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1 **Habitat diversity and structure regulate British bird**
2 **richness: implications of non-linear relationships for**
3 **conservation**

4

5

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1 **Abstract**

2 Spatial environmental heterogeneity (EH) is an important factor determining species
3 richness among many taxa across spatial scales. Increased EH may support higher diversity
4 mainly by providing a higher number of ecological niches. However, the shapes of the EH-
5 diversity relationships and their influence on diversity measures at landscape scales are
6 poorly understood. We used random forests regression models to assess the relationships
7 between different components of EH and bird species richness across Great Britain. Bird
8 data were obtained using BTO/JNCC/RSPB Breeding Bird Survey methods across 335 UK
9 Countryside Survey (CS) 1-km squares in 2000. Data on components of EH, including;
10 vegetation, habitat diversity, and habitat structure were collected in associated field surveys.
11 Using the results of our EH component-bird richness models, we applied the case of the
12 likely decline of the ash tree, a species of conservation concern and a key component of
13 British landscape complexity, to create predictive scenarios of future bird richness. We
14 found that EH components had a strong positive effect on bird richness and identified six
15 key components that explained over 70% of variance in bird richness. Bird richness
16 responses were strongly dependent on the specific EH components and were generally non-
17 linear, especially for habitat structural variables, such as lines of trees and hedges. Our
18 predictive scenarios showed a decrease in bird species richness only for simulated ash tree
19 decreases within the habitat structural variables of over 90%, and only for areas where this

20 tree species was a particularly abundant component of the landscape. Our findings, showing
21 that bird richness responses differ for EH components, and that non-linear responses are
22 common, could help the ‘design’ of landscapes that enhance bird diversity. In particular, our
23 study indicates that, in some cases, increasing the occurrence of key structural components
24 of habitat (such as ensuring a minimum of 700 m of managed hedges or a minimum of 70
25 individual trees per km square), could have disproportionately positive impacts on bird
26 richness.

27

28 **Keywords:** ash tree, Countryside Survey, environmental heterogeneity, linear features,
29 random forests models, predictive diversity maps

30 **1. Introduction**

31 A major concern for ecologists and conservationists is understanding why some areas are
32 richer in species than others. Spatial environmental heterogeneity (EH), understood as all
33 aspects of complexity, diversity, structure or variability of the environment (Stein *et al.*,
34 2015), is known to be an important factor for determining species richness and abundance
35 among many taxa across spatial scales (Stein *et al.*, 2014). Increased EH might support a
36 higher diversity by providing higher numbers of ecological niches in the form of habitat
37 types, resources or structural diversity (Tews *et al.*, 2004). Based on this, one might expect
38 positive and linear relationships between EH and species diversity (Seiferling *et al.*, 2014).
39 Although examples of negligible or negative relationships can be found, most studies show
40 such positive relationships (see review by Stein *et al.* (2014)). However, the study of non-
41 linear patterns may be particularly important for understanding complex EH-diversity
42 relationships (Stein *et al.*, 2014), and could help in the identification of environmental
43 tipping points (Oliver *et al.*, 2015).

44 Models based on island biogeography have suggested that EH can have a unimodal effect
45 on species diversity (Kadmon and Allouche, 2007), arising from the trade-off between the
46 increase of ecological niches and the effects of the reduction in area of suitable habitats for
47 each individual species. This trade-off may be strongly dependent on the scale of
48 observation, as larger-scale diversity patterns may be driven by demographic processes,

49 while small-scale patterns may instead reflect behavioural processes (Chocron *et al.*, 2015).
50 In a meta-regression study, Tamme *et al.* (2010) found that negative EH-diversity
51 relationships are more common at smaller scales. Factors such as the level of urbanization
52 (Seiferling *et al.*, 2014) or the size (area coverage) of the niches required by the species
53 considered (Allouche *et al.*, 2012) could also affect the shape of the EH-diversity curve.

