



## Article (refereed) - postprint

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1 **Title:** The relative value of field survey and remote-sensing for biodiversity assessment

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27 **Summary**

28 1. The importance of habitat for biodiversity is well established but the two most commonly used  
29 methods to measure habitat (field survey and remote-sensing) have seldom been explicitly compared.

30 2. We compare high resolution sample-based field survey (Countryside Survey) with medium  
31 resolution remote-sensed habitat data (the highest resolution of Land Cover Map available) for Great  
32 Britain. Variation in abundance of 60 bird species from 335 1 km squares was modelled using habitat  
33 predictors from the two methods. Model comparisons assessed the explanatory power of (a) field  
34 survey versus remote-sensed data and (b) coarse information on habitat areas (Broad Habitats) versus  
35 fine grained information on Landscape Features.

36 3. Field survey data (combining Broad Habitat and Landscape Feature predictors) explained more  
37 variation in bird abundance than remote-sensed data (comprising Broad Habitat predictors only) for  
38 57 species and had significantly higher mean explanatory power, averaged across 60 species models.  
39 The relative explanatory power of remote-sensing, as a proportion of that provided by field data, was  
40 measured at 74%, averaged across 60 species models. Predictions from field survey Broad Habitat data  
41 were more accurate than those from either remote-sensed Broad Habitat data, or field survey  
42 Landscape Feature data, averaged across 60 species models.

43 4. High resolution data generate more reliable models of predicted local population responses to  
44 land use change than lower resolution remote-sensing data. Collection of field data is typically costly  
45 in time, labour and resources, making use of remote-sensing more feasible for assessment at larger  
46 spatial extents if data of equivalent value are produced, but the cost-benefit threshold between the  
47 two is likely to be context-specific. However, integration of field survey with remote-sensed data  
48 provides accurate predictions of bird distributions, which suggests that both forms of data should be  
49 considered for future biodiversity surveys.

50

51 **Key-words:**

52 Bird abundance, Broad Habitats, habitat association modelling, land use survey methods, landscape

53 composition, landscape features, predictive model, spatial resolution

54

## 55 **Introduction**

56 Land-use is a major factor influencing biodiversity (Benton, Vickery, & Wilson 2003; Foley *et al.* 2005),  
57 making land-use change (through impacts to land cover in natural and human-modified landscapes)  
58 an important potential driver of species' declines (Butchart *et al.* 2010). Identification of land-use  
59 impacts on biodiversity requires spatially and temporally matched data on habitat and species  
60 distributions (Kerr & Ostrovsky 2003; Turner *et al.* 2003; Rose *et al.* 2014). Biodiversity-habitat  
61 association studies are likely to be most informative for environmental management when examining  
62 relationships at high resolution (where the minimum area of habitat units measured is low, therefore  
63 giving fine spatial grain), but over large geographic areas (Whittingham *et al.* 2007; Brambilla *et al.*  
64 2009; Rose *et al.* 2014). Analyses of this type have the potential to reflect assemblage responses to  
65 habitats at multiple scales (Blackburn & Gaston 2002), including scales relevant both biologically and  
66 for management administration (Mattison & Norris 2005). Despite this, pragmatic trade-offs result in  
67 a tendency for high resolution biodiversity-habitat analyses to cover relatively small areas  
68 (Whittingham *et al.* 2005), while larger scale (hereafter meaning 'spatial extent') studies typically have  
69 lower resolution (Siriwardena, Cooke, & Sutherland 2011; Rose *et al.* 2014). Funding limitations favour  
70 cost-effective solutions to habitat data requirements. Improved understanding of the comparative  
71 strengths and weaknesses of alternative forms of habitat data available at national scales would  
72 facilitate optimal resource allocation for research (Kerr & Ostrovsky 2003; Turner *et al.* 2003; Rose *et*  
73 *al.* 2014).

74

75 We compared high resolution (hereafter meaning resolution in terms of both spatial grain and habitat  
76 classification), nationally representative field survey data for Great Britain (Countryside Survey 2000)  
77 with lower resolution, remote-sensed data (Land Cover Map 2000), at the same spatial extent, for  
78 assessment of bird-habitat associations. The explanatory power of field data and remote-sensed data

79 in models of spatial variation in abundance of 60 bird species across Great Britain was assessed. The  
80 design aimed to test and quantify the improvement in predictions generated by field survey data, over  
81 and above those yielded using remote-sensed data, as a result of the higher resolution and accuracy  
82 of habitat mapping and classification in field survey (Saveraid *et al.* 2001). Such comparisons are rarely  
83 possible because field survey (habitats and birds) and remote-sensed habitat data collected at  
84 comparable spatial and temporal scales are scarce. The relative value of the two methods for  
85 predicting large scale patterns has yet to be assessed (Müller & Brandl 2009).

86

87 Field survey has traditionally been the main method of detailed habitat assessment (Rodwell 2006;  
88 Fuller 2012), informing about land-use impacts on a variety of taxa (Aviron *et al.* 2005; Whittingham  
89 *et al.* 2005). Field survey can be used to record habitat types based on plant species composition and  
90 its resolution is limited mainly by human expertise for field measurement of habitats and the effort  
91 required. Accurate, high resolution habitat data are produced, but typically demand considerable  
92 resources (Kerr & Ostrovsky 2003) and may pose prohibitive logistical challenges at large scales  
93 (Müller & Brandl 2009).

94

95 Remote-sensing (from satellites or airborne sensors) is developing as a method for habitat assessment  
96 with a variety of imagery becoming available (Turner *et al.* 2003; Recio *et al.* 2013; Shirley *et al.* 2013).  
97 Large scale remote-sensing data tend to be lower in resolution (Rose *et al.* 2014), while higher  
98 resolution sources such as lidar are typically unavailable at national scales (Simonson, Allen & Coombes  
99 2014). Many sources of remote-sensed imagery such as Landsat (Fuller *et al.* 2005; Shirley *et al.* 2013),  
100 Google Earth (Hughes, Martin & Reynolds 2011) and lidar (Simonson, Allen & Coombes 2014), are  
101 available in raster format, which requires considerable processing effort to produce vector (polygon)  
102 formats suitable for analysis. Novel remote-sensed imagery has great potential for use in biodiversity  
103 modelling, but methods to convert raw pixel information into usable data on habitats or management  
104 require development (Shirley *et al.* 2013; Shereen, Bonthoux & Balent 2014). Here we use Land Cover

105 Map 2000, which has a resolution of >0.5 ha, because bird data and field data were available for the  
106 same period.

