



Factors influencing Hen Harrier, *Circus cyaneus*, territory site selection and breeding success.

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1 Original Research Paper

2 **Factors influencing Hen Harrier, *Circus cyaneus*, territory site selection and breeding**
3 **success.**

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19 **Keywords:** birds of prey; conservation; habitat models; nest success; productivity.

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21

22 **Summary**

23 **Capsule**

24 Our findings regarding Hen Harrier territory site selection and breeding success in Ireland offer
25 an opportunity for the development of initiatives and conservation activities aimed at
26 enhancing the suitability of upland areas for breeding Hen Harriers and ensuring the long-term
27 future of the species.

28 **Aims**

29 To investigate landscape-scale associations between habitat composition and Hen Harrier
30 territory site selection, and to explore the influence of habitat and climate on breeding success.

31 **Methods**

32 We used multi-model inference from Generalised Linear Models and Euclidean distance
33 analyses to explore the influence of habitat, topographic, anthropogenic and climatic factors on
34 Hen Harrier territory selection and breeding success in Ireland, based on data from national
35 breeding surveys in 2010 and 2015.

36 **Results**

37 Hen Harrier territories were associated with heath/shrub and pre-thicket coniferous forests.
38 Comparisons between territories and randomly-generated pseudo-absences (upland and
39 lowland) showed that breeding pairs preferentially select for these habitats. Breeding success
40 was negatively influenced by rainfall early in the breeding season and by climatic instability
41 and was positively influenced by the presence of heather moorland and bog.

42 **Conclusions**

43 The results suggest that breeding success in a degraded landscape is compromised by the
44 synergistic effects of climate, landscape composition and management. Effective conservation
45 of Hen Harriers in Ireland will therefore rely on landscape-scale initiatives.

46

For Peer Review

47 **Introduction**

48 Upland areas, typically found at higher elevation than enclosed farmland (O'Rourke & Kramm
49 2009), are of high conservation importance and support a diverse and characteristic assemblage
50 of habitats and species (Thompson *et al.* 1995; Roche *et al.* 2014). However, uplands are also
51 subject to a suite of pressures that result in the degradation and fragmentation of habitats (e.g.
52 Douglas *et al.*, 2008; O'Riordan *et al.*, 2015; O'Rourke & Kramm 2009; Ratcliffe, 2010;
53 Renou-Wilson *et al.* 2011). This has led to the decline of many upland bird populations
54 (Marquiss *et al.* 1985; Brawn *et al.* 2001; Julliard *et al.* 2004)

55 Afforestation (the planting of forest in an area where there was little or no previous
56 tree cover) has resulted in greater losses in upland bird populations than any other single factor
57 (Thompson *et al.* 1988; Ratcliffe 2010). Following afforestation, the composition of avian
58 assemblages associated with plantation forests is not temporally stable; while young plantation
59 forests are associated with a diverse range of bird species (Wilson *et al.* 2006), bird
60 communities change as the plantation ages, with forest species succeeding those of open
61 habitats (Wilson *et al.* 2006). Furthermore, afforestation has negative implications for upland
62 species beyond the immediate transformation of open habitats. For example, forest fragments
63 act as reservoirs for generalist predators (Small & Hunter 1988; Andren 1992; Kurki *et al.*
64 1998), increasing the risk of depredation for ground-nesting birds near forest edges and/or
65 driving avoidance of habitat patches associated with forest edges (Douglas *et al.* 2011; Wilson
66 *et al.* 2014). Thus, the links between habitat abundance, quality and/or connectivity and the
67 persistence of a species requires a nuanced understanding of the focal species' ecology. Thus
68 far, afforestation has precipitated the decline of many upland, open-habitat species, including
69 the Hen Harrier (*Circus cyaneus*; O'Flynn 1983).

70 Bird populations can also be negatively affected by temperature (Wingfield 1984) and
71 rainfall (Elkins 1984) mediated by effects on reproductive success related to the
72 thermoregulatory inefficiencies of young chicks (Nye 1964; Elkins 1984) and associated adult
73 brooding behaviour. In cold environments, both chicks and adults may expend more energy
74 counteracting heat loss, leading to greater food demands (Weathers 1979). This can result in
75 adults spending more time foraging (Redpath *et al.* 2002), thus increasing chick vulnerability
76 via exposure or, conversely, substantially increase brooding time which can result in chick
77 mortality via starvation (Beintema & Visser 1989). The effects of cold temperatures may be
78 exacerbated by rainfall as the downy feathers of young chicks are not fully water-repellent; wet
79 chicks lose heat more rapidly than dry chicks (Nye 1964). However, while both temperature
80 and rainfall have been shown to affect Hen Harrier breeding performance (García & Arroyo
81 2001; Redpath *et al.* 2002a; Schipper 1979), their impacts are not consistent across the species'
82 range. For example, Hen Harrier brood size was positively related to temperature in Scotland
83 (Redpath *et al.* 2002a) while the opposite was true in Spain (García & Arroyo 2001). Thus,
84 understanding the relationship between climate and breeding performance in this species
85 requires discrete, region-specific studies.

86 Hen Harriers are medium sized, ground-nesting birds of prey that are widely distributed
87 throughout Eurasia, including the UK and Ireland (Millon *et al.* 2002; Redpath *et al.* 2002;
88 Amar *et al.* 2008; Ruddock *et al.* 2016; Sachslehner *et al.* 2016). Populations have declined
89 across the species' range and they are now a Species of European Conservation Concern
90 (SPEC; Staneva & Burfield, 2017). They are listed under Annex I of the EU Birds Directive
91 (European Council Directive 79/409/EEC) which requires EU Member States protect them
92 where they occur within national boundaries. This includes the designation of Natura 2000
93 sites, or Special Protected Areas (SPAs), as per Article 4 (Directive 2009/147/EC), and the
94 implementation of ongoing monitoring initiatives such as the regular national surveys of

95 breeding Hen Harriers in Ireland (Norriss *et al.* 2002; Barton *et al.* 2006; Ruddock *et al.* 2012;
96 Ruddock *et al.* 2016). Ireland's afforestation goals are ambitious, with forest estate coverage
97 expected to expand from the current 11% of total land cover to 18% by 2046 (National Parks
98 & Wildlife Service 2015). This represents a considerable change in land-use with implications
99 for Hen Harrier conservation, particularly as forest plantations mature and become unusable
100 for nesting and foraging (Picozzi 1978; Wilson *et al.* 2012).

101 Hen Harriers typically utilise upland habitats during the breeding season, often nesting
102 in heather moorlands (Redpath *et al.* 1998; Amar *et al.* 2008; Watson 2017). In areas where
103 their preferred habitat is not available, Hen Harriers are known to utilise other habitats, such as
104 cereal fields and young forest plantations (Millon *et al.* 2002; Sachslehner *et al.* 2016);
105 Ruddock *et al.*, 2016; Wilson *et al.*, 2009, 2012b) where the dense understory provides nesting
106 habitat and foraging opportunities (Redpath *et al.* 1998; Madders 2000). The breeding success
107 of Hen Harriers can be affected by many factors, including food availability (Amar & Redpath
108 2002; Amar *et al.* 2003), predation (Irwin *et al.*, 2012; Ruddock *et al.*, 2016), habitat (Amar *et*
109 *al.* 2008; Wilson *et al.* 2012) and climate (García & Arroyo 2001; Redpath *et al.* 2002).
110 Breeding success rates exhibit considerable spatial variation and the average number of chicks
111 raised to fledging in Ireland is lower than observed in the UK (Fielding *et al.* 2011; Irwin *et al.*
112 2012). The subsequent survival of juveniles, and the proportion of which are recruited into the
113 Irish breeding population, is largely unknown at present.