54 Another key issue for understanding how EH regulates species diversity is that these
55 relationships may depend heavily on the definition of EH, or on the measured heterogeneity
56 components. For example, fern species richness in the Alps had different response curves for
57 habitat diversity, land cover, elevation or climate variables (Marini *et al.*, 2011). Scottish
58 soil-fauna diversity had hump-shaped relationships with land-cover percentages, but linear
59 ones with habitat diversity (Vanbergen *et al.*, 2007). Understanding the contribution of
60 different components of EH to these relationships may be critical, but presents several
61 challenges.

62 The interaction between different components of EH makes the study of individual
63 variables difficult, as autocorrelation and indirect effects on diversity might be common in
64 these systems. Although the study of the interactions between different EH components and
65 their disparate effects on diversity should help to explain the observed array of EH-diversity
66 relationships, this topic has rarely been addressed (Stein *et al.*, 2014). Understanding how
67 individual components of EH influence overall EH-diversity relationships could help with

68 conservation planning, as optimal levels for the maintenance of biodiversity could be
69 identified independently for different, manageable EH components.

70 In this study, we tested how a combination of different components of EH could explain
71 bird richness gradients across Great Britain (GB) and studied the shape of relationships
72 between individual EH components and bird richness. Birds are good indicators of the
73 general health of biodiversity and ecosystems (Furness and Greenwood, 2013). Maintaining
74 bird diversity is important due to its role in the provision of cultural and ecosystem services
75 (Whelan *et al.*, 2008). Some aspects of EH, such as habitat diversity or structural
76 complexity, including, for example, the presence of linear landscape features such as
77 hedgerows, have been shown to affect bird abundance (Pearce-Higgins and Grant, 2006) and
78 diversity at local scales within certain habitat types (Pickett and Siriwardena, 2011;
79 Zellweger *et al.*, 2016; Sullivan *et al.*, 2017). However, nationally representative data
80 demonstrating how fine-grain EH regulates bird richness is lacking, largely due to the lack
81 of highly resolved co-located bird and habitat/landscape feature surveys. Here we use fine-
82 grain (field) environmental data to characterize habitats in terms of heterogeneity features,
83 as opposed to the standard approach of considering habitat extent. Detailed measurements of
84 landscape features are often neglected in EH-diversity studies despite their potential
85 importance at certain scales (Tews *et al.*, 2004) because they are rarely recorded
86 comprehensively in the field. Given that particular fine-scale landscape features are
87 generally not dominant in the landscape and that they add structural complexity, which is

88 additional to existing habitat heterogeneity, they can be considered to be positive
89 contributors to heterogeneity as well as to habitat amount.

90 In order to assess the relationships between EH and bird richness across GB, we first
91 tested the extent to which a combination of EH components explained the observed
92 differences in bird richness between squares. Second, we tested whether the responses of
93 bird richness were similar for each of the key EH components. Finally, to give an example
94 of how understanding these relationships can be useful in conservation and management
95 planning, national scale predictive maps of bird richness were created. We used the case of
96 the decline of the ash tree (*Fraxinus excelsior*), a species of conservation concern and a key
97 component of British landscape complexity (Mitchell *et al.*, 2014), to create scenarios of
98 future bird richness.

99 **2. Materials and methods**

100 *2.1 Environmental heterogeneity variables*

101 This study focused on features considered likely to be relevant for bird diversity at the 1-km
102 scale that contribute to overall EH. We analysed biotic EH components (Stein *et al.*, 2014)
103 including; land cover, habitat features and vegetation. These components are important at
104 landscape scales (Tews *et al.*, 2004), and include aspects of both spatial and, in particular,

105 structural diversity, such as borders between habitats or individual trees. Abiotic EH
106 components, such as climate or soil, were not used because their heterogeneity is difficult to
107 detect at 1-km scale and they often influence bird richness indirectly through resource
108 provision and vegetation effects (Ferber *et al.*, 2014).