107

108 Remote-sensing at large scales may be more cost-effective than field survey for timely collection of  
109 large scale habitat data (Gould 2000; Kerr & Ostrovsky 2003; Turner *et al.* 2003; Fuller *et al.* 2005), but  
110 tends to result in lower spatial resolution than field survey, being constrained by the pixel size of the  
111 imagery used and the lack of spectral difference between particular habitat types (Kerr & Ostrovsky  
112 2003; Turner *et al.* 2003). Habitat classification by remote-sensing is indirect (based on reflectance of  
113 lasers or light) and spectral confusion can reduce accuracy (Kerr & Ostrovsky 2003; Turner *et al.* 2003).  
114 We hypothesised that field data, highly resolved in both spatial grain and habitat classification, would  
115 better predict bird abundance than lower resolution remote-sensing.

116

117 Broad classifications of habitat at the field scale (hereafter referred to as Broad Habitats), including  
118 land cover categories of human-modified (e.g. arable), semi-natural (e.g. dwarf shrub heath), and  
119 natural (broadleaved woodland) landscapes, are routinely collected by both field survey and remote-  
120 sensing (Howard *et al.* 2003; Morton *et al.* 2011). Features of habitat measured at high resolution  
121 (referred to here as Landscape Features) including hedges and individual trees (trees outside typical  
122 woodland habitat), are recorded by field survey but, although raster photographic data frequently  
123 capture images of both hedges and individual trees, interpretation to identify them has yet to be done  
124 for Great Britain (Tebbs & Rowland 2014). The inclusion of Landscape Features is one factor  
125 contributing to the high resolution of field surveys relative to some large scale remote-sensing  
126 products. Broad Habitats typically cover a larger proportion of land surface area than Landscape  
127 Features (Fuller *et al.* 2002; Firbank *et al.* 2003). Broad Habitat definitions may incorporate  
128 information on multiple habitat types, for example broadleaved woodland describes a guild of tree  
129 species, but do not discriminate features including characteristic understory flora, woodland rides and  
130 glades, which may be important components of a habitat matrix. Conversely, the broad habitat matrix

131 may have a stronger influence on breeding birds. We hypothesised that Broad Habitats would be more  
132 important for determining bird abundance than Landscape Features (Siriwardena, Cooke, &  
133 Sutherland 2011).

134

135 This article tests the following hypotheses about how data perform in predicting spatial variation in  
136 bird abundance:

- 137 1. High resolution field data will outperform lower resolution remote-sensed data, due to the  
138 combined effects of more accurate Broad Habitat data from field survey and the inclusion of  
139 Landscape Features as additional variables unavailable in the remote-sensed data.
- 140 2. Broad Habitats (from field data or remote-sensing) will outperform Landscape Features (from  
141 field data).

142 The outcomes will provide valuable information on the advantages and constraints of the use of  
143 different data types for objective decision making about landscape management to put against  
144 resource and scaling considerations.

145

## 146 **Materials and methods**

147 DATA

### 148 *Field Survey Habitats (Countryside Survey)*

149 Field data on total land cover (including Broad Habitats and Landscape Features) were collected across  
150 a randomly stratified sample of 569 1km squares, targeting rural land in Great Britain in 1998/1999 as  
151 part of Countryside Survey 2000 (Howard *et al.* 2003). A subset of data from 335 squares, where  
152 breeding bird surveys took place, was used for the current analysis (see *Breeding bird survey* and *Bird*  
153 *abundance response variables* below). Field surveyors mapped and described land cover by  
154 combinations of points, lines and polygons, at a scale of approximately 1:5500 (Howard *et al.* 2003),  
155 identifying land cover for every parcel within the square. All features present in non-urban areas above  
156 minimum length (<20m), area (0.04 ha) and point (individual trees diameter at breast height >5cm)

157 criteria were mapped. The Broad Habitat classification was based on hierarchical nomenclature  
158 corresponding to the Joint Nature Conservation Committee (JNCC) Broad Habitats, which  
159 encompasses the entire range of UK habitats (Jackson 2000; Howard *et al.* 2003; Norton *et al.* 2012).

160

#### 161 *Remote-sensed Habitats (Land Cover Map)*

162 Remote-sensed land cover data were obtained from Land Cover Map 2000, a UK-wide satellite-based  
163 survey (Fuller *et al.* 2002). Land cover was derived from satellite scenes recorded during ‘winter’  
164 (October 1997 to April 1998) and ‘summer’ (mid-May to August 1998) periods. The main sensor was  
165 Landsat, which identified coarse segments (>0.5 ha). Interpretative work trained a computer  
166 classification system to assign polygons to ‘22 classes based on Broad Habitats’ (Jackson 2000; Fuller  
167 *et al.* 2002). Landscape Feature data were not available from remote-sensing. Data were extracted for  
168 the 335 1km squares for which contemporaneous field data were available, allowing direct  
169 comparison between the data sets.

170

#### 171 *Habitat Predictor Variables*

172 A subset of habitat variables were considered for inclusion in models based on *a priori* knowledge of  
173 habitats predicted to influence breeding birds (Siriwardena, Cooke, & Sutherland 2011). The subset  
174 comprised 15 out of 27 classes based on Broad Habitats available in both field data and remote-  
175 sensing: broadleaved/mixed woodland, coniferous woodland, arable and horticulture, improved  
176 grassland, neutral grassland, calcareous grassland, acid grassland, bracken, dwarf shrub heath, fen  
177 marsh swamp, bog, standing open water and canals, montane habitats, inland rock, built up areas and  
178 gardens (Table S1). Two Broad Habitats were not considered: ‘boundary and linear features’ (due to  
179 lack of data and inconsistencies in recording) and ‘rivers and streams’ (remote-sensed data for this  
180 category could not be distinguished from the Broad Habitat ‘standing open water’). The habitat  
181 classification ‘sea’ was used as a proxy for any of the ten coastal habitat classifications to make the  
182 study tractable. The Landscape Features considered were drawn from the variables available in the



183 field data, where these matched habitats described as important for birds in the literature (Table S1  
184 displays the variables used for 60 species analyses). To avoid inclusion of large numbers of predictor  
185 variables for which sample sizes were low, Landscape Features were considered for inclusion only if  
186 they were present in 10% or more of the 335 squares sampled. Landscape Features considered  
187 included linear (bank, ditch, dry stone wall, fence, stream, woody linear feature) and point (pond,  
188 scrub, tree) features. Three Landscape Feature composites, 'woody linear feature' (hedges, lines of  
189 trees, and belts of trees), 'ditch' (roadside ditches and other ditches) and 'bank' (stone and earth  
190 banks), were considered (see '*Hypotheses*' below, Cramp and Simmons 2006).

