenic  
413 factors. In CHE, agricultural arable fields represented just 1.00% (range: 0-17.61%) of the  
414 landscape surrounding sampled sites, but these patches were positively associated with badger  
415 site use. Under colder conditions, where earthworms are more likely to be scarce, agriculture  
416 patches can provide complementary alternate food resources for badgers (e.g. barley, wheat  
417 and oats - Kruuk & Parish, 1985; Remonti *et al.* , 2011; Byrne *et al.* , 2012). In WLE sites,  
418 with more productive foraging conditions (Kruuk & Parish, 1985), other factors became more  
419 important, especially those that disturbed badgers (i.e. distance to human settlements and  
420 main roads; Cresswell *et al.* , 1989; Skinner *et al.* , 1991; Clarke *et al.* , 1998). The proportion  
421 of agricultural patches and the distance to main roads was not significantly different between  
422 the two topo-climate types (see Fig. S2), thus a badger's decision on which habitats to

423 occupy, or avoid, is probably driven by landscape context/composition, linked to food  
 424 resources, but not by differences in the relative availability of habitat types.  
 425  
 426 *Implications in relation to human-induced rapid environmental change (HIREC) (B)*  
 427 UKCP09 climate projections (Murphy *et al.* , 2009), based on the IPCC's Special Report on  
 428 Emissions Scenario (SRES) A1B (i.e. medium emissions scenario, MES), predict that winter  
 429 mean minimum temperature for Northern Scotland may increase between 1-3°C (central  
 430 estimate) by the 2050s. Certainly, we observed greater badger occupancy in warmer (lower  
 431 elevation) sites, and therefore if conditions warmed by ca. 2°C we would anticipate that more  
 432 areas of Highland Scotland would have temperatures better suited to badgers (Fig. 3). But, as  
 433 we show here, models based on this single factor are likely to prove simplistic and naïve.  
 434 Scotland's human population is predicted to increase by ca. 10% (Highlands, ca. 5%) for the  
 435 period 2012-2037 (Population Projections for Scottish areas, 2014), leading to an increased  
 436 demand for transport network/road development (19%, 2005-2022), which will most likely  
 437 encompass the Scottish countryside (Transport Scotland, 2009). In addition, improved  
 438 conditions for farming and a greater demand for food will likely lead to more agricultural land  
 439 conversion in Scotland, particularly in the drier east (Brown *et al.* , 2008). In combination,  
 440 these co-factors, interactive with specific topo-climate responses, might skew or nullify the  
 441 veracity of simple climate models attempting to project future badger population trends.  
 442 These types of effect have substantial ramifications for understanding species responses at  
 443 high-latitude range-edges, subject to 'improving' climatic conditions (VanDerWal *et al.* ,  
 444 2012). We show that it may prove faulty, or superficial, to assume that species will simply  
 445 benefit from warming conditions along the formerly cold-edge of their distribution  
 446 (Humphries *et al.* , 2004). If these zones become more important in acting as critical refugia  
 447 for range-shifting species (sensu Lomolino & Channell, 1995) then specific conservation

measures may be needed to ensure that other HIREC factors, such as landscape modification/agriculture, urbanisation and road-building/traffic do not counteract any improvements in environmental conditions resulting from weather more suitable for the species in question (see Oliver and Morecroft, 2014). This is especially important where the influence of these interactive constraints may also increase with global warming (White & Ward, 2011), potentially tipping populations into a failing cascade (Chevin *et al.*., 2010; Newman & Macdonald, 2015).

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**Table 1** Environmental characteristics of Northern Scotland (Data collated from MLURI, 1993; SCROL, 2011; MET, 2012) adapted from Kilshaw *et al.*, (2016). See geographic divisions in Fig. 1. SD – Standard Deviation.

	North	East	South	West
Human Population Density ind/km <sup>2</sup>	8	36.6	58.2	19
<b>Main habitats</b>				
Dwarf shrub heath	44%	20%	21%	11.5
Coniferous/broadleaved	9%	13%	15%	17%
Rough grassland	2.40%	2%	7%	11%
Improved grassland	4.40%	12.60%	18%	10
Arable	2.10%	36.50%	47%	0.7
<b>Climate</b>				
Annual rainfall (mm)	500-4000+	700-1500	<700	<1000-3500+
Annual snowfall (days)	40-100+	20-100+	20-60	10-60
Annual ground frost (days)	<90-140+	<90-150+	20-80+	60-140+
Mean annual temp (Celsius)	0-8C	6-9C	9	8-9.4
<b>Topography</b>				
Mean elevation ± SD (m)	266 ± 206	244 ± 209	275 ± 217	188 ± 159