114 Hen Harriers were once widespread in Ireland until historic habitat loss resulted in
115 substantial reductions in both range and abundance (O'Flynn 1983; Whilde 1993). The
116 population showed some signs of recovery during the mid-20th Century, peaking at a reported
117 200-300 pairs in the 1970s (Watson 2017) though the decline resumed thereafter due to habitat
118 loss and persecution (see Barton *et al.* 2006; Norriss *et al.* 2002; Ruddock *et al.* 2012, 2016).
119 The current Hen Harrier population in Ireland is moderately small, with fewer than 157

120 breeding pairs being recorded in 2015 (Ruddock *et al.* 2016). Thus, the species is of
121 considerable conservation concern in Ireland (Colhoun & Cummins 2013). In 2007, six SPAs
122 were established for Hen Harrier conservation in the Republic of Ireland. Afforestation, forest
123 management, development (e.g. windfarms) and recreational activities are regulated in these
124 areas and they include important breeding habitats such as heather moorland, bogs, rough
125 grassland and young conifer plantations (Wilson *et al.* 2009). However, all SPAs contain
126 considerable forest cover, primarily in the form of non-native conifer plantations (Moran &
127 Wilson-Parr 2015). This is typical of upland areas in Ireland where large tracts of upland
128 habitats have been afforested in recent decades (O'Leary *et al.* 2000).

129 Here we used data derived from national breeding Hen Harrier surveys, together with
130 data on landscape, climate and man-made features to explore local factors affecting the location
131 of breeding-pair territories and landscape-scale factors affecting breeding success and
132 productivity. We hypothesise that: i) Hen Harrier territories will be strongly associated with
133 pre-thicket coniferous forests; ii) breeding performance will be negatively affected by the
134 amount of coniferous forest in the landscape; and iii) the effect of SPAs will be
135 indistinguishable from that of non-designated areas. We discuss our findings in the context of
136 previous work on the habitat associations of Hen Harriers in Ireland and Hen Harrier
137 conservation. Consequently, we provide recommendations regarding habitat management and
138 investigative avenues for future research which would provide a basis for the development of
139 ecologically appropriate conservation and management measures.

140

141 **Materials and methods**

142 ***Data sources and preparation***

143 A total of 668 records collected during national breeding Hen Harrier surveys in Ireland
144 in 2010 and 2015 were provided by the National Parks and Wildlife Service (NPWS). These
145 data were collected by an extensive network of staff, members and volunteers from the NPWS,
146 Irish Raptor Study Group (IRSG), BirdWatch Ireland (BWI) and Golden Eagle Trust (GET),
147 university researchers, as well as independent commercial and voluntary ornithological
148 surveyors working across Ireland (Ruddock *et al.*, 2012, 2016). Two discrete datasets were
149 derived from the raw data. The first was concerned with territory selection and included point
150 data representing centroids of all confirmed territories ($n = 236$; 2010 = 128, 2015 = 108; Fig.
151 1a). The second was concerned with breeding success and productivity ('breeding success',
152 hereafter). Thus, only territory centroids with known nest-success outcomes (i.e. success or
153 failure) were included ($n = 191$; 2010 = 94, 2015 = 97; Fig. 1b). To account for spatial
154 autocorrelation, i.e. clustering of presence records, Moran's I Index scores (Moran 1950) were
155 calculated for each point using the Spatial Analyst function in the ArcGIS toolbox.

156 We investigated the effect of several variables on Hen Harrier territory location and
157 breeding success, including: forest composition (broadleaved or coniferous); coniferous forest
158 age; land class; temperature; rainfall; hilliness; elevation; SPA (inside/outside site boundary);
159 proximity to windfarms; proximity to post-thicket coniferous forest; and proximal road density
160 (Table 1). Data temporally relevant to the 2010 and 2015 Hen Harrier surveys (i.e. nest
161 site/success, climate, weather, forest age) were grouped accordingly. Non-forest land class
162 variables were assumed to be temporally consistent between surveys.

163 Forest data were extracted from the CORINE 2012 Land Cover dataset (European
164 Environment Agency 2016) and were augmented with data from Coillte (public forests in
165 Ireland), NPWS (private forests in Ireland) and the Forest Service Northern Ireland (public and
166 private forests). Forest data were classified by type (broadleaved or coniferous); mixed forest
167 where conifers accounted for $\leq 50\%$ of the total area were classified as broadleaved and mixed

168 forest with >50% conifers were classified as coniferous. Coniferous forests were further
169 divided into three age categories, according to known Hen Harrier nest site selection
170 preferences (Irwin *et al.* 2012; Wilson *et al.* 2012b): i) early (0 – 2 years, post-planting); ii)
171 pre-thicket (3 – 12 years, post-planting); and iii) post-thicket (≥ 13 years, post-planting). Post-
172 thicket forest data were merged with CORINE coniferous data, which represent mature forests.
173 Early and pre-thicket forest data were then erased from the composite CORINE-post-thicket
174 shapefile. The accuracy of derived forest shapefiles in describing total forest coverage was
175 visually assessed via comparison with satellite optical imagery.

176 In order to investigate the effects of land-use, additional, non-forest land cover variables
177 were extracted from the CORINE dataset: two composites (arable; heath/shrub) and four raw
178 variables (bog; natural grassland; pasture; urban; Table 1). Temperature ($^{\circ}\text{C}$) and rainfall (mm)
179 data were downloaded from Met Éireann (<http://www.met.ie>) and the Met Office
180 (<https://data.gov.uk>). Data for 27 weather stations were included, based on the temporal
181 resolution of their data (i.e. weekly measurements). Data for the breeding season, March –
182 August inclusive, were included in the analyses. Rainfall data were further split into two sub-
183 sets according to breeding season stage: early-to-mid breeding season ('early' hereafter; March
184 – May, inclusive) and mid-to-late breeding season ('late' hereafter; June – August, inclusive).
185 Mean weekly rainfall and associated variance were calculated for each period. Temperature
186 measurements were found to be strongly correlated when separated into early and late breeding
187 season sub-sets, therefore derived metrics - minimum weekly temperature and associated
188 variance - spanned the entire breeding season. Variance was taken as a proxy for climatic
189 stability. For example, low daily variance in rainfall would suggest that the amount of rain that
190 fell on a daily basis was temporally consistent. In contrast, high variance could suggest
191 irregular patterns of rainfall or a trend in rainfall over time. Interpolated regularised raster
192 surfaces (Aggrey 2002) grid-based data structures) were constructed at 1km resolution for each

193 climate metric using the Spline function in ArcGIS 10.4.1 (ESRI 2015), giving 100% coverage
194 to the island of Ireland.