191

192 For subsequent use as model covariates, habitat and landscape feature variables were summed at the  
193 1km square level as: area of cover in m<sup>2</sup> (Broad Habitat areas); the sum of length in metres (linear  
194 features); and counts (point features). These values are likely to reflect habitats potentially used by  
195 many bird species breeding in the square, given the mobility of birds and typical territory sizes; a 1 km  
196 square could be occupied by multiple breeding pairs for the majority of the bird species considered.  
197 Potential model covariates, as listed above, were centred by subtracting the sample mean and scaled  
198 by dividing by the sample standard deviation (Schielezeth 2010).

199

#### 200 *Breeding Bird Surveys*

201 Breeding bird surveys were carried out between April and June 2000 on the sample of 335 1km squares  
202 for which habitat data was measured (Wilson & Fuller 2002). Bird counts were recorded along  
203 transects in three distance bands by skilled contract workers or volunteers (Gregory & Baillie 1998;  
204 Wilson & Fuller 2002). Four separate transects were covered per square on each of two visits (April to  
205 mid-May and mid-May to June), giving representative coverage of habitats in each square that was  
206 more intensive than the two-transect method used in the BTO/JNCC/RSPB Breeding Bird Survey  
207 (Wilson & Fuller 2002). Bird data and habitat data were collected as far as possible within a year of  
208 one another. Difficulties in obtaining complete imagery in any one year (due to cloud) made

209 mismatches in timing unavoidable. Habitats in some polygons will have changed between years  
210 (Norton et al. 2012), particularly in arable areas, but crop rotations are likely to limit changes at the  
211 1km square scale.

212

### 213 *Bird Abundance Response Variables*

214 Response variables were individual bird species counts (60 species total, Table 3) for each 1km square.  
215 Bird species selected for analysis had the highest non-zero counts for the 335 survey squares, omitting  
216 managed species (e.g. ring-necked pheasant *Phasianus colchicus*) and highly colonial species (e.g. rook  
217 *Corvus frugilegus*). Carrion crow *Corvus corone* counts included hooded crow *Corvus cornix* counts.  
218 Counts were summed across all four transects and distance bands, omitting birds in flight. The  
219 maximum count across visits was selected as the observed value for each species at each square (Table  
220 S1), aiming to capture breeding numbers at peak detectability for early and late breeders. Relative  
221 abundance (observed counts) was modelled, not absolute abundance or density, so not adjusting for  
222 imperfect detection. Only one bird dataset was used, the two habitat datasets differed little in gross  
223 habitat measures (Fuller *et al.* 2002) and the focus was not on differences between species. Therefore,  
224 accounting for detection rather than modelling relative abundance was not expected to change the  
225 results (all models for each species would be adjusted by approximately similar constants), but would  
226 add unnecessary complexity which can have drawbacks, especially for large scale analyses (Banks-Leite  
227 *et al.* 2014).

228

229 Some zero counts may occur where range-restricted bird species do not occur in all regions. To avoid  
230 such uninformative (with respect to land-use relationships) zeroes, 1 km squares were excluded from  
231 analyses if they occurred in a 10 km national grid square within which no individual of a given species  
232 was recorded as present in the 1988-91 breeding bird atlas (Gibbons, Reid, & Chapman 1993). The  
233 number of squares used for each species-specific analysis therefore varied (Table 3).

234

235 ANALYSES

236 *Hypotheses*

237 For each bird species, an *a priori* hypothesis regarding habitat influences on abundance was  
238 formulated by examining habitat preferences (see Cramp and Simmons 2006). This identified variables  
239 to be included as potential predictor variables for each species (see ‘Habitat predictor variables’, Table  
240 S1). All models included a categorical variable assigning lowland or upland squares, based on  
241 Environmental Zones (Wilson & Fuller 2002).

242

243 *Model structure*

244 Species-specific analyses modelled bird counts as a function of habitat predictors in Generalized Linear  
245 Models, with a Poisson error structure and log link function, as is typical of analysis for breeding bird  
246 survey data (Siriwardena, Cooke, & Sutherland 2011). Negative binomial errors were not used as they  
247 sometimes resulted in extremely high predicted values for certain bird species in squares with high  
248 density of hedges or trees. Five models were generated per species, each of which corresponded to  
249 one of five ‘*Model Sets*’ differing in the type of habitat predictors and their data set of origin (Table 1).  
250 This allowed comparison of separate models including field data and/or remote-sensed data, and also  
251 Broad Habitats and Landscape Feature predictors, as well as the two in combination (hereafter,  
252 ‘Combined Habitats’). Broad Habitats were available in both data sets, while Landscape Features were  
253 available only in field data, so the number of variables compared between models was sometimes  
254 unequal. Explanatory power was measured as the percentage of deviance explained. The focus was on  
255 specific quantities of deviance explained by variables from different datasets or groupings, and not on  
256 parsimony, which was favoured deviance over a possible alternative Akaike’s Information Criterion.  
257 Predictive power was assessed through cross-validation (see below).

258

259 *Bootstrapped model comparisons*

260 To determine whether there was an overall significant difference in explanatory power between

261 'Model Sets' across all 60 species, a bootstrapping procedure was adopted. Comparisons between any  
262 two 'Model Sets' was assessed by calculating the within-species difference in explanatory power  
263 (defined by percent deviance explained), then taking the mean of these differences across all species.  
264 This provided a clear test statistic which bootstrap-based samples could be compared against. Under  
265 the null hypothesis that the two model sets show no difference in power, the observed differences  
266 across the 60 species were randomly sampled with replacement and then randomly assigned to be  
267 negative or positive with equal probability, thus simulating from the null distribution. From this  
268 sample, the test statistic was re-calculated by taking the mean across the 60 values and stored. The  
269 whole process was repeated 1000 times in order to obtain 1000 values of the test statistic under the  
270 null hypothesis which the observed test statistic can be compared to. P-values were calculated as the  
271 proportion of occurrences of re-sampled mean difference estimates that exceeded the test statistic,  
272 thus measuring the probability that the true value of the test statistic was larger.