**Table 2** Environmental covariates selected to explain badger site occupancy patterns in Northern Scotland.

Covariate	Code	Description	Units	Data range (min - max)
<b>TOPOGRAPHY</b>				
Elevation *, <sup>a</sup> <u><sup>b</sup></u>	Elev	Elevation above sea level	meters	5.9 - 521.3
<b>CLIMATE</b>				
Winter minimum daily temperature *, <sup>a</sup> <u><sup>b</sup></u>	WTemp	Average mean daily minimum temperature, for winter months (November to April) 2007 to 2011	°C	-1.44 – 3.03
Winter daily temperature variation <sup>a</sup> <u><sup>b</sup></u>	WTempA	Average difference between average mean daily minimum and maximum temperature, for winter months (November to April) 2007 to 2011	°C	11.94 – 16.15
Winter precipitation *, <sup>a</sup> <u><sup>b</sup></u>	Rain	Average precipitation for winter months (November to April) 2007 to 2011	mm	50.39 – 244.17
Days of snow lying <sup>c</sup>	DSL	Average number of days with snow for winter months (November to April) 2007 to 2011	#	2.66 – 10.93
Days of ground frost *, <sup>a</sup> <u><sup>b</sup></u>	DGF	Average number of days with ground frost for winter months (November to April) 2007 to 2011	#	11.75 - 21.94

## LAND-COVER

Agriculture * <sup>b</sup> <sub>1</sub>	Agric	Percentage of total buffer area occupied by Arable and horticulture fields	%	0 - 25.91
Mixed forest * <sup>b</sup> <sub>1</sub>	Mix	Percentage of total buffer area occupied by Broad leaved, mixed and yew woodland	%	0 – 42.48
Coniferous forest *, <sup>a</sup> <sub>1</sub> <sup>b</sup> <sub>2</sub>	Conif	Percentage of total buffer area occupied by Coniferous woodland	%	0 – 100
Grassland * <sup>b</sup> <sub>1</sub>	Grass	Percentage of total buffer area occupied by Rough low-productivity grassland, Acid grassland, Improved grassland, Neutral Grassland and Calcareous grassland	%	0 – 89.98
Dwarf Shrub Heather *, <sup>a</sup> <sub>1</sub> <sup>b</sup> <sub>2</sub>	Heath	Percentage of total buffer area occupied by Dwarf Shrub Heather (including open and dense dwarf shrub heath). Ericaceous vegetation on peat > 0.5 m deep is recorded as ‘bog’.	%	0 – 98.02
Bog * <sup>b</sup> <sub>2</sub>	Bog	Percentage of total buffer area occupied by Bog, Fen, Marsh and Swamp	%	0 – 99.54
Water * <sup>b</sup> <sub>2</sub>	Water	Percentage of total buffer area occupied by Freshwater	%	0 – 61.83
Distance to nearest river * <sup>b</sup> <sub>2</sub>	DistRi	Linear distance to the nearest river/stream	meters	0.41 – 1594.1
Habitat richness <sup>a</sup> <sub>2</sub> <sup>b</sup> <sub>2</sub>	HRich	Number of different land cover classes in each 500m buffer	#	1 - 7

## DISTURBANCE

Distance to nearest main road *, <sup>a</sup> <u><sup>b</sup></u>	DistMR	Linear distance between camera-trap station and nearest main road (road_a+primary_road+highway)	meters	21.87 - 10168
Main road extension *, <sup>a</sup> <u><sup>b</sup></u>	MRExt	Main road (road_a+primary_road+highway) total extension inside 500m buffer	meters	0 - 1956.5
Distance to nearest secondary road *, <sup>a</sup>	DistSR	Linear distance between camera-trap station and nearest secondary road (road_b+minor_road)	meters	40.7 - 10735
Secondary road extension *, <sup>a</sup>	SRExt	Secondary road total extension inside 500-m buffer (road_b+minor_road)	meters	0 – 1595.2
Distance to nearest human settlement *, <sup>a</sup> <u><sup>b</sup></u>	DistSet	Linear distance between camera-trap station and nearest human settlement	meters	118.21 – 6046.3
Human presence *, <sup>a</sup>	Humans	Humans captures per 100 trap nights	#	0 – 205.2
<b>COMPETITION</b>				
Competition with sympatric carnivores <sup>b</sup>	ALLC	Number of most abundant sympatric carnivore species (Red fox <i>Vulpes</i> <i>vulpes</i> ; wild-living cats <i>Felis silvestris</i> ; Pine marten <i>Martes martes</i> ) captures per 100 trap nights	#	0 – 37.66

\* - covariates tested when modelling detection probability in all stages. <sup>a</sup> - covariates used in stage-1 (inter-area) occupancy analysis. <sup>b</sup> - covariates used in stage-2 (context-specific) occupancy analysis. <sup>c</sup> – excluded covariates.

**Table 3** Model selection results for stage 1 “Inter-area variability in occupancy probability across Northern Scotland” analysis of badger occupancy. The most parsimonious models ( $\Delta AICc < 2$ ) are highlighted. Covariate abbreviations are presented in Table 2.  $p$ —probability of detection,  $\psi$ —probability of occupancy.