195 We used a 30 arc-second Digital Elevation Model (DEM) from NASA's Shuttle Radar
196 Topography Mission (SRTM; <https://eros.usgs.gov/>) to derive elevation data for each point
197 ('elevation'). Shapefiles describing SPA boundaries and the locations of windfarms – given as
198 centroids - across Ireland, correct to 2016, were provided by the NPWS. Road data were
199 downloaded from OpenStreetMap.org (<https://www.openstreetmap.org>). Only *roads*, *link*
200 *roads* and *tracks* were included in our analyses (see
201 <https://wiki.openstreetmap.org/wiki/Key:highway> for more on OSM highway categories), all
202 of which included road types which were present in areas used by Hen Harriers. Road density
203 was calculated as a function of the total length of roads divided by total polygon area (see
204 sections 2.2 and 2.3). Shapefile and raster processing and manipulation were carried out using
205 the statistical program R (R Core Team 2017), particularly the packages *raster* (Hijmans 2017),
206 *rgeos* (Bivand & Rundel 2017), *rgdal* (Bivand *et al.* 2017) and *maptools* (Bivand & Lewin-
207 Koh 2017) and ArcGIS 10.4.1 (ESRI 2015).

208

209 ***Territory selection models***

210 Putative Hen Harrier territories were assessed based on interpretation of (i) nest locations, (ii)
211 Hen Harrier observations, (iii) Hen Harrier activity, and (iv) the behavioural category by which
212 each record was defined during each breeding Hen Harrier survey (see Ruddock *et al.*, 2016).
213 Hen Harrier territory sites were compared to hypothetical territory sites (i.e. pseudoabsences)
214 in the wider landscape to establish the ecological distinctiveness of territories relative to other
215 habitat mosaics. Pseudoabsences (*pal*) were randomly generated within the altitudinal range
216 of confirmed Hen Harrier territories ($n = 500$; 36m – 570m). Each point (i.e. territory or

217 pseudoabsence) was buffered to three distances (Graf *et al.* 2005) – 1 km, 2 km and 5 km - that
218 were chosen to represent variable foraging distances from the nest and to ease comparisons
219 with previous studies (Arroyo *et al.* 2014; Schipper 1977; Wilson *et al.* 2009). Breeding Hen
220 Harriers in Ireland have been reported to travel over 11 km from an active nest, via GPS
221 tracking (Irwin *et al.* 2012) and males in Scotland have been observed travelling up to 9 km
222 from nests (Arroyo *et al.* 2014). However, typical foraging ranges are reported to be much
223 smaller (Arroyo *et al.* 2014). Moreover, the maximum distance travelled from a nest site does
224 not necessarily equate to consistent trends in foraging strategy and may not be representative
225 of typical Hen Harriers in Ireland. Hence, conservative distances were used. The total area of
226 each land cover variable and forest category and road density were calculated within each
227 buffer. The effect of spatial scale was explored by constructing GLMMs for individual
228 variables across all buffers. The most suitable buffer distance for each variable was chosen, *a*
229 *priori*, based on the size of the regression coefficients from these exploratory models; selected
230 scales had the largest coefficients. Euclidean distances were calculated from each point to the
231 nearest windfarm and stand (edge) of post-thicket forest. Elevation (m above sea level) was
232 extracted for each point.

233 Territory selection was examined using binomial, log-linked Generalised Linear Mixed
234 Models (GLMMs) and model weighting using the R packages lme4 (Bates *et al.* 2015) and
235 *MuMIn* (Bates *et al.* 2015). The presence or pseudoabsence of a territory was fitted as the
236 dependent variable; Moran's *I* scores were fitted as a random factor. Predictor variables were
237 tested for multicollinearity, ensuring that Tolerance values were >0.2, Variance Inflation Factor
238 (VIF) values were <10.0 and bivariate correlations had an $r < 0.5$ (Quinn & Keogh 2002).
239 Variables were standardized to have a $\bar{x} = 0$ and $\sigma = 1$ prior to analysis, thus permitting the direct
240 comparison of regression coefficients. We used the Akaike Information Criterion (AIC) to rank
241 all possible model permutations. The top subset of models was defined by the threshold ΔAIC

242 ≤ 2 units (Burnham & Anderson 2002). The model with the lowest Akaike weight (ω_i) was
243 identified as being the best approximating model within the top subset of N models. To
244 determine the relative importance of each variable, the $\Sigma\omega_i$ of all models containing the focal
245 variable within the top subset was calculated (McAlpine *et al.* 2006), where the $\Sigma\omega_i$ of
246 omnipresent variables = 1. The effect size (β coefficient) of each variable was determined via
247 multi-model inference and model averaging (Burnham & Anderson 2002). Variables were
248 ranked, first by $\Sigma\omega_i$, and, secondarily where variables had equal $\Sigma\omega_i$ values, by the magnitude
249 of their regression coefficients. The performance of the best approximating model was assessed
250 using a 60% training set and a 40% test set with 10-fold cross-validation (R package *caret*;
251 Kuhn 2017).

252 Territory records and *pa1* were augmented by an additional set of pseudoabsences (*pa2*)
253 to facilitate inferential exploration of habitat choice via ecological distance analysis. To create
254 *pa2*, we generated 500 randomly-placed points across the remaining Irish landscape, beyond
255 elevational constraints described above. These additional locations provided a broader context
256 for interpretation of ecological distances between territory locations and *pa1*. Principal
257 Component Analysis was used to reduce climate and habitat variables associated with all
258 locations to five hypothetical axes with eigenvalues >1 . We calculated a single measure of
259 ecological, Euclidean distance between groups (territories, *pa1*, *pa2*) in *n*th-dimensional space
260 across all Principal Components simultaneously. Euclidean distances were calculated using the
261 R package *pdist* (Wong 2013) and the base function *dist*.

262

263 ***Breeding performance models***

264 Breeding performance models were constructed to explore factors affecting Hen Harriers at
265 mixed landscape scales using the methods described for territory models (see *Territory*
266 *selection models*, above) but on the subset of territories with known nest success outcomes (i.e.

267 success/failure). Territory centroids were assumed to be nest locations (and are referred to as
268 such, hereafter) based on the best available data. Additional point data for each nest location
269 was extracted for SPA (inside or outside the boundary); minimum temperature; the variance of
270 minimum temperature across the breeding season; mean weekly rainfall in the early breeding
271 season; and mean weekly rainfall in the late breeding season. 86 nests were located inside SPAs
272 with 112 occurring outside SPA boundaries (2010 = 36:65; 2015 = 50:47).

273 Breeding performance was examined using a poisson GLMM; the number of chicks
274 successfully fledged (Fig. 1b) was fitted as the dependent variable and Moran's I was fitted as
275 a random factor. Model construction, selection and evaluation followed the same methods
276 described for territory selection models (see *Territory selection models*, above). In addition,
277 the relative abundance of each habitat was explored across all buffered distances for nest
278 locations and across the total area of each SPA.