273

#### 274 *Goodness-of-fit and cross validation*

275 Practical implications of differences between field data and remote-sensing in prediction were  
276 assessed by comparing fitted and observed values for the 'Field Data Combined Habitats' and 'Remote-  
277 sensed Broad Habitat' model sets, the sets comprising all available field data and remote-sensed data  
278 respectively (Table 3). Mean Absolute Error (MAE) between fitted and observed values was calculated  
279 for each species. This was chosen over Mean Square Error because it provides a more easily  
280 interpretable output (i.e. birds per 1km<sup>2</sup>). A cross-validation procedure assessed the predictive  
281 performance of the datasets. For each species, data were partitioned into a randomly selected training  
282 dataset of 80% of squares (rounded to the nearest integer) and a testing dataset comprising the  
283 remainder of the squares. Models were fitted to the training data and then used to predict bird counts  
284 with for the testing dataset and MAE was recalculated.

285

#### 286 **Results**

287 MODEL PERFORMANCE

288 Figure 1 displays the mean explanatory power (% deviance explained) across all 60 species for the five  
289 'Model Sets' differing in habitat predictors (Table 2). Mean explanatory power was lowest for species  
290 models derived from Landscape Features from field data alone (14%). Broad Habitats explained  
291 intermediate amounts of deviance (remote-sensed 24%, field data 28%) but this increased when they  
292 were combined with Landscape Features from field data (remote-sensed data 29%, field data 33%)  
293 (Figure 1). Figure 2 shows the explanatory power for 60 individual bird species separated into the five  
294 'Model Sets'.

295

296 FIELD DATA VERSUS REMOTE-SENSED DATA

297 In a comparison of all data available, field data outperformed remote-sensed data in predicting bird  
298 abundance. 'Field Data Combined Habitats' had higher explanatory power than 'Remote-sensed Broad  
299 Habitats' for 57 of 60 species (Fig. 2) and significantly higher mean explanatory power across all species  
300 (Table 2, Fig. 1). When considering Broad Habitat data alone, field data had higher explanatory power  
301 than remote-sensed data for 49 of 60 species (Fig. 2) and significantly higher mean explanatory power  
302 across all species (Table 2, Fig. 1). The superior performance of Broad Habitats from field data was  
303 enhanced by inclusion of Landscape Features to form Combined Habitats models (Table 2). 'Field Data  
304 Combined Habitats' had higher explanatory power than 'Remote-sensed Combined Habitats' for 49 of  
305 60 species (Fig. 2) and significantly higher mean explanatory power across all species (Table 2, Fig. 1).  
306 The mean improvement in explanatory power of field data over remote-sensed data was greater for  
307 Combined Habitats than for Broad Habitats alone (mean difference in percent deviance averaged  
308 across 60 species models: Combined Habitats = 3.82, Broad Habitats = 3.76, Table 2).

309

310 Differences between field data and remote-sensing for prediction were further assessed by comparing  
311 observed and fitted values for the 'Remote-sensed Broad Habitats' and 'Field Data Combined Habitats'  
312 model sets (Table 3). Mean absolute error between fitted and observed values (MAE) averaged across

313 squares demonstrated a closer fit for field data (MAE lower for 53/60 species, MAE averaged across  
314 60 species = 2.74) compared to remote-sensed data (MAE lower for 7/60 species, MAE averaged across  
315 60 species = 2.92, Table 3). This result was robust to cross-validation, out-of-sample predictions were  
316 closer to observed values for field data (MAE lower for 46/60 species, MAE averaged across 60 species  
317 = 2.92) compared to remote-sensed data (MAE lower for 12/60 species, MAE averaged across 60  
318 species = 3.12, MAE equal for 2/60 species, Table S2).

319

## 320 BROAD HABITATS VERSUS LANDSCAPE FEATURES

321 Comparing the two components of the field data set demonstrated that Broad Habitats outperformed  
322 Landscape Features in prediction of bird abundance. *'Field Data Broad Habitats'* had higher  
323 explanatory power than *'Field Data Landscape Features'* for 55/60 species, while *'Remote-sensed*  
324 *Broad Habitats'* had higher explanatory power than Landscape Features for 53/60 species (Fig. 2).  
325 Broad Habitats from both field data and remote-sensed data had significantly higher mean  
326 explanatory power than Landscape features (mean difference in percent deviance averaged across 60  
327 species models: +13.87 for field data Broad Habitats, +10.11 for remote-sensed Broad Habitats Table  
328 2, Fig. 1).

329

## 330 Discussion

331 Our results support the hypothesis that national-scale field survey data outperform remote-sensed  
332 equivalents as predictors of spatial variation in bird abundance, providing more accurate models of  
333 breeding bird counts (Figs 1 & 2, Table 2). The explanatory power of remote-sensed data alone, as a  
334 percentage of that provided by the Field Data Combined models (which generally had the highest  
335 explanatory performance), was 74% (Table 2). The extent to which increases in explanatory power  
336 produce better predictions of bird numbers is a key issue. Measures of observed versus fitted values  
337 suggest that more reliable predictions of bird numbers are likely to be obtained from field survey data  
338 than from remote-sensed data. Examples of more accurate predictions resulting from field data ranged

339 in magnitude from small errors for species such as wheatear *Oenanthe oenanthe* (mean observed  
340 count per square = 1.06, MAE = 0.01 counted birds averaged across 86 squares), to errors of nearly  
341 two individual birds for species such as meadow pipit *Anthus pratensis* (mean observed count per  
342 square = 13.31, MAE = 1.99 counted birds averaged across 319 squares, Table 3). This result was robust  
343 for sites not used to train the models (cross-validation) across the majority of bird species (Table S2),  
344 indicating that biodiversity-habitat associations produced without detailed habitat data may result in  
345 significantly suboptimal recommendations for environmental management. Potential implications of  
346 the disparity in assessment accuracy extend to further applications such as predictions of effects of  
347 climate (Foley *et al.* 2005), policy change (Mattison & Norris 2005) and Environmental Impact  
348 Assessments (Treweek 1996).

349

350 Widespread declines in biodiversity (Butchart *et al.* 2010) and growing pressures on land use (Foley *et*  
351 *al.* 2005) are increasing demand for large scale data on land-use and biodiversity for policy and  
352 environmental management. The strength of our analyses relates to the novel combination of large  
353 geographic scale with fine-grained observation of Landscape Features and national monitoring  
354 methods for estimating bird populations from an unbiased random sample of countryside. The results  
355 of this study suggest that investment in future analyses should consider the scale and detail required  
356 to optimise understanding of biodiversity-habitat associations, and produce better-informed  
357 environmental management. The results offer a baseline against which performance of remote-  
358 sensing can be assessed as advances in technology improve the resolution (in terms of spatial grain  
359 and habitat classification) and accuracy of the data produced.