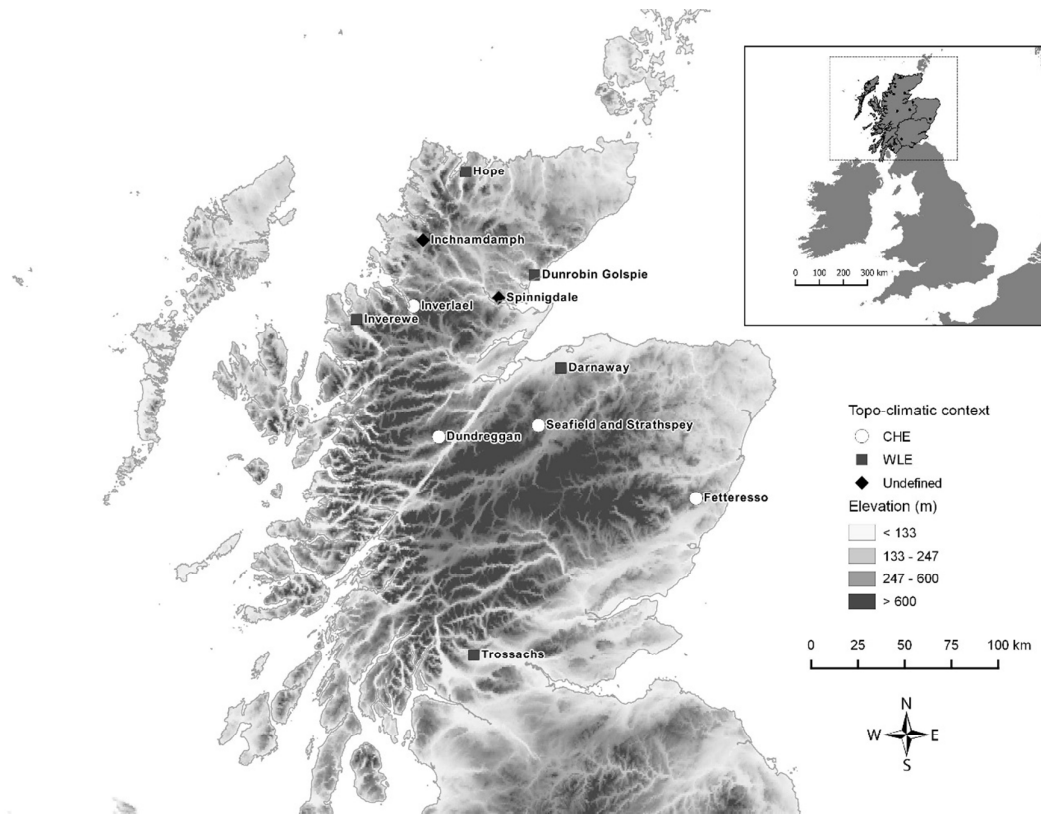
Hypothesis	Model	K	AICc	$\Delta AICc$	AICcw
Climate: temperature	$\psi(WTemp) p(WTemp)$	4	764.65	0	0.39
Topography: elevation	$\psi(Elev) p(WTemp)$	4	765.71	1.06	0.23
Disturbance: main roads	$\psi(DistMR+MRext) p(WTemp)$	5	767.48	2.83	0.09
Disturbance: Human presence	$\psi(DistSet+Humans) p(WTemp)$	5	768.52	3.86	0.06
Null model	$\psi(.) p(WTemp)$	3	768.8	4.15	0.05
General climate	$\psi(WTemp+WTempA+Rain+DGF)$ $p(WTemp)$	7	769.45	4.8	0.04
Land-cover: Non-forest habitat	$\psi(Heath) p(WTemp)$	4	769.62	4.97	0.03
Climate: rainfall	$\psi(Rain) p(WTemp)$	4	769.73	5.08	0.03
Land-cover: Forest habitat	$\psi(Conif) p(WTemp)$	4	770.26	5.61	0.02
Land-cover: Habitat richness	$\psi(HRich) p(WTemp)$	4	770.74	6.09	0.02
Climate: ground frost	$\psi(DGF) p(WTemp)$	4	770.83	6.18	0.02
Climate: temperature variation	$\psi(WTempA) p(WTemp)$	4	770.89	6.24	0.02
Disturbance: secondary roads	$\psi(DistSR+SRext) p(WTemp)$	5	772.63	7.98	0.01
General disturbance	$\psi(DistMR+MRext+DistSR+SRext+DistSet+Humans) p(WTemp)$	9	774.63	9.98	0

**Table 4** Model selection results for stage-2 “*Context-specific responses to local environmental conditions*” analyses of badger occupancy. Only models with  $\Delta AICc < 2$  and the ‘Null model’ are shown. Covariate abbreviations are presented in Table 2.  $p$ —probability of detection,  $\psi$ —probability of occupancy (or site use).