279

280

281 3. Results

282 Hen Harrier territory locations exhibited significant spatial autocorrelation ($I = -0.003 \pm 0.005$,
283 $p < 0.0001$; Fig. 2). There was no evidence of site fidelity between years, even assuming that
284 the nearest territories were established by the same pair; 2010 territories were located at least
285 141m ($\bar{x} = 3.80\text{km} \pm 7.61\text{km}$) from the nearest territory in 2015, The top subset ($\Delta\text{AIC} \leq 2$)
286 consisted of 18 models (see Appendix I, Table 1A). The best approximating model for territory
287 site selection was positively influenced by heath/shrub, pre-thicket forest and bog at 1km,
288 indicating that Hen Harrier territories were strongly associated with habitats that ostensibly
289 offer an appropriate nesting environment. There was a negative association with pasture at 2km
290 and with broadleaved woodland at 5km, two habitats that are not typically associated with

291 breeding Hen Harriers. Territories were also positively associated with increased elevation,
292 being found at higher altitudes than *pa1* (Fig. 3). The predictive accuracy of the best-
293 approximating model, assessed via 10-fold cross-validation, was 0.82 (± 0.02).

294 According to single-metric *n*th-dimensional Euclidean distance analyses, territory
295 locations were on average 17% further away from *pa2* than *pa1* and 27% further away than
296 *pa1* and *pa2* were from each other (Fig. 4). This indicates that Hen Harriers are not only
297 utilising upland habitats as territory locations but that they are specifically utilising the
298 landscape according to a narrow range of habitat features.

299 Hen Harrier territory locations with known breeding success outcomes exhibited
300 significant spatial autocorrelation ($I = -0.118 \pm 0.001$, $p = 0.002$). The top subset ($\Delta AIC \leq 2$)
301 consisted of 23 models (Appendix I, Table 1B). The best approximating model for breeding
302 success was negatively influenced by mean weekly rainfall early in the breeding season, mean
303 weekly minimum temperatures and the variance in mean weekly minimum temperature. The
304 direction? of the climatic effects suggests that chicks are most vulnerable to stochastic changes
305 in minimum temperature, possibly exacerbated by rainfall that could cause prolonged chilling,
306 during the early stages of the breeding season. There were positive associations with mean
307 weekly rainfall late in the breeding season, heath/shrub habitat at the 1km scale and bog at
308 2km. Both habitats are typically associated with breeding Hen Harriers elsewhere in the
309 species' range. In contrast to territory analyses, coniferous forest age classes did not feature in
310 the best approximating model for breeding success (Fig. 4). The predictive accuracy of the
311 best-approximating model, assessed via 10-fold cross-validation, was 0.76 (± 0.01).

312

313 4. Discussion

314 Across the 2010 and 2015 Hen Harrier national survey data, the influence of land class and
315 associated parameters on the utilisation of habitats for territories contrasted with their influence
316 on subsequent breeding success and productivity.

317 Hen Harrier territories in Ireland were found to be positively associated with
318 heath/shrub, bog, high elevation and pre-thicket coniferous forest (i.e. 0-2 years old and 3-12
319 years old). The positive association with typically preferred habitat (i.e. bog and heath/shrub),
320 reinforced by breeding success models, emphasises the importance of these habitats for
321 breeding and foraging Hen Harriers (e.g. Redpath *et al.* 1998; Madders 2000; Amar *et al.* 2008;
322 Arroyo *et al.* 2009). There was a particular association with pre-thicket forests (i.e. 0-12 years
323 post-planting). While previous studies at a number of locations across Ireland and the UK have
324 described similar associations with pre-thicket forest (Madders 2000; Barton *et al.* 2006;
325 Wilson *et al.* 2009; O'Donoghue 2010; Irwin *et al.* 2012), this is the first to do so on such a
326 large scale. Pre-thicket forest undergrowth may consist of heather (*Ericaceae* sp.), gorse (*Ulex*
327 sp.) and bramble (*Rubus fruticosus* agg.), providing nest security against potential predators
328 (O'Flynn 1983) and making these areas attractive to breeding Hen Harriers. Utilisation of these
329 habitats by Hen Harriers as described by territory selection models and *n*th dimensional
330 ecological distance analyses may, therefore, be indicative of a lack of more suitable nesting
331 and/or foraging habitat in the wider landscape. Furthermore, areas of ostensibly suitable upland
332 habitat may also be degraded and/or exposed to disturbance via peat extraction (O'Riordan *et*
333 *al.* 2015), over-grazing (Douglas *et al.* 2008), burning or changes to land management (Renou-
334 Wilson *et al.* 2011). These factors may have implications for adult behaviour and subsequent
335 chick survival, creating a potential ecological trap where Hen Harriers select breeding habitats
336 that ultimately result in reduced fitness (Schlaepfer *et al.* 2002). This was previously reported
337 at one study site in Ireland (Slieve Aughty SPA; Wilson *et al.* 2012b). The current study shows
338 that this phenomenon may be occurring across the island of Ireland, on a much wider scale,

339 and with greater implications for Hen Harrier populations, than previously thought. Further
340 afforestation of open upland areas and maturation of the existing forest estate will result in
341 further fragmentation of foraging habitat, decreasing the overall landscape suitability for
342 breeding Hen Harriers and ultimately impacting on breeding success.

343 The location of nests relative to SPA boundaries (i.e. inside or outside) was consistently
344 retained across the top subset of breeding success models, including the best approximating
345 model. This is the first scientific evidence that the best areas for Hen Harriers were selected
346 during the SPA designation process. Proposed interventions within SPAs (e.g. road
347 construction, clear-felling, afforestation) are subject to a suite of regulations in Ireland, many
348 of which are aimed at mitigating disturbance of breeding Hen Harriers in high sensitivity areas
349 (i.e. 'Red Areas', NPWS 2015). The apparent success of SPAs in facilitating greater breeding
350 success appears to be skewed by increased success in locations where heather and moorland
351 nesting and foraging habitats may be of higher quality and/or less fragmented. It is important
352 to note, however, that over 50% of the breeding Hen Harrier population was located outside of
353 the six breeding Hen Harrier SPAs during both survey years and that the Hen Harrier
354 population in the SPA network has declined over this time (Ruddock *et al.* 2012, 2016). The
355 value of the wider countryside to Hen Harrier conservation is twofold. First, a species with a
356 wider breeding range will be more robust to pressures acting at a site level. Second, it is
357 possible that, due to the maturation of the forest estate in Ireland combined with other pressures
358 in SPAs, the breeding population could drop below a critical level. A sufficiently large and
359 persistent population outside of the SPA network could improve the recolonization potential
360 for those SPAs that are at risk of local extinctions. It is essential, therefore, that conservation
361 initiatives aimed at bolstering Hen Harrier populations in Ireland embrace a landscape-scale
362 approach and do not focus on SPAs alone.