360

361 Broad Habitats provided more reliable predictions than Landscape Features, across the 60 species  
362 tested. This may be because Broad Habitats integrate multiple habitat characteristics over larger areas  
363 (Benton, Vickery & Wilson 2003), while Landscape Features reflect more specific habitat features as  
364 well as being correlated with basic land cover (Siriwardena, Cooke, & Sutherland 2011). Models

365 combining both Broad Habitats and Landscape Features performed better than either set alone,  
366 regardless of the source (field survey or remote-sensing) of Broad Habitat data. This suggests  
367 possibilities for enhancement of national monitoring of breeding birds. Wildlife surveys collecting  
368 additional detail on landscape features (length of linears, count of points), for combination with  
369 available remote-sensed data may benefit understanding of large scale biodiversity-habitat  
370 associations. Although Broad Habitats were found to outperform Landscape Features, no attempt was  
371 made to control the number of input variables from the two sets that were included in any given  
372 model. Overall, a mean of 6.07 Broad Habitat predictors were included per species, higher than the  
373 mean of 3.13 Landscape Feature predictors included per species (Table S1). Studies focussed on the  
374 roles of these two habitat variable types should test their relative benefits explicitly with adequate  
375 controls (Siriwardena, Cooke, & Sutherland 2011).

376

377 Landscape Features (e.g. woody linear features, individual trees, scrub, rivers, streams, stone walls,  
378 ditches, fences, banks, ponds) can have important effects (positive or negative) on many species by  
379 providing sources of food, nest sites or protection from/exposure to predators (Fuller 2012). As such,  
380 measures of Landscape Features are important from the perspective of applied management. Habitats  
381 impact bird abundance at multiple scales simultaneously and the context within which a given habitat  
382 occurs may influence suitability for breeding birds (Benton, Vickery & Wilson 2003). Broad Habitats  
383 may determine basic breeding suitability of an area for a given species (e.g. yellowhammer *Emberiza*  
384 *citrinella* – arable specialist), while Landscape Features may provide resources making them an  
385 important determinant of breeding abundance of a species within the habitat matrix (e.g.  
386 yellowhammer - trees and hedges, Whittingham *et al.* 2005). Therefore, to predict land-use impacts  
387 on biodiversity, simultaneous understanding of all habitat effects is required. Field survey, but not  
388 remote-sensing, recorded Landscape Features in the present study (Fuller *et al.* 2002; Howard *et al.*  
389 2003), but their impact on model performance suggests that future surveys aiming to inform  
390 biodiversity-habitat associations, both field survey and remote-sensing, should aim to record both



391 Broad Habitats and Landscape Features. Where pragmatism favours collection of either Broad Habitat  
392 or Landscape Feature data but not both (due to limits on survey complexity or time, e.g. as part of  
393 'citizen science' data protocols), Broad Habitats should typically be prioritised. Remote-sensed Broad  
394 Habitat data may often be relatively accessible (Shirley *et al.* 2013; Shereen, Bonthoux & Balent 2014)  
395 and under such circumstances field survey efforts might best prioritise Landscape Features to be used  
396 in combination. This may change in the future if remote-sensed Landscape Feature data are developed  
397 (Tebbs & Rowland 2014). Combinations of remote-sensed data and field survey have previously  
398 yielded important results in attempts to identify land use impacts on biodiversity (Fuller *et al.* 1998;  
399 Nagendra & Gadgil 1999; Saveraid *et al.* 2001). While the best performance was yielded by the using  
400 both Broad Habitats and Landscape Features from field survey, our results suggest that the  
401 performance benefits lost by using remote-sensed Broad Habitats combined with field survey  
402 Landscape Features might be outweighed by potential cost reductions under some circumstances (Fig.  
403 1, Fig. 2, Table 2).

404

405 The extra performance yielded by field data may be due to greater resolution (in terms of both spatial  
406 grain and habitat classification) and accuracy compared with remote-sensing. Broad Habitat areas  
407 were more accurately mapped by field survey (minimum mappable unit 20 m<sup>2</sup>) than by remote-sensing  
408 (pixel-based measures interpreted from satellite images, pixel size 25 m<sup>2</sup>, minimum mappable unit >  
409 50 m<sup>2</sup>) and Broad Habitat classification was more accurate by field survey (survey based on plant  
410 species composition) than remote-sensing (computer-based interpretation of satellite land cover  
411 image reflectance) (Fuller *et al.* 2002; Howard *et al.* 2003). Remote-sensing technology has developed  
412 since the data were collected, with resolution, scale, accuracy and availability of data increasing (Recio  
413 *et al.* 2013, Shirley *et al.* 2013); for example, the Land Cover Map for 2007 incorporates an Ordnance  
414 Survey polygon framework to improve habitat mapping (Morton *et al.* 2011). However breadth of  
415 habitat classification and pixel size, key differentials with field data, remain the same. The ability of  
416 remote-sensed data to predict bird abundance is likely to improve with technological advancements.

417

418 Addressing the relative costs of field survey and remote-sensing methods is an important issue.  
419 Countryside Survey 2007 field survey cost £4.1m for a randomly stratified sample of squares, whilst  
420 Land Cover Map 2007 cost £1.8M for all GB squares. Field data benefits therefore come at an increased  
421 cost of approximately 128%. However, cost measurement for either field survey or remote-sensing is  
422 not straightforward. For field survey, mapping comprises just one element of the survey (besides soils,  
423 freshwaters and extensive vegetation sampling. For remote-sensing, many development costs involved  
424 in early surveys may not be incurred in the future. Therefore, these costs do not necessarily represent  
425 the scale of costs for future surveys.