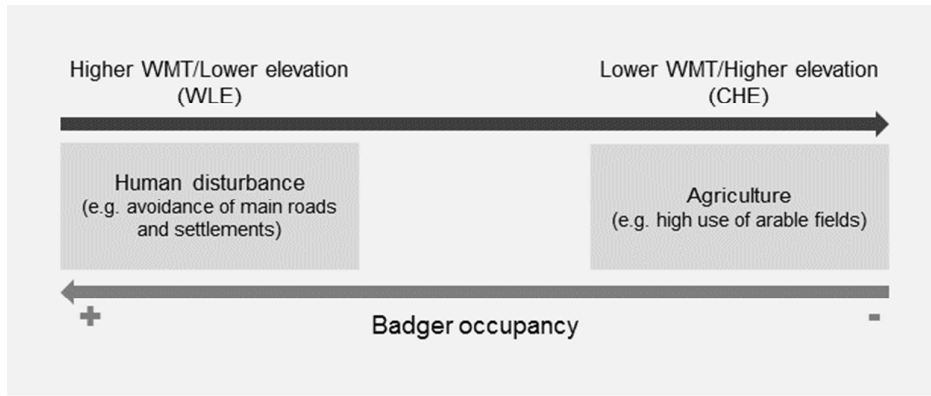
Topo-climatic type	Model	K	AICc	$\Delta AICc$	AICcw
"Warmer and Lower elevation"					
context (WLE)					
	$\psi(\text{DistSet}) p(\text{WTemp})$	4	381.05	0.00	0.38
	$\psi(\text{DistMR}) p(\text{WTemp})$	4	382.16	1.11	0.22
	$\psi(.) p(\text{WTemp})$	3	387.15	6.10	0.02
"Colder and Higher elevation "					
context (CHE)					
	$\psi(\text{Agric}) p(\text{WTemp})$	4	224.68	0.00	0.74
	$\psi(.) p(\text{WTemp})$	3	232.49	7.81	0.01

**Table 5** Model-averaged beta coefficient estimates on the logit scale [ $\beta$  (SE)] for environmental covariates (abbreviations are presented in Table 2) included in best-fitting models of badger occupancy.  $p$  — probability of detection,  $\psi$  — probability of occupancy (or site use).

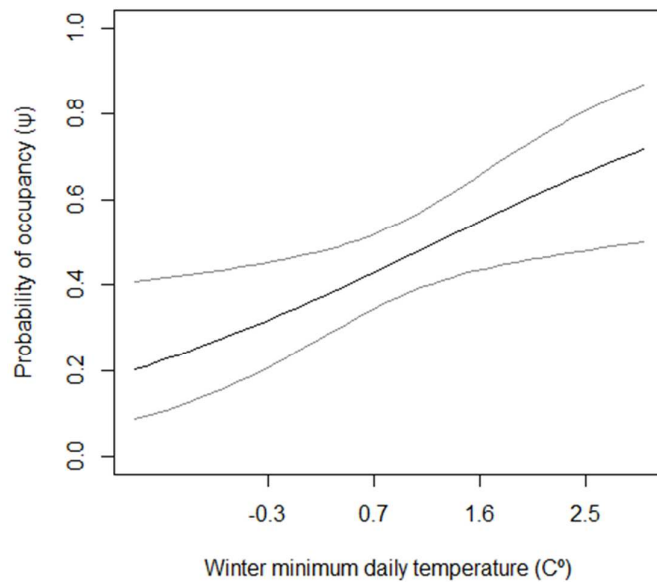
Parameter	Category	Covariate	Stage-1: <i>Inter-area</i> <i>variability in occupancy</i> <i>probability across</i> <i>Northern Scotland</i>	Stage-2: <i>Context-specific</i> <i>responses to local environmental</i> <i>conditions</i>	
				"Warmer and Lower elevation" context (WLE)	"Colder and Higher elevation" context (CHE)
$\psi$	Climate	WTemp	0.48 (0.19) <sup>a</sup>		
	Topography	Elev	-0.43 (0.19) <sup>a</sup>		
	Disturbance	DistSet		0.92 (0.40) <sup>a</sup>	
		DistMR		0.80 (0.33) <sup>a</sup>	
	Land cover	Agric			1.27 (0.67) <sup>a</sup>
$p$	Climate	WTemp	0.86 (0.13) <sup>a</sup>	0.60 (0.15) <sup>a</sup>	0.87 (0.28) <sup>a</sup>



**Figure 1** Location of study areas target of camera-trapping surveys in Northern Scotland (WLE – Warmer and Lower elevation context; CHE – Colder and Higher elevation context). Land cover is classified as montane habitat above 600m (LCM 2007), therefore considered less suitable for badger occurrence. Regions surveyed during this study and characterized in table 1 are shown in the overview map (top-right corner).



**Figure 2** Schematic representation of the main factors explaining badger occupancy in Northern Scotland (WMT – Winter minimum daily temperature).



**Figure 3** Response plot of badger occupancy (or site use) probability as a function of winter mean minimum daily temperature in Northern Scotland.



## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Temperature and elevation comparison between CHE and WLE context.

**Figure S2** Comparison between of the most important covariates identified in stage-2 (i.e. context specific) occupancy analysis for the CHE and WLE context.

**Table S1** Period of sampling for each study area.

**Table S2** Variables characterization per study area.

**Table S3** Model selection results for detection probability.

**Table S4** Study area division for stage-2 “*Context-specific responses to local environmental conditions*” occupancy analysis.