109 The EH predictors used were based on data collected during the UK Countryside Survey
110 of 2000 (CS2000) (Howard *et al.*, 2003). CS2000 compiled detailed information on the
111 landscape across a randomly stratified sample of nationally representative 569 1-km squares
112 of rural GB collected in 1998/1999. The sample was stratified according to the UK Institute
113 of Terrestrial Ecology (ITE) land classes which classify all 1km squares across GB
114 according to a range of biophysical variables (Bunce *et al.*, 1991). The variation of these
115 biophysical variables was minimised within the strata and maximised between strata. A
116 subset of 335 squares, for which bird survey data was collected as well as EH variables, was
117 used for this study. During the CS2000 surveys, the landscape was mapped and described at
118 a scale of 1:500, identifying the land cover of each parcel within each square, as well as a
119 wide variety of point and linear landscape features. All of the features present in non-urban
120 areas with a minimum length (>20m) and area (>0.04ha (minimum mappable unit (MMU)))
121 together with point features (including individual trees with diameter at breast height
122 (DBH)>5cm and other significant features below the MMU, such as ponds or patches of
123 scrub) were recorded.

124 Three types of CS-derived variables were used as components of EH within a square:
125 plant species diversity, habitat cover diversity and the presence of a range of landscape
126 features. The total number of plant species per square, recorded across all plot types in the
127 CS2000 surveys (Barr *et al.*, 2003), was used to characterise plant richness. Habitat cover
128 percentage estimates recorded in the CS2000 surveys were based on the UK Broad Habitats
129 classification (Jackson, 2000). As this study was specifically focused on identifying the
130 importance of aspects of heterogeneity other than ‘areas of habitat type’, rather than on
131 understanding the detailed ecology of either individual British bird species or groups of
132 them, ‘areas of habitat types’ were not explicitly included as predictors. Instead, a Shannon’s
133 habitat-cover diversity index (Magurran, 2013) for each square was used, as this was simpler
134 to interpret as a component of overall EH at the national scale. The Boundary and Linear
135 Features Broad Habitat was used as an EH variable by itself; in CS, it is recorded as areas
136 composed of linear landscape components which are greater than 20m in width, such as
137 grass strips, motorway, road and railway verges, wide field boundaries, etc.

138 Structural landscape features included attributes recorded on an area, linear or point basis.
139 Area features included; scattered trees and scrub (at densities well below those that would
140 constitute woodland) recorded on top of the habitat which was recorded as the main cover
141 (e.g. Neutral Grassland Broad Habitat), wide tree and scrub belts recorded as an area in their
142 own right, and clumps of trees and patches of scrub in areas above the MMU but not
143 constituting the main habitat (as per scattered trees and scrub). Linear features included

144 rivers, streams, ditches, hedges, fences, walls and lines of trees. Point features included
145 variables such as individual trees or small patches of trees or scrubs (below MMU). Table
146 S.1 shows the variables used as EH predictors of bird diversity.

147

148 *2.2 Bird richness*

149 Bird species richness data were collected in 335 CS2000 squares between April and June of
150 2000 (Wilson and Fuller, 2001) and are used as the response variable. Bird counts were
151 recorded along four line transects, measuring up to 4 km within each square, on each of two
152 separate visits during the early and late breeding season; the standard surveying
153 methodology of the BTO/JNCC/RSPB Breeding Bird Survey (BBS, Harris *et al.*, 2017) was
154 followed. The greater spatial intensity of survey should provide a more comprehensive
155 assessment of square-level bird abundance and species presence than the standard BBS
156 method. Bird richness for all squares was calculated by counting all the different species
157 recorded along any of the four transects (Table S.2).

158

159 *2.3 Random forests models and variable selection*

160 EH component variables can be highly correlated and may interact producing complex, non-
161 linear effects on bird diversity. The Random Forests (RF) regression (Breiman, 2001) does

162 not assume linear responses and is often used for its ability to handle complex interactions
163 between variables (Breiman, 2001; Prasad *et al.*, 2006). In recent years, RF tools have
164 assisted scientists in solving feature selection problems (Genuer *et al.*, 2010), through
165 feature importance analysis (Nicodemus *et al.*, 2010) and studying the shape of the predictor
166 effects on the response variables (Palczewska *et al.*, 2014). Here, we use RFs to determine
167 which components of EH, in combination, best predict species richness.