363 Hen Harrier breeding success and productivity were affected by temperature and
364 climatic instability (i.e. the variation in minimum temperature) throughout the breeding season
365 and by rainfall in the early breeding season. The mechanisms by which temperature and rainfall
366 influence Hen Harrier breeding success are unclear at present, as studies elsewhere in the
367 species' range reveal regionally variable effects (e.g. García & Arroyo 2001; Redpath *et al.*
368 2002a; Schipper 1979). This suggests that climate may be masking discrete ecological and
369 behavioural phenomena. For example, poor foraging opportunities in the surrounding
370 landscape may be placing a larger provisioning burden on both parents who consequently have
371 to travel greater distances to find food (e.g. see flight distances in Irwin *et al.* 2012). Decreased
372 parental attendance may also result in greater vulnerability of eggs and chicks to predation.
373 Potential predators of Hen Harrier nests in Ireland include red foxes (*Vulpes vulpes*), badgers
374 (*Meles meles*), pine martens (*Martes martes*), American minks (*Neovison vison*), stoats
375 (*Mustela erminea*), buzzards (*Buteo buteo*), ravens (*Corvus corax*) and hooded crows (*Corvus*
376 *corone corvix*). Such predators are often more abundant in fragmented habitats (Andren 1992;
377 Kurki *et al.* 1998) and can have substantial negative impacts on ground-nesting birds (Paton
378 1994; Fletcher *et al.* 2010). Foxes and pine martens have been observed depredating Hen
379 Harrier chicks in studies using remote-sensing camera traps (Irwin *et al.* 2012; Monaghan
380 2015; Ruddock *et al.* 2016; Fernández-Bellon *et al.* 2017). Furthermore, increased rainfall may
381 place an additional thermoregulatory burden on young chicks via increased metabolic costs
382 and greater food demands (Weathers 1979; Olsen & Olsen 1992; Redpath *et al.* 2002). These
383 impacts could be exacerbated by the stochastic effects of an increasingly unpredictable climate
384 such that young chicks are rendered particularly vulnerable to chilling during the coldest
385 periods. Thus, the synergistic effects of reduced parental attendance, increased predation risk
386 and increased energetic demands of exposed chicks via unsupported thermoregulation could

387 go some way to explaining the observed impacts of climate on Hen Harrier breeding success
388 in the current study.

389 Our findings have implications for the long-term viability and security of Hen Harrier
390 populations in Ireland under continued land use change and future climate change. The early
391 months of the Hen Harrier breeding season are predicted to get increasingly warmer and wetter
392 under future climate change scenarios, while summer months (i.e. late breeding season) will
393 be drier (Gleeson *et al.* 2013). Many studies have demonstrated the impacts of climate change
394 on breeding birds via several mechanisms, including egg-laying phenology (Crick *et al.* 1997;
395 Geyer *et al.* 2011), disease (Benning *et al.* 2002) and changes in prey availability (e.g. Pearce-
396 Higgins 2010). For example, a decline in the availability of upland invertebrates can lead to
397 reduced productivity of insectivorous passerine species which comprise a large proportion of
398 the Hen Harrier's diet. Such phenological mismatches, along with other changes in species
399 interactions, may be among the most important negative impacts of climate change (Cahill *et*
400 *al.* 2012). Furthermore, climate change impacts may be exacerbated by changes in land
401 management that could simultaneously reduce the proportion of suitable foraging habitat in the
402 landscape (e.g. Kleijn *et al.* 2010). It is therefore imperative that the potential impacts of
403 climate change on Irish Hen Harrier breeding performance and distribution are mitigated using
404 long-term conservation strategies.

405

406 Hen Harriers in Ireland currently face an uncertain future. Rainfall and climatic
407 instability early in the breeding season were found in this study to have strong negative effects
408 on subsequent breeding success, suggesting that the population is at further risk under future
409 climate change. Hen Harriers in this study preferentially selected pre-thicket coniferous forests,
410 that provide nesting and foraging opportunities, for territory locations. However, this habitat

411 was also negatively associated with breeding success. Given our understanding of Hen Harrier
412 ecology, including factors known to affect productivity, it seems likely that there are synergistic
413 effects across and between climate, landscape composition and management, parent and chick
414 behaviour, and predation that are resulting in egg and/or chick mortality and, hence, negatively
415 impacting breeding success and, consequently, population levels. The cumulative effects of
416 climate, habitat, parental attendance, prey abundance and predation result in reduced
417 availability of optimum nesting and foraging habitat at the landscape scale. Afforestation of
418 upland areas, along with maturation of the existing 'usable' forest estate, therefore pose the
419 greatest threats to the ecological security of Hen Harriers in Ireland while pre-thicket conifer
420 plantations represent an ecological trap, attracting breeding pairs to a sub-optimal landscape.
421 An optimal habitat mosaic would offer nest concealment and protection from predators and
422 sufficient prey to support near-nest foraging throughout the critical stages of the breeding
423 season. Furthermore, it is clear that while some SPAs benefit breeding Hen Harriers, the
424 majority of the breeding population are found outside of the SPA network and the population
425 within the SPA network has declined, making the conservation of the species in a broader
426 context more important than ever before. Effective conservation of Hen Harriers in Ireland
427 therefore relies on landscape-scale initiatives, including the creation /restoration of suitable
428 nesting and breeding habitat and protection for this species within and beyond the boundaries
429 of the SPA network.

430

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443

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Appendices

Appendix I

Table A1. Generalised Linear Mixed Model (GLMM) results for variables affecting Hen Harrier territory site selection. Models within the top subset of n models ($\Delta\text{AIC} < 2$) are given. t = confirmed territory/pseudoabsence; a = arable (5km); b = bog (1km); bf = broadleaved forest (5km); df = distance to mature coniferous forest; dw - distance to windfarm; e = elevation; ef = coniferous forest (0-2 years post-planting; 1km); h = heath/shrub (1km); lf = coniferous forest (13+ years; 1km); m = Moran's I (random factor to account for spatial autocorrelation); n = natural grassland (5km); p = pasture (5km); pf = coniferous forest (3-12 years; 1km); r = road density. Models were ranked according to their Akaike's Information Criterion (AIC) value; the best approximating (i.e. top-ranked) model is given in bold.

Formula	AIC	ΔAIC
$t \sim bf + b + ef + e + h + p + pf + (m)$	416.09	0.00
$t \sim b + ef + e + h + p + pf + (m)$	416.19	0.10
$t \sim bf + b + ef + e + h + p + pf + (m)$	416.22	0.13
$t \sim bf + b + ef + e + df + h + p + pf + (m)$	416.23	0.14
$t \sim bf + b + ef + e + n + h + p + pf + (m)$	416.24	0.15
$t \sim b + ef + h + p + pf + (m)$	416.50	0.41
$t \sim b + ef + e + lf + h + p + pf + (m)$	416.78	0.69
$t \sim b + ef + lf + n + h + p + pf + (m)$	416.83	0.74
$t \sim bf + b + ef + e + lf + h + p + pf + (m)$	417.03	0.94
$t \sim b + ef + e + h + p + pf + (m)$	417.41	1.32
$t \sim a + bf + b + ef + df + lf + h + p + pf + (m)$	417.42	1.33
$t \sim a + bf + b + ef + h + p + pf + (m)$	417.44	1.35
$t \sim b + ef + e + df + h + p + pf + (m)$	417.53	1.44
$t \sim b + ef + lf + n + h + p + pf + (m)$	417.55	1.46
$t \sim bf + b + ef + e + df + lf + h + p + pf + (m)$	417.89	1.80
$t \sim bf + b + ef + n + h + p + pf + dw + (m)$	417.92	1.83
$t \sim b + ef + n + h + p + pf + r + (m)$	418.02	1.93
$t \sim bf + b + ef + e + df + lf + n + h + p + pf + (m)$	418.05	1.96