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### Biosketches (A)

André P. Silva is a conservation biologist currently undertaking a Ph.D. at the Department of Animal Ecology, Uppsala University (<http://katalog.uu.se/profile/?id=N13-2210>). He has been working on the ecology and genetics of endangered mammals, with special emphasis on carnivores. Presently, he is studying the distribution and population structure of small felids in India to understand potential consequences of environmental changes and future efficiency of protected areas.

Gonçalo Curveira-Santos is a Ph.D. student at the cE3c (<http://ce3c.ciencias.ulisboa.pt/member/gonccedilalo-curveira-santos>). His main research field

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2  
3 846 is the conservation ecology of mammals. Particularly, he is interested in the ecological  
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5 847 strategies involved in carnivore adaptation to changing environments and the functional  
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7 848 conservation role of agriculture and forestry landscapes. During the forthcoming years he will  
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9 849 focus on the spatial ecology of mammalian carnivores in Neotropical agro-ecosystems.  
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11 850 Ultimately, he aims to contribute to the development of integrative management approaches  
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13 851 in a conservation context by investigating the correspondence between the spatial unit and its  
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15 852 functional role, linking patterns to processes.  
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17 853  
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19 854 Author contributions: A.P.S, G.C.S and L.M.R conceived the ideas; K.K. collected the data,  
20  
21 855 L.S conducted the GIS analyses, G.C.S led the occupancy analyses with the contribution of  
22  
23 856 A.P.S and L.M.R; and A.P.S and G.C.S led the writing with the contribution of all co-authors.  
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## 1 Supporting information

**Table S1** Period of sampling for each study area. Note that camera trapping surveys occurred across three Autumn-Winter seasons (2010-2013).

Topo-climatic type	Study area	Sampling period					
		Out	Nov	Dec	Jan	Feb	Mar
"Warmer and Lower elevation" context (WLE)	Darnaway						
	Dunrobin						
	Inverewe						
	Hope						
	Trossachs						
"Colder and higher elevation" context (CHE)	Dundreggan						
	Fetteresso						
	Inverlael						
	Seafeld and						
	Strathspey						
Discarded	Inchnadamph						
	Spinningdale						

2 **Table S2** Variables characterisation per study area. Covariate abbreviations are presented in Table 2.

Topo-climatic type	Study area	Elev	WTemp	WTempA	Rain	DSL	DGF	Agric	Mix	Conif	Grass	Heath	Bog	Water	DistRi	HRI ch	DistMR	MRExt	DistSR	SRExt	DistSet	Humans	ALLC	
"Warmer and Lower elevation " context (WLE)	Darnaway	Avg	79.5	1.2	15.4	59.3	4.6	19.2	5.9	4.5	59.7	26.3	2.4	0.0	1.1	245.8	4.2	1860.7	59.1	660.6	374.3	1516.8	0.4	1.1
		SD	48.8	0.5	0.2	4.1	0.6	1.4	8.8	5.3	22.3	21.0	3.9	0.0	2.6	212.7	0.9	1090.5	196.5	430.1	560.5	703.1	0.8	1.8
		Max	189.7	1.9	15.5	62.2	5.0	20.2	25.9	20.1	94.6	81.9	12.2	0.0	7.8	628.7	6.0	3795.3	796.1	1488.6	1478.9	2649.9	2.6	6.5
		Min	28.2	0.8	15.0	50.4	3.6	16.8	0.0	0.0	17.2	0.1	0.0	0.0	0.0	2.1	3.0	320.6	0.0	9.2	0.0	289.3	0.0	0.0
	Dunrobin	Avg	132.2	1.2	13.7	79.0	4.5	17.0	2.3	1.8	36.2	24.0	30.5	4.3	0.2	500.9	4.4	1591.4	54.0	692.3	373.6	1281.8	16.2	4.7
		SD	86.9	0.4	0.2	5.7	0.4	1.0	5.0	2.7	24.6	12.3	27.2	10.8	0.6	326.1	1.0	989.3	194.8	533.4	531.3	585.8	47.9	6.4
		Max	297.7	1.7	14.0	83.1	4.8	17.7	15.3	8.5	69.9	41.1	78.7	33.2	2.1	1194.1	6.0	3415.6	702.5	1760.5	1595.2	2115.9	172.7	23.4
		Min	34.9	0.9	13.4	67.3	3.7	15.6	0.0	0.0	0.0	9.6	0.1	0.0	0.0	119.0	3.0	336.3	0.0	134.2	0.0	398.6	0.0	0.0
	Inverewe	Avg	77.3	2.5	12.2	170.9	4.5	13.5	0.0	7.3	10.1	17.8	47.0	3.1	12.0	493.9	4.7	3058.5	189.0	3107.1	57.4	3727.0	25.1	9.3
		SD	81.5	0.6	0.2	19.7	0.9	0.5	0.0	8.5	19.9	17.6	23.7	5.9	17.3	435.0	1.4	2004.2	382.1	1473.5	206.8	2207.2	59.0	12.2
		Max	220.9	3.0	12.4	190.8	5.5	14.1	0.1	26.2	69.0	58.5	90.6	16.7	45.6	1392.9	7.0	6417.2	1031.3	5477.2	745.6	6046.3	205.2	37.7
		Min	7.6	1.9	11.9	148.7	3.6	13.1	0.0	0.0	0.0	0.0	7.5	0.0	0.0	47.3	2.0	117.4	0.0	266.5	0.0	118.2	0.0	0.0
	Hope	Avg	64.8	1.0	13.4	111.9	4.2	14.0	2.2	8.8	8.8	17.2	44.6	8.0	18.6	431.7	4.1	2273.9	168.1	662.5	468.0	2160.5	1.1	6.1
		SD	65.9	0.7	3.7	36.9	1.3	4.9	6.2	9.7	18.5	11.2	25.7	21.3	19.9	427.1	1.6	1603.2	362.9	611.1	480.0	1541.6	2.5	7.7
		Max	221.0	2.0	15.7	154.5	5.8	20.5	23.1	32.4	65.6	45.0	84.2	80.7	61.8	1594.1	7.0	5073.9	1313.7	2179.4	1044.8	4849.1	9.1	28.6
		Min	5.9	-0.2	0.6	10.3	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.9	21.9	0.0	4.8	0.0	180.6	0.0	0.0
	Trossachs	Avg	112.3	1.2	15.0	175.1	3.1	17.3	0.6	8.3	49.0	28.2	12.9	0.1	0.3	253.3	3.7	1364.4	231.4	894.4	313.4	1524.6	0.1	3.8
		SD	85.2	0.3	0.4	6.6	0.6	0.2	1.7	11.4	24.5	24.6	18.0	0.5	0.8	235.6	1.3	1086.8	414.3	673.9	463.6	717.2	0.4	4.4
		Max	275.3	1.5	15.3	194.3	3.9	17.4	6.6	41.5	94.7	80.6	44.4	1.8	3.0	717.1	6.0	3448.6	962.0	2383.7	1253.3	2888.1	1.8	17.9
		Min	16.7	0.8	14.4	170.4	2.7	17.1	0.0	0.0	1.9	0.0	0.0	0.0	0.0	18.2	2.0	126.8	0.0	84.5	0.0	591.3	0.0	0.0