426

427 Technological developments are increasing data quality yielded by both field survey and remote-  
428 sensing whilst reducing costs. Advances in field data collection efficiency have occurred in parallel with  
429 those in remote-sensing and we estimate it to take an average of 2 person days to collect detailed field  
430 data from a 1 km square using Countryside Survey field protocols, which are then available for  
431 immediate analysis. Methods such as lidar offer possibilities for improving the resolution of remote-  
432 sensed data, but costs associated with this method are considerably higher than those of acquiring  
433 satellite data and processing costs for data at national scales are currently likely to be prohibitive  
434 (Mason *et al.* 2003; Turner *et al.* 2003, Müller & Brandl 2009). The remote-sensed data in this study  
435 recorded land cover for the whole of Great Britain while the field survey was limited to sample 1 km  
436 squares. One important consequence of this extra spatial coverage from remote-sensing is that it  
437 allows out-of-sample predictions beyond bird survey areas. As the area of interest for a study  
438 increases, the cost of field survey would increase relative to the cost of remote-sensing and at some  
439 threshold outweigh any benefit (given that funding of field surveys of the entire land surface of Great  
440 Britain seems implausible) (Blackburn & Gaston 2002). The threshold scale at which this shift occurs  
441 may be reduced if developments in the resolution and cost efficiencies of remote-sensing outstrip  
442 equivalent developments in field survey. As the resolution, accuracy and relative costs of remote-

443 sensing and field survey methods develop, further comparisons should be made to measure progress  
444 in biodiversity-habitat associations to inform policy decision regarding allocation of research funding.  
445 Such comparisons should consider a range of taxa due to the varying importance of resolved  
446 information for different organisms.

447

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452

#### 453 **Data Accessibility**

454 Countryside Survey & Land Cover Map: Countryside Survey and Land Cover Map data are publicly  
455 accessible via <http://countrysidesurvey.org.uk/>. Due to confidentiality of location data, spatial  
456 information is available subject to a licence agreement. Details are available here:  
457 <http://countrysidesurvey.org.uk/data-access>

458

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**Table 1. Five ‘Model Sets’ differing in the origin of habitat predictors used**

Five ‘Model Sets’ (each applied to all 60 bird species) were produced. ‘Model Sets’ varied based upon inclusion of predictors from Broad Habitats, Landscape Features or Combined Habitats (both Broad Habitats and Landscape Features) and also based on the data source of Broad Habitats (field data or remote-sensed). Landscape Features were sourced from field data only. NA = Not applicable.

Model Set Name	Landscape Feature Data Source	Broad Habitat Data Source
Field Data Landscape Features	Field Data	NA
Remote-sensed Broad Habitats	NA	Remote-sensed
Field Data Broad Habitats	NA	Field Data
Remote-sensed Combined Habitats	Field Data	Remote-sensed
Field Data Combined Habitats	Field Data	Field Data



**Table 2. Summary of seven comparisons between ‘Model sets’ testing two main hypotheses of habitat data performance in prediction of bird abundance**

Hypothesis (the hypothesis of interest), Comparison (the ‘Model set’ comparisons aimed at testing each hypothesis), Model set 1 & 2 (the two ‘Model Sets’ being compared, see Table 2), Best performance (the result of the comparison, which of the two sets being compared performed best in prediction of bird abundance), Test Statistic (estimated mean difference in explanatory power, measured as percent deviance explained, across 60 bird species). C.I. (bootstrapped 95 % Confidence Interval), p (bootstrapped p-value), Lower model % (explanatory power of the lower performing model from the comparison as a percentage of the explanatory power of the better performing model from the comparison).

Hypothesis	Model Set 1	Model Set 2	Best Performance	Test Stat.	C.I. 2.5%	C.I. 97.5%	p	Lower model %
<b>Field Data versus Remote-sensed</b>	Field Data Combined Habitats	Remote-sensed Broad Habitats	<b>Field Data</b>	8.61	-2.80	2.77	< 0.001	74
	Field Data Broad Habitats	Remote-sensed Broad Habitats	<b>Field Data</b>	3.76	-1.79	1.84	< 0.001	86
	Field Data Combined Habitats	Remote-sensed Combined Habitats	<b>Field Data</b>	3.82	-1.62	1.64	< 0.001	88
<b>Broad Habitats versus Landscape Features</b>	Field Data Broad Habitats	Field Data Landscape Features	<b>Broad Habitats</b>	13.87	-4.13	4.45	< 0.001	50
	Remote-sensed Broad Habitats	Field Data Landscape Features	<b>Broad Habitats</b>	10.11	-3.40	3.38	< 0.001	58

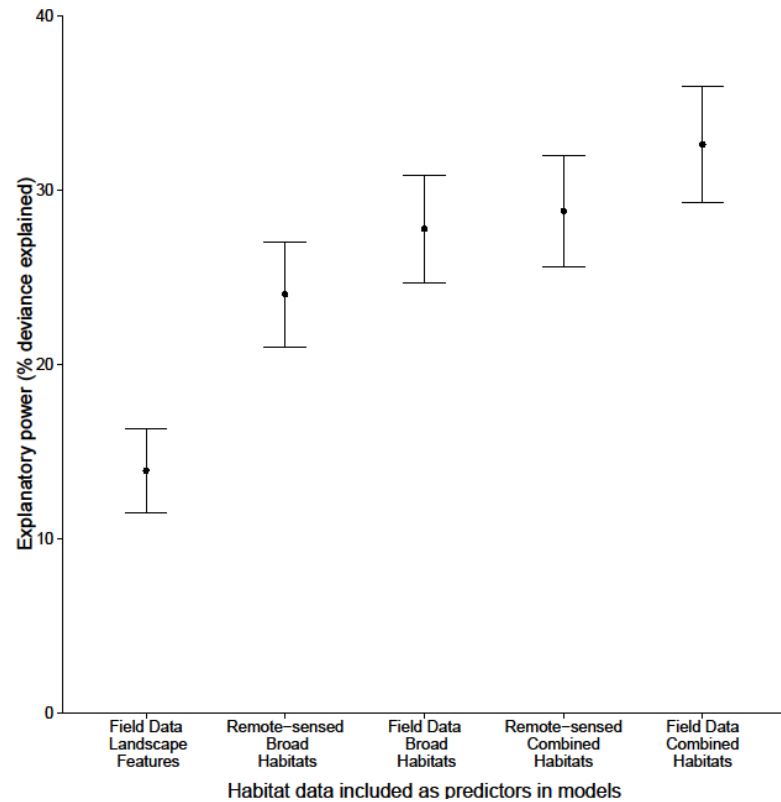
**Table 3 Comparison of error between fitted and observed values for models based on field data and remote-sensing**

Comparing Field Data Combined Habitats (combining Broad Habitat + Landscape Feature predictors) and Remote Sensed Data (Broad Habitat predictors only). Sample size = number of 1km squares used for species-specific analysis. Zeros = number of squares with zero count. Max observed = maximum observed count. Mean observed = mean observed count. MAE = mean absolute error between fitted and observed values. Scaled MAE = MAE divided by mean count for species. Values in bold indicate smaller error for Field Data or Remote Sensed Data.