Table 2A. Generalised Linear Mixed Model (GLMM) results for variables affecting Hen Harrier breeding success. Models within the top subset of n models ($\Delta\text{AIC} < 2$) are given. c = breeding success (i.e. number of chicks successfully raised to fledging); a = arable (5km); b = bog (2km); bf = broadleaved forest (2km); df = distance to mature coniferous forest; dw = distance to windfarm; e = elevation; ef = coniferous forest (0-2 years post-planting; 5km); h = heath/shrub (1km); lf = coniferous forest (13+ years; 5km); m = Moran's I (random factor to account for spatial autocorrelation); n = natural grassland (2km); p = pasture (5km); pf = coniferous forest (3-12 years; 2km); r = road density; re = rain early in the breeding season; rl = rain late in the breeding season; s = inside/outside Special Protection Areas (SPA); t = minimum weekly temperature; tv = variance in minimum weekly temperature. Models were ranked according to their Akaike's Information Criterion (AIC) value; the best approximating (i.e. top-ranked) model is given in bold.

Formula	AIC	ΔAIC
$c \sim b + e + h + t + tv + re + rl + (m)$	580.26	0.00
$c \sim b + ef + e + h + t + tv + pf + re + rl + s + (m)$	580.45	0.19
$c \sim bf + ef + e + h + t + tv + re + rl + (m)$	580.69	0.43
$c \sim b + dl + ef + e + h + p + re + rl + (m)$	580.73	0.47
$c \sim b + bf + ef + t + tv + re + rl + (m)$	581.10	0.84
$c \sim dw + h + t + p + re + rl + (m)$	581.14	0.88
$c \sim b + dw + e + lf + t + tv + p + pf + re + rl + (m)$	581.15	0.89
$c \sim bf + dw + h + t + tv + p + pf + re + rl + s + (m)$	581.25	0.99
$c \sim dw + e + h + t + tv + re + rl + s + (m)$	581.32	1.06
$c \sim b + bf + ef + lf + h + t + n + re + rl + r + s + (m)$	581.39	1.13
$c \sim a + b + ef + t + n + re + rl + (m)$	581.42	1.16
$c \sim a + bf + e + h + t + re + rl + r + (m)$	581.42	1.16
$c \sim b + bf + dw + e + tv + re + rl + r + s + (m)$	581.49	1.23
$c \sim a + b + e + h + t + tv + re + r + (m)$	581.51	1.25
$c \sim a + b + ef + lf + h + t + tv + p + re + rl + (m)$	581.51	1.25
$c \sim b + dl + dw + ef + h + t + p + pf + re + rl + (m)$	581.57	1.31
$c \sim a + dl + dw + e + h + t + tv + pf + re + rl + s + (m)$	581.77	1.51
$c \sim b + dw + e + lf + t + tv + p + re + rl + (m)$	582.01	1.75
$c \sim a + b + dl + lf + t + tv + re + r + s + (m)$	582.05	1.79
$c \sim a + b + dw + ef + e + h + n + re + rl + r + (m)$	582.07	1.81
$c \sim bf + dl + ef + e + lf + h + tv + pf + re + rl + r + s + (m)$	582.12	1.86
$c \sim a + b + bf + dl + dw + ef + h + t + tv + p + re + rl + r + s + (m)$	582.12	1.86
$c \sim a + b + bf + dw + e + lf + h + t + n + p + re + rl + r + (m)$	582.20	1.94

Table 1. Variables used in Hen Harrier territory site selection and breeding performance models. ‘Raw’ variables were not manipulated prior to analyses. Variables are listed according to the order in which they occur in the main text. References are given to support the inclusion of each variable.

Variable	Data product	Manipulation	Source	References
Broadleaved forest	Polygon data	Raw	Coillte; NPWS; Forest Service Northern Ireland	Moran & Wilson-Parr 2015
Coniferous forest	Polygon data	Raw	Coillte; NPWS; Forest Service Northern Ireland	Madders 2000; Wilson <i>et al.</i> 2009; Wilson <i>et al.</i> 2012; Sachslehner <i>et al.</i> 2016
Arable	Polygon data	Composite data: Complex cultivation patterns; land principally occupied by agriculture; non-irrigated arable land	CORINE	Wilson <i>et al.</i> 2012; Feys <i>et al.</i> 2013; Sachslehner <i>et al.</i> 2016; Geary, Haworth & Fielding 2018
Heath/shrub	Polygon data	Composite data: Moors and heathland; sparsely vegetated areas; transitional woodland shrub	CORINE	Madders 2000; Amar & Redpath 2004; Cormier <i>et al.</i> 2008; Arroyo <i>et al.</i> 2009; Wilson <i>et al.</i> 2012
Bog	Polygon data	Raw	CORINE	Madders 2000; Arroyo <i>et al.</i> 2009; Irwin <i>et al.</i> 2011; Wilson <i>et al.</i> 2012
Natural grassland	Polygon data	Raw	CORINE	Madders 2000; Amar & Redpath 2004; Arroyo <i>et al.</i> 2009; Wilson <i>et al.</i> 2012
Pasture	Polygon data	Raw	CORINE	Madders 2000; Amar & Redpath 2004; Arroyo <i>et al.</i> 2009; Wilson <i>et al.</i> 2012
Urban	Polygon data	Raw	CORINE	Tapia, Dominguez & Rodriguez 2004
Temperature	Point data	Interpolated raster	Met Éireann; Met Office	García & Arroyo 2001; Redpath <i>et al.</i> 2002

Rainfall	Point data	Interpolated raster	Met Éireann; Met Office	García & Arroyo 2001; Redpath <i>et al.</i> 2002
Elevation DEM	Surface raster	Raw	NASA	Geary <i>et al.</i> 2018
SPA boundaries	Polygon data	Raw	NPWS	Ruddock <i>et al.</i> 2012; Moran & Wilson-Parr 2015; Ruddock <i>et al.</i> 2016
Roads	Polyline data	Raw	OpenStreetMap	Tapia <i>et al.</i> 2004
Windfarms	Point data	Raw	NPWS	Fernández-Bellon <i>et al.</i> 2015; Wilson <i>et al.</i> 2017
Hen Harrier territories	Point data	Raw	NPWS	Ruddock <i>et al.</i> 2012; Ruddock <i>et al.</i> 2016

Legends to figures

Figure 1. (a) Confirmed territory locations and (b) mean productivity (number of chicks fledged) of Hen Harriers in Ireland in 2010 and 2015, combined.