"Colder and higher elevation " context (CHE)

Undefined

Dundreggan	Avg	247.9	0.3	14.0	161.2	7.3	18.3	0.3	3.0	27.2	39.2	15.1	5.1	3.2	359.0	4.4	1029.8	375.0	3325.4	0.0	2841.1	0.4	6.6
	SD	106.5	0.4	0.3	14.6	0.7	0.1	1.4	8.1	28.9	31.2	13.8	13.1	5.8	308.0	1.5	866.7	487.0	1448.2	0.0	1375.3	1.3	5.6
	Max	411.5	0.7	14.3	178.2	8.0	18.3	5.9	33.2	77.8	90.0	46.0	51.1	23.3	1148.5	7.0	2533.8	1059.8	5744.5	0.0	5053.2	5.2	22.1
	Min	80.2	-0.1	13.7	143.8	6.6	18.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.4	2.0	45.7	0.0	595.5	0.0	348.1	0.0	1.3
Fetteresso	Avg	281.9	0.3	13.5	100.2	5.9	21.1	2.8	1.6	62.2	15.7	13.8	3.1	0.1	314.7	3.9	7392.2	0.0	1822.4	0.0	3411.5	0.9	13.2
	SD	62.5	0.4	0.7	11.1	0.7	0.4	4.9	2.8	23.8	21.0	14.9	8.1	0.5	276.7	1.6	1237.4	0.0	862.8	0.0	993.9	2.2	8.3
	Max	389.9	1.0	14.1	110.0	6.5	21.9	17.6	7.8	100.0	69.2	54.2	34.2	1.8	997.6	7.0	10168.2	0.0	3209.5	0.0	4915.3	9.1	29.9
	Min	186.0	-0.1	12.6	86.1	5.0	20.5	0.0	0.0	13.8	0.0	0.0	0.0	0.0	37.2	1.0	5427.8	0.0	243.9	0.0	1638.4	0.0	1.3
Inverlael	Avg	267.4	0.2	14.0	174.1	6.9	16.8	0.1	10.8	9.4	17.0	36.7	22.4	0.4	347.7	4.0	1737.3	435.9	2434.0	7.8	2196.6	0.7	3.3
	SD	164.3	1.0	1.0	21.3	1.9	0.2	0.2	14.1	11.2	22.0	30.9	36.3	0.9	306.2	1.4	1501.0	748.0	1429.1	29.3	1314.0	2.0	2.5
	Max	521.3	1.4	15.1	200.4	9.0	17.0	0.8	42.5	32.8	62.0	98.0	99.5	2.7	1135.1	6.0	4543.0	1956.5	4800.9	109.6	4661.7	6.5	9.1
	Min	8.1	-1.1	13.0	147.4	4.6	16.5	0.0	0.0	0.0	0.0	0.5	0.0	0.0	21.0	2.0	58.8	0.0	431.4	0.0	399.7	0.0	0.0
Seafield and Strathspey	Avg	333.4	-0.8	16.0	80.2	9.4	19.9	0.5	5.7	49.1	18.7	23.6	1.3	0.0	327.9	4.6	1422.0	97.3	873.5	292.7	1565.0	3.0	2.2
	SD	34.3	0.3	0.4	16.4	0.7	0.2	1.4	8.9	18.6	15.8	18.8	3.8	0.2	219.4	1.0	818.1	269.9	622.1	449.2	546.7	3.7	2.1
	Max	392.8	-0.6	16.1	115.3	10.9	19.9	4.9	36.8	88.7	49.5	61.5	14.4	0.7	780.1	6.0	2968.5	907.1	1949.9	989.4	2572.5	14.3	7.8
	Min	277.5	-1.4	14.9	72.6	9.1	19.4	0.0	0.0	23.1	0.0	0.0	0.0	0.0	72.7	3.0	204.3	0.0	4.8	0.0	645.7	0.0	0.0
Inchnadamph	Avg	171.4	0.2	12.9	225.6	6.7	14.6	0.0	1.9	0.5	31.8	46.6	10.3	8.9	331.1	3.4	1206.2	212.2	9427.5	0.0	1628.4	0.5	4.0
	SD	64.5	0.2	0.1	12.6	0.3	0.2	0.0	5.0	1.1	25.7	30.0	20.5	14.3	208.0	1.0	840.9	421.7	846.2	0.0	883.5	0.6	5.6
	Max	278.7	0.4	13.1	244.2	7.2	14.8	0.0	19.1	3.0	67.7	97.0	74.9	34.8	741.5	5.0	3098.7	1003.1	10734.6	0.0	3202.5	1.3	22.1
	Min	67.7	-0.1	12.8	213.5	6.5	14.3	0.0	0.0	0.0	0.0	3.2	0.0	0.0	29.4	2.0	69.6	0.0	8261.2	0.0	141.1	0.0	0.0
Spinningdale	Avg	79.4	0.2	15.0	91.5	5.2	20.0	1.7	9.2	28.5	11.6	30.8	2.0	15.2	652.9	4.8	1014.8	272.7	953.7	219.7	1404.3	1.5	10.3
	SD	49.8	0.4	0.6	10.3	0.7	0.3	5.4	10.1	17.8	13.9	26.8	4.2	18.3	538.9	0.9	757.7	464.3	664.9	417.4	617.2	2.7	8.4
	Max	201.7	0.7	15.7	102.0	5.8	20.5	23.1	32.4	65.6	45.0	84.2	13.8	61.8	1594.1	6.0	2406.1	1313.7	2179.4	1044.8	2545.5	9.1	28.6
	Min	20.5	-0.2	14.3	77.5	4.3	19.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	22.6	3.0	21.9	0.0	4.8	0.0	459.5	0.0	1.3