168 A RF regression model with 1000 trees was used to establish the response of bird species
169 richness, derived from the 335 CS bird surveys, to 25 EH predictors (Table S1). This RF
170 model was used to rank the explanatory power (importance) of each predictor. The mean
171 decrease in accuracy (MDA) and the Gini index (Breiman, 2001) were used to assess EH-
172 variable importance. The MDA index uses the left-out data samples not used for training the
173 RF model (out-of-bag data) to cross-validate the response predictions, by comparing the
174 accuracies of the final model with a model in which a given variable has been randomly
175 permuted. The Gini index uses the impurity measurements (how effectively a tree splits the
176 data) after a tree-node split for a given variable. Measuring the total Gini impurity decrease
177 across all of the trees in the forest gives a reliable variable importance measure.

178 Subsequent analyses were based on RF models using the six EH-variables identified as
179 being most important (Table 1). Although co-linearity cannot be completely removed and it
180 might influence the assessment of the variables' response analysis, feature selection reduces
181 complexity and correlation between predictors and simplifies interpretation. Robust and

182 objective selection of high ranking predictors can be challenging. Although the MDA and
183 Gini indices can be useful in the ranking and comparison of predictor importance, there is no
184 standard method of selecting variables for RF models. Several methods have been suggested
185 based on decreased model accuracy after discarding an arbitrary number of variables (Díaz-
186 Uriarte and De Andres, 2006; Genuer *et al.*, 2010). In order to avoid the use of arbitrary
187 accuracy thresholds, we excluded lower importance variables progressively, with reference
188 to the accuracy decrease curve after removing all of the variables one by one (Ishwaran *et*
189 *al.*, 2010). The randomForest package (Liaw and Wiener, 2002) in R (R Development Core
190 Team, 2013) was used to build and to analyse the RF models.

191 *2.4 Response of bird richness to EH variability*

192 The six highest ranked EH variables (Table 1) were analysed. First, scatterplots of bird
193 richness for each square were plotted against the EH variables, a linear regression model
194 was created and the Pearson correlation coefficient calculated. Density graphs of bird
195 richness and each predictor were plotted to get an overview of the data distribution shapes.
196 Correlations between the predictors were estimated to identify possible highly correlated
197 predictors.

198 Second, to account for possible non-linear relationships between bird richness and
199 explanatory variables, as well as complex multivariable interactions, RF analysis tools were

200 used. A new RF model was created using EH variables selected for importance. Then, a
201 feature contribution (FC) analysis was performed (Palczewska *et al.*, 2014). The FC is
202 calculated by recording the increments of the predicted response after each tree node split by
203 a given variable. The FC is the sum of all the increments for each observation for each
204 variable, divided by the number of trees. Plotting the FC against the value of each variable is
205 an effective means of separating and visualising the effect of a studied variable in isolation
206 on variations in the response variable predictions. The non-linearity of the FC plots was
207 tested by fitting the FC of each variable with a k-nearest neighbors (*knn*) regression model
208 and comparing its explanatory power to that of a linear regression. The forestFloor package
209 (Welling *et al.*, 2016) in R was used to calculate the FC and to fit the *knn* models.

210 *2.5 Predictive models*

211 National scale predictive models of bird richness were created. The top ranked EH variables
212 were up-scaled for all of GB, using satellite-derived land-cover data from the UK Land
213 Cover Map of 2000 (LCM2000, Fuller *et al.*, 2002) and the ITE Land Classification (Bunce
214 *et al.*, 1991). Broad Habitat (Jackson, 2000) percentages for each square were calculated
215 from LCM2000. These variables (land cover and land class) were then used to train RF
216 models to predict the most important EH component variables for each GB 1km square.
217 Modelled EH variables for each 1km square were then used to feed the RF model built with
218 the key variables (see previous section) to obtain a predictive map of bird richness for GB.