Species	Sample size	Zeros	Max observed	Mean observed	MAE Field Data	MAE Remote Sensed	Scaled MAE Field Data	Scaled MAE Remote Sensed
Blackbird	328	79	79	8.41	<b>4.44</b>	4.84	<b>0.53</b>	0.58
Blackcap	256	104	21	2.29	<b>1.75</b>	1.82	<b>0.76</b>	0.80
BlueTit	305	98	71	6.23	<b>4.19</b>	4.63	<b>0.67</b>	0.74
Bullfinch	271	202	6	0.45	<b>0.58</b>	0.60	<b>1.30</b>	1.34
Buzzard	232	99	9	1.24	<b>1.08</b>	1.11	<b>0.87</b>	0.89
Carrion Crow	335	80	69	6.74	<b>7.59</b>	8.45	<b>1.13</b>	1.25
Chaffinch	322	51	72	13.51	<b>1.53</b>	1.67	<b>0.11</b>	0.12
Chiffchaff	262	144	22	1.63	<b>1.22</b>	1.31	<b>0.75</b>	0.81
Coal Tit	297	189	21	1.15	<b>1.63</b>	1.80	<b>1.42</b>	1.56
Collared Dove	260	164	23	1.70	5.55	<b>5.54</b>	<b>3.26</b>	3.26
Cuckoo	308	208	6	0.54	<b>0.67</b>	0.68	<b>1.25</b>	1.28
Curlew	255	169	53	1.85	<b>2.26</b>	2.35	<b>1.22</b>	1.27
Dunnock	310	108	22	2.87	<b>1.98</b>	2.11	<b>0.69</b>	0.73
Garden Warbler	241	174	9	0.53	<b>0.69</b>	0.70	<b>1.31</b>	1.33
Goldcrest	295	163	23	1.91	<b>1.70</b>	1.83	<b>0.89</b>	0.96
Goldfinch	273	109	21	2.71	<b>2.21</b>	2.33	<b>0.82</b>	0.86
G.S. Woodpecker	255	169	7	0.58	<b>0.56</b>	0.62	<b>0.96</b>	1.06
Great Tit	305	114	40	3.27	<b>2.18</b>	2.26	<b>0.67</b>	0.69
Greenfinch	284	128	31	3.48	<b>2.89</b>	3.10	<b>0.83</b>	0.89

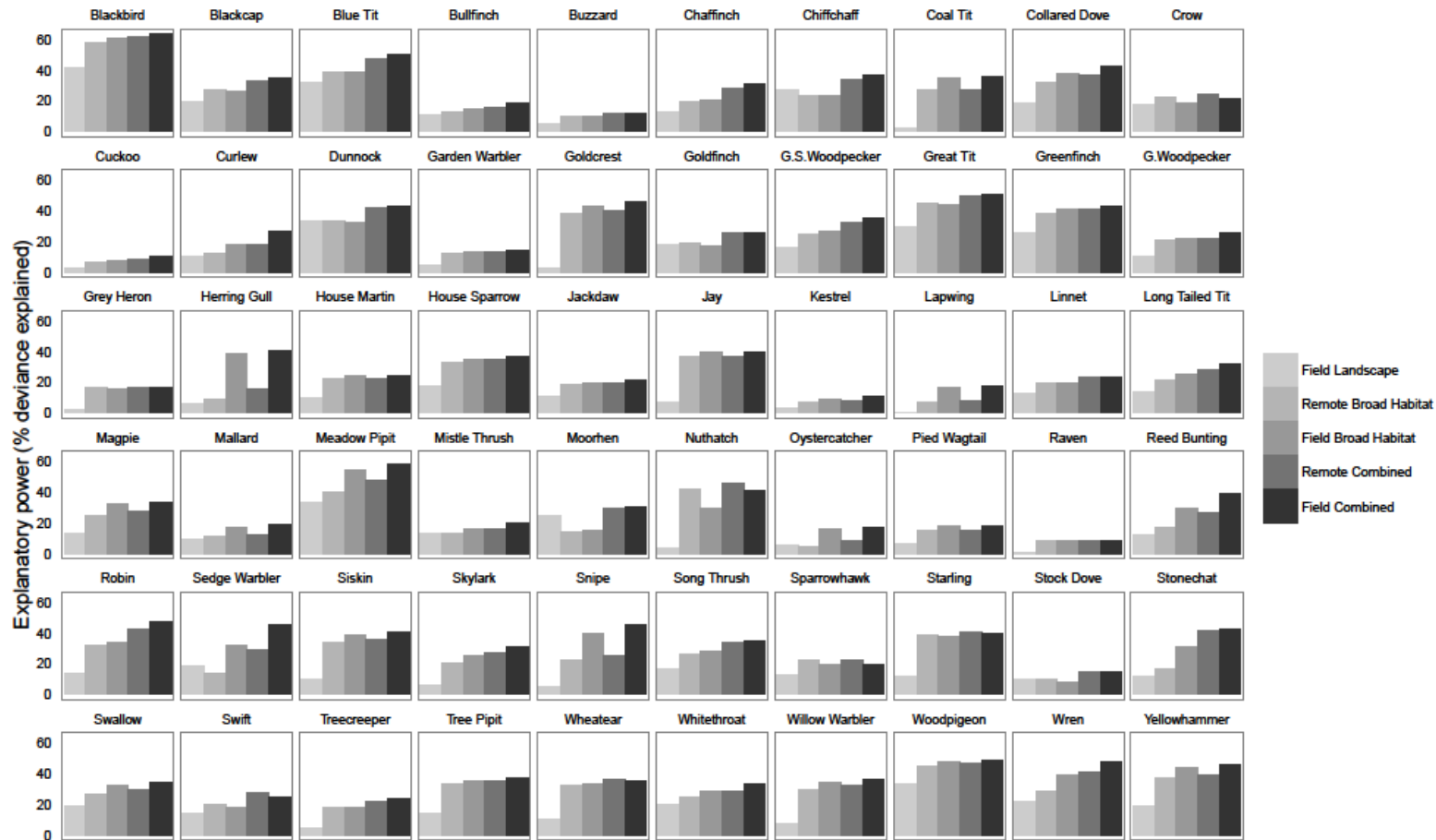
Green Woodpecker	192	132	15	0.72	0.83	0.83	<b>1.16</b>	1.16
Grey Heron	296	252	92	0.73	0.16	0.17	<b>0.22</b>	0.23
Herring Gull	172	125	200	4.84	<b>6.23</b>	7.25	<b>1.29</b>	1.50
House Martin	292	187	417	4.06	5.71	<b>5.51</b>	<b>1.41</b>	1.36
House Sparrow	308	156	99	5.65	<b>5.24</b>	5.51	<b>0.93</b>	0.98
Jackdaw	280	119	107	6.90	<b>7.12</b>	7.14	<b>1.03</b>	1.04
Jay	222	155	20	0.65	<b>0.70</b>	0.72	<b>1.08</b>	1.10
Kestrel	304	218	3	0.35	<b>0.44</b>	0.46	<b>1.29</b>	1.32
Lapwing	290	214	71	1.97	<b>2.78</b>	2.83	<b>1.41</b>	1.44
Linnet	264	127	41	3.80	<b>3.88</b>	3.96	<b>1.02</b>	1.04
Long Tailed Tit	269	180	22	1.35	<b>1.40</b>	1.59	<b>1.04</b>	1.18
Magpie	240	88	30	3.21	<b>2.65</b>	2.84	<b>0.83</b>	0.89
Mallard	322	193	31	2.22	<b>2.54</b>	2.67	<b>1.14</b>	1.20
Meadow Pipit	319	117	202	13.31	<b>9.34</b>	11.33	<b>0.70</b>	0.85
Mistle Thrush	302	160	11	1.26	<b>1.26</b>	1.29	<b>1.00</b>	1.02
Moorhen	239	185	10	0.53	<b>0.65</b>	0.74	<b>1.23</b>	1.40
Nuthatch	167	117	24	0.84	0.93	<b>0.91</b>	<b>1.10</b>	1.08
Oystercatcher	199	132	24	2.07	<b>2.49</b>	2.76	<b>1.20</b>	1.33
Pied Wagtail	329	143	10	1.53	<b>1.30</b>	1.33	<b>0.85</b>	0.87
Raven	163	112	8	0.69	0.90	<b>0.89</b>	<b>1.30</b>	1.28
Reed Bunting	266	205	15	0.73	<b>0.80</b>	0.98	<b>1.11</b>	1.35
Robin	322	65	49	7.79	<b>4.60</b>	5.23	<b>0.59</b>	0.67
Sedge Warbler	222	170	25	1.21	<b>1.32</b>	1.69	<b>1.09</b>	1.39
Siskin	179	127	13	1.07	<b>1.13</b>	1.19	<b>1.05</b>	1.12
Skylark	332	102	87	6.92	<b>5.85</b>	6.30	<b>0.85</b>	0.91
Snipe	244	201	35	0.49	<b>0.59</b>	0.70	<b>1.20</b>	1.42
Song Thrush	323	105	20	2.72	<b>1.93</b>	2.06	<b>0.71</b>	0.76
Sparrowhawk	277	234	2	0.18	0.26	<b>0.25</b>	<b>1.46</b>	1.42
Starling	315	156	380	10.57	11.20	<b>10.56</b>	<b>1.06</b>	1.00
Stock Dove	235	158	12	0.94	<b>1.16</b>	1.19	<b>1.23</b>	1.26
Stonechat	146	96	12	1.05	<b>0.94</b>	1.26	<b>0.90</b>	1.20