**Table S3** Model selection results for detection probability in every stage of analysis. The most parsimonious models ( $\Delta AICc < 2$ ) are highlighted. Covariate abbreviations are presented in Table 2. p—probability of detection,  $\psi$ —probability of occupancy (or site use).

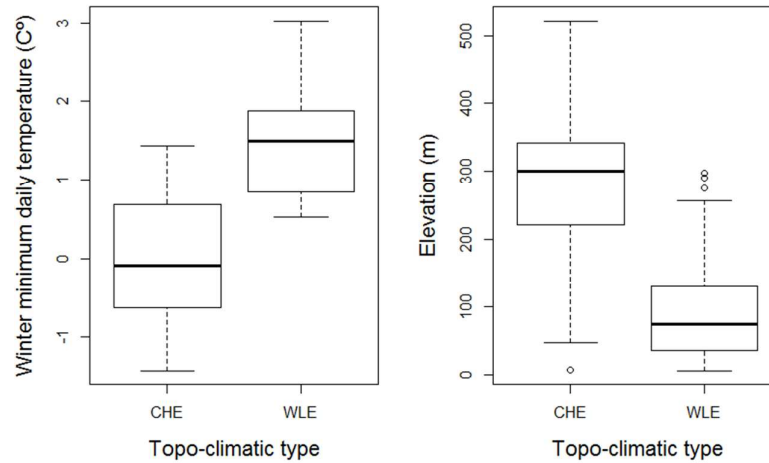
Model	Stage-1: <i>Inter-area variability in occupancy probability across Northern Scotland</i>			Stage-2: <i>Context-specific responses to local environmental conditions</i>					
	"All sites"			"Warmer and Lower elevation " context			"Colder and Higher elevation " context		
	AICc	$\Delta AICc$	AICcw	AICc	$\Delta AICc$	AICcw	AICc	$\Delta AICc$	AICcw
$\psi(.) p(.)$	832.04	63.25	0	402.06	14.91	0	242.07	9.58	0.01
$\psi(.) p(Alt)$	810.17	41.37	0	399.39	12.24	0	244.27	11.77	0
$\psi(.) p(WTemp)$	768.8	0	1	387.15	0	0.81	232.49	0	0.69
$\psi(.) p(Rain)$	834.03	65.24	0	400.22	13.07	0	244.27	11.77	0
$\psi(.) p(DGF)$	825.63	56.83	0	397.12	9.97	0.01	240.92	8.43	0.01
$\psi(.) p(Agric)$	832.12	63.32	0	404.2	17.05	0	236.89	4.4	0.08
$\psi(.) p(Mix)$	828.33	59.53	0	398.25	11.1	0	242.8	10.31	0
$\psi(.) p(Conif)$	828.68	59.89	0	397.52	10.37	0	242.48	9.99	0
$\psi(.) p(Grass)$	833.63	64.84	0	402.13	14.98	0	241.95	9.46	0.01
$\psi(.) p(Heath)$	833.94	65.14	0	403.93	16.78	0	244.15	11.65	0
$\psi(.) p(Bog)$	833.46	64.66	0	404.23	17.08	0	244.26	11.77	0
$\psi(.) p(Water)$	829.01	60.21	0	395.12	7.97	0.02	243.04	10.54	0
$\psi(.) p(DistRi)$	833.68	64.88	0	403.92	16.78	0	238.61	6.12	0.03
$\psi(.) p(DistMR)$	830.38	61.59	0	400.76	13.61	0	236.5	4	0.09
$\psi(.) p(MRExt)$	833.04	64.25	0	393	5.85	0.04	242.74	10.24	0
$\psi(.) p(DistSR)$	828.15	59.36	0	393.03	5.88	0.04	237.66	5.17	0.05
$\psi(.) p(SRExt)$	833.08	64.28	0	394.36	7.21	0.02	244.37	11.88	0
$\psi(.) p(DistSet)$	830.2	61.41	0	397.1	9.95	0.01	243.24	10.75	0
$\psi(.) p(Humans)$	820.61	51.81	0	392.88	5.73	0.05	244.03	11.53	0