Figure 2. Relative importance of variables in explaining the locations of confirmed Hen Harrier territories relative to pseudoabsences at multiple spatial scales (1 km, 2 km and 5 km, selected *a-priori*), except for elevation which was extracted at each point location. D_{-} = distance to. Variables were ranked according to the sum of their Akaike weights within the top set of models ($\Delta AIC < 2$). Black bars indicate variables that were present in the best approximating model; white bars indicate variables otherwise included in the top subset. Standardised coefficients \pm SEs and p values are given to the right, where * = $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$. The inset plot describes model accuracy as evaluated using randomly split 60:40 training:test datasets with 10-fold cross-validation.

Figure 3. Euclidean distances (\pm 1SD) across five Principal Component scores for pairwise combinations Hen Harrier territory locations (t), upland pseudoabsences (pa1) and pseudoabsences distributed across the rest of Ireland (pa2).

Figure 4. Relative importance of variables in explaining the breeding success of nesting Hen Harriers at multiple spatial scales (1 km, 2 km and 5 km, selected *a-priori*). Variables were ranked according to the sum of their Akaike weights within the top set of models ($\Delta AIC < 2$). Black bars indicate variables that were present in the best approximating model; white bars indicate variables otherwise included in the top subset. Standardised coefficients \pm SEs and p values are given to the right, where * = $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$. The inset plot describes model accuracy as evaluated using randomly split 60:40 training:test datasets with 10-fold cross-validation.

Figure 5. (a) Habitat composition of Special Protection Areas (SPAs) in Ireland which contained (b) successful Hen Harrier nests (i.e. produced ≥ 1 fledged chick) in 2010 and 2015. Natural grassland was omitted as it comprised a small fraction of available habitats across all SPAs. MMM = Mullaghanish to Musheramore Mountains; SAM = Slieve Aughty Mountains SPA; SBe = Slieve Beagh; SBM = Slieve Bloom Mountains; SMW = Stacks to Mullaghareirk Mountains, West Limerick Hills and Mount Eagle; SSM = Slievefelim to Silvermines Mountains. SPA areas were derived from the NPWS SPA shapefile 2017_06.

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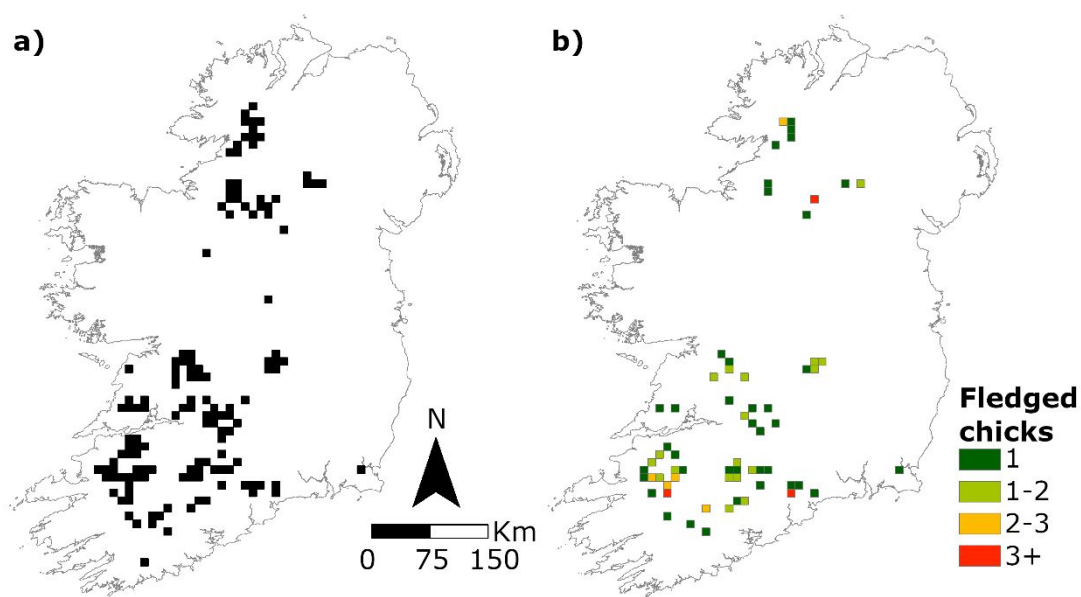


Figure 1.

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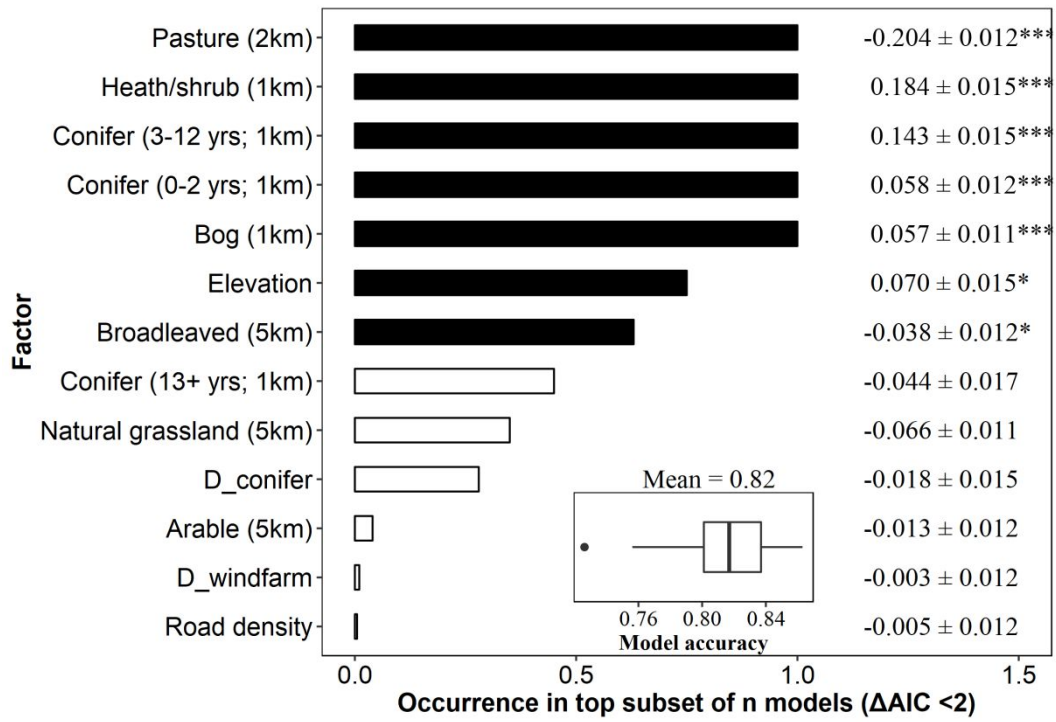


Figure 2.