Swallow	320	91	34	5.38	<b>3.69</b>	4.00	<b>0.69</b>	0.74
Swift	267	172	120	2.74	<b>3.56</b>	3.66	<b>1.30</b>	1.34
Treecreeper	277	220	5	0.32	<b>0.42</b>	0.45	<b>1.31</b>	1.40
Tree Pipit	232	182	14	0.62	<b>0.77</b>	0.77	<b>1.23</b>	1.25
Wheatear	248	162	16	1.06	<b>1.13</b>	1.14	<b>1.06</b>	1.08
Whitethroat	262	131	20	2.00	<b>1.77</b>	1.89	<b>0.89</b>	0.94
Willow Warbler	323	104	49	6.34	<b>4.91</b>	5.13	<b>0.78</b>	0.81
Woodpigeon	309	82	108	13.72	<b>9.86</b>	10.01	<b>0.72</b>	0.73
Wren	335	48	47	10.39	<b>5.47</b>	6.50	<b>0.53</b>	0.63
Yellowhammer	260	131	20	2.39	<b>1.88</b>	1.98	<b>0.79</b>	0.83
				Mean	2.74	2.92	1.02	1.08



**Figure 1. Mean explanatory power ( $\pm$  95% Confidence Interval) across 60 bird species for five ‘Model Sets’ generated from field data and remote-sensed data**

‘Field Landscape’ = Landscape feature predictors from field data. ‘Remote Broad Habitat’ = Broad Habitat predictors from remote-sensed data. ‘Field Broad Habitat’ = Broad Habitat predictors from field data. ‘Remote Combined’ = Broad Habitat predictors from remote-sensed data + Landscape Features from field data, ‘Field Combined’ = Broad Habitat predictors from field data + Landscape Features from field data. Significant differences: Field Landscape versus Field Broad Habitat/Remote Broad Habitat/Field Combined ( $p < 0.001$ ), Remote Broad Habitat versus Field Broad Habitat/Remote Combined/Field Combined ( $p < 0.001$ ), Field Broad Habitat versus Field Combined ( $p < 0.001$ ), Remote Combined versus Field Combined ( $p < 0.001$ ), (Table 2).



**Figure 2. Explanatory power for 60 individual bird species models generated from field data and remote-sensed habitat predictors**

*'Field Landscape'* = Landscape Feature predictors from field data (Countryside Survey). *'Remote Broad Habitat'* = Broad Habitat predictors from remote-sensed data (Land Cover Map). *'Field Broad Habitat'* = Broad Habitat predictors from field data. *'Remote Combined'* = Broad Habitat predictors from remote-sensed data + Landscape Features from field data, *'Field Combined'* = Broad Habitat predictors from field data + Landscape Features from field data.

## **Supporting Information**

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

**Table S1. Bird species, sample sizes and habitat predictors included in hypotheses**

**Table S2 Comparison of error between fitted and observed values for models based on field data and remote-sensing in out-of-sample prediction**