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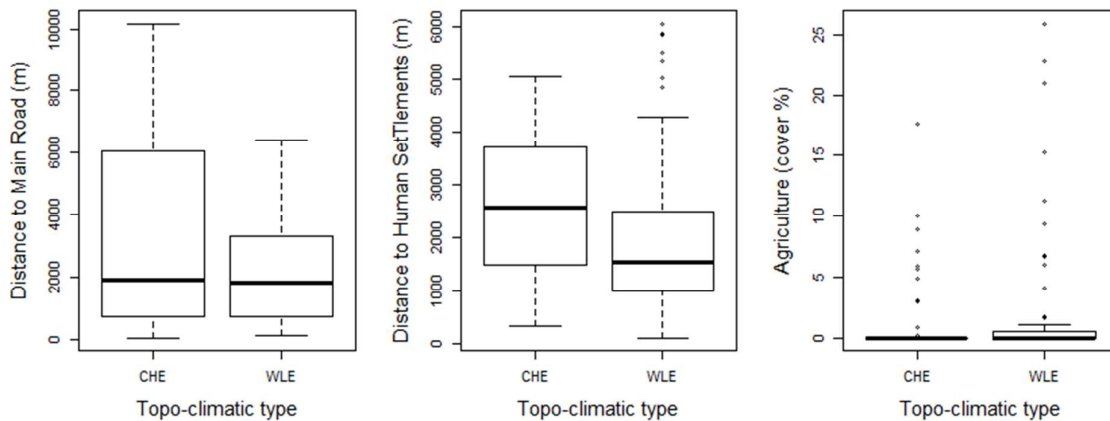
**Table S4** Study area division for stage-2 “*Context-specific responses to local environmental conditions*” occupancy analysis according to average site’s Temperature (WTemp) and Elevation (Elev) values. See Table 2 for variables description.

Topo-climatic type	Study area	Winter minimum daily temperature (C°) (average*)	Elevation (m) (average*)
"Warmer and Lower elevation" context (WLE)	Darnaway	1.2	79.5
	Dunrobin	1.2	132.2
	Inverewe	2.5	74.0
	Hope	1.3	64.8
	Trossachs	1.2	112.3
"Colder and Higher elevation" context (CHE)	Dundreggan	0.3	247.9
	Fetteresso	0.3	281.9
	Inverlael	0.2	267.4
	Seafeld and Strathspey	-0.8	333.4
Undefined (discarded)	Inchnadamp	0.2	171.4
	Spinningdale	0.2	79.4
<b>Global average across all sites</b>		0.7	173.2

\* – Average across sites in each study area.



**Fig. S1** Comparison between average site values in "Colder and Higher elevation" context (CHE) and "Warmer and Lower elevation" context (WLE) study area types for Temperature and Elevation – covariates used to define the distinct topo-climatic contexts.



**Fig. S2** Comparison between average site values in "Colder and Higher elevation" context (CHE) and "Warmer and Lower elevation" context (WLE) study area topo-climatic types for the most important covariates identified in stage-2 (i.e. context-specific) occupancy analysis. No significantly difference in the distance to the main roads and in the percentage of agriculture coverage between topo-climatic types were detected (U=2515, U=2024; all



22  $p>0.05$ ; respectively). However, these groups differed significantly in the distance to human  
23 settlements ( $U=2955$ ,  $p=0.005$ ).

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