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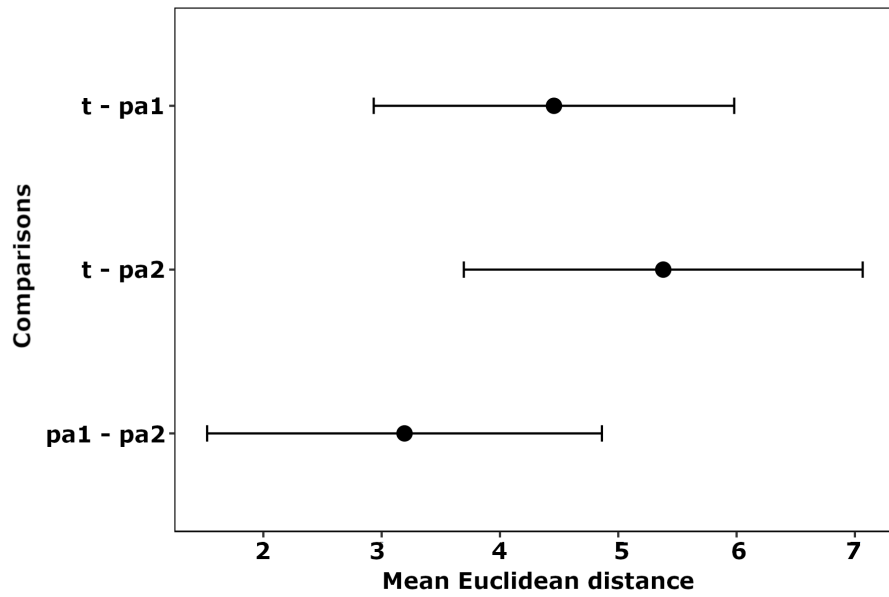


Figure 3.

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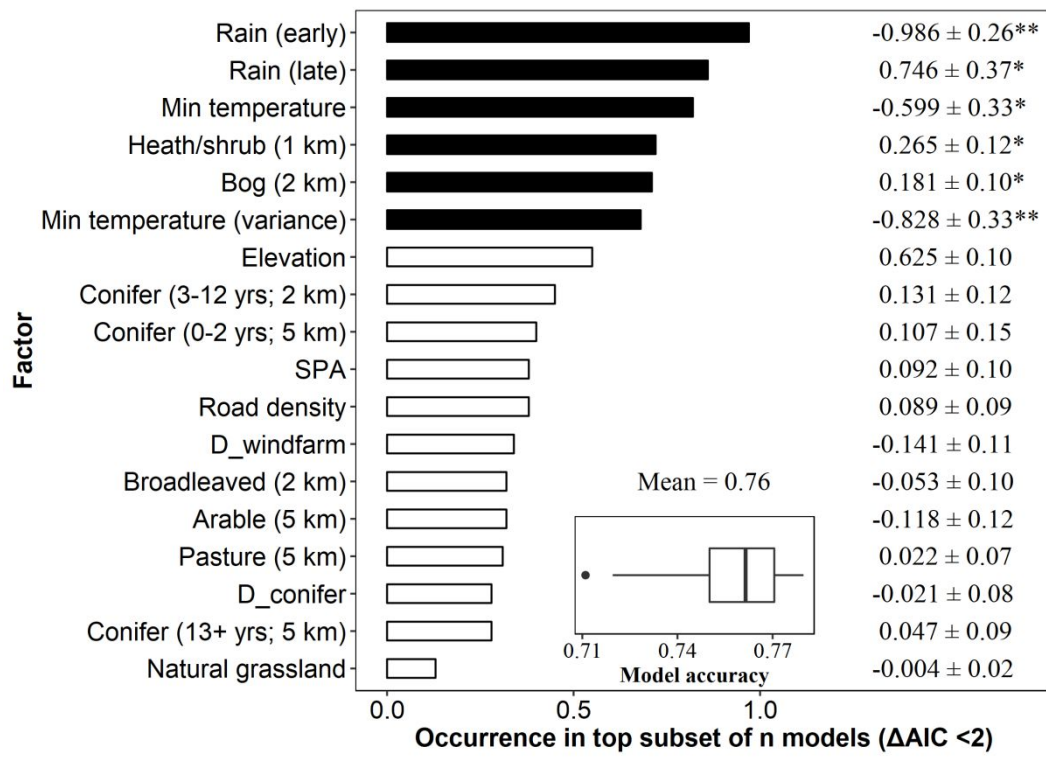


Figure 4.

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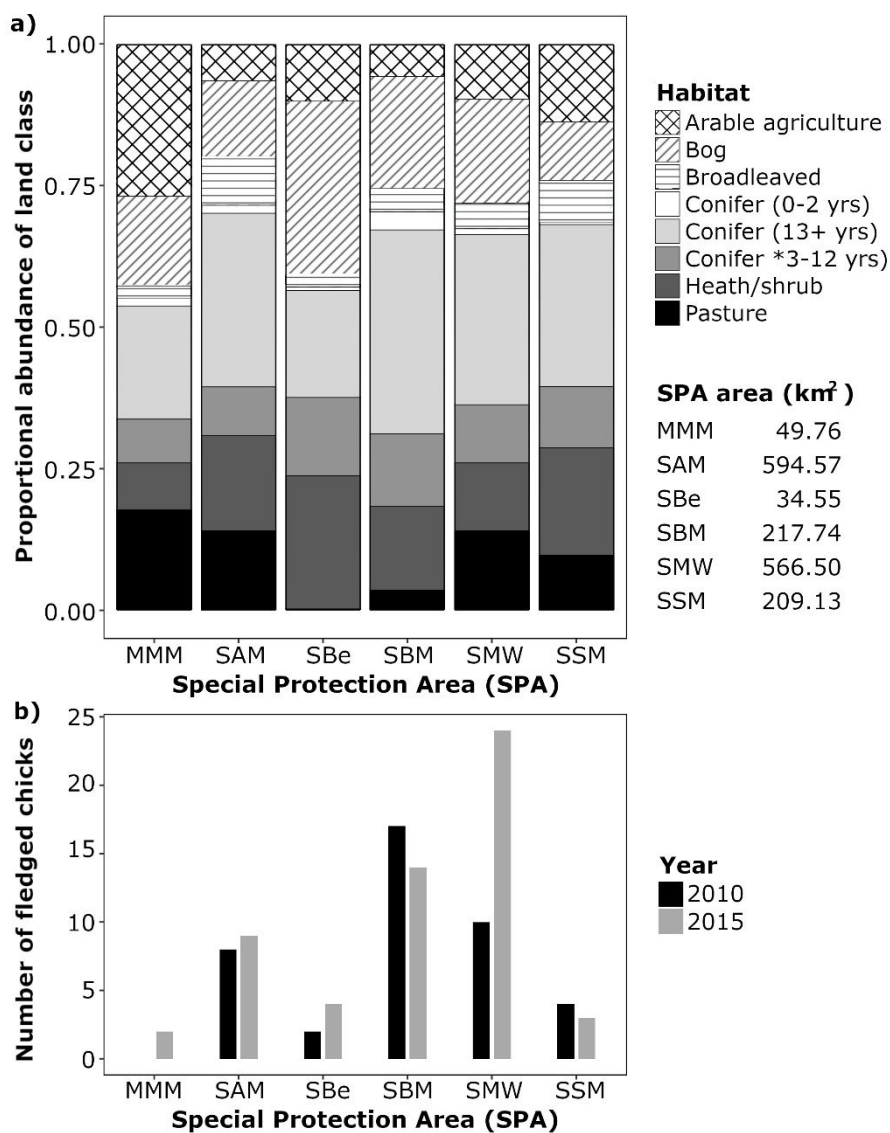


Figure 5.