219 To test a scenario of how changes to key EH variables may impact on bird richness,
220 predictive bird richness models were created representing potential losses in GB ash tree
221 coverage from ash dieback, as would be seen in the top ranked EH variables (N.B. further
222 impacts would be likely to result from the loss of ash in woodland, which were not
223 considered here). Data derived from CS2000, which estimate the percentages of ash trees in
224 the different linear and point features at national scales and for each ITE Land class
225 (Maskell *et al.*, 2013), were used to alter the values of our bird richness predictors. These
226 predictors were then used to model (and map) bird richness changes under different ash loss
227 scenarios. The amount of ash trees present in linear and point features varied, ranging from
228 constituting between 1 and 26% of lines of trees (mean \pm sd: $3.9 \pm 4.2\%$), from 17 to 100%
229 of hedges ($36.1 \pm 20.58\%$) and from 0 to 41% of individual trees ($14.3 \pm 10.8\%$). These
230 three variables were modified using hypothetical values of ash tree percentage decrease
231 across GB, creating 11 scenarios: from 100% of ash (current state) to 0% of ash, with steady
232 decreases of 10%. For each ash tree percentage scenario, a modelled bird richness map was
233 created. Finally, the effects of potential ash tree losses were studied by detecting the 1-km
234 squares with severe bird richness decreases for each scenario.
235

236 **3. Results**

237 *3.1 Model accuracies and variable selection*

238 The RF model including the 25 EH variables explained over 71% of the variance in bird
239 richness, showing a strong association between bird richness and EH components. Very
240 similar variance-explained results were obtained with a RF internal cross validation and with
241 a 7-fold cross validation (this also applied to subsequent models). According to both
242 variable importance indices, lines of trees were the most important EH component
243 explaining bird richness. Plant richness, habitat diversity and boundary habitat at the square
244 level were also ranked in the top six EH variables, together with two other structural
245 variables: hedges (linear) and individual trees (point) (Fig. 1a and 1b). Table 1 summarises
246 the model's top ranked EH variables. Figure 2 shows that accuracy of the models (the
247 variance in bird richness that they explain) did not improve with the addition of extra
248 explanatory variables after the six top-ranked ones. As the top six most important variables
249 are the same for both indices according to Fig. 1a and 1b, those were the EH variables
250 selected to create a new RF model. The RF model that included the six top ranked variables
251 explained 71% of the variance in bird richness. This model was used to analyse the
252 responses of bird richness to EH.

253

254 3.2 Response of bird richness to EH variability

255 Plots of bird richness against the six analysed EH variables showed diverse relationships
256 (Fig. S.1). The Pearson correlation coefficient between bird richness and each EH variable,
257 in all cases, was higher than 0.45. The EH variables were correlated with one another to
258 various degrees, from near zero (hedges and habitat diversity) to 0.63 (hedges and lines of
259 trees).

260 The FC analysis showed different response shapes for different EH variables (Fig. 3).
261 These results support the idea that EH-richness relationships can be strongly dependent on
262 the measured EH component. The response of bird richness to the two linear features (lines
263 of trees and hedges) and to boundary habitat, showed saturating patterns, with a sharp
264 increase above a certain threshold value for the predictors. The effect of a line of trees on
265 increased bird richness was negative for values of zero to 100-120 m. Values for lines of
266 trees bigger than these values had a positive effect on bird richness, and this effect increased
267 asymptotically, saturating for a values of around 700 m. A similar pattern was observed for
268 hedges: values from 0 to 30 m had a negative effect on bird richness, while this effect was
269 increasingly positive from 30 m, stabilizing for values bigger than 1,200 m. The effect of the
270 boundary habitat also stabilised for values bigger than 15,000 m², and indeed values of
271 under 10,000 m were associated with negative effects on bird richness. For boundary habitat,
272 however, the positive effects on bird richness were weaker than for lines of trees or hedges.

273 The effect of individual trees on bird richness also followed an asymptotic pattern of
274 increase, but increased smoothly until saturating for values of 70-80 trees per km². Values of
275 under 20-25 trees per km² had a negative association with bird richness. Plant richness below
276 90-100 species across the whole 1km square was also associated with a negative effect on
277 bird species richness. At values of over 90-100 species, the effect became positive, but the
278 intensity of the effect started to decrease slightly after 150 species. The response of bird
279 richness to habitat diversity was the only one to follow a linear pattern (Table 2), as
280 expected from previous studies. A Shannon habitat diversity index value of higher than 1.7
281 positively affected bird richness, and the intensity of the effect increased linearly for higher
282 values.

283 For the response of bird richness to habitat diversity, the R^2 of the linear model was very
284 similar to the R^2 of the *knn* fitted model, the latter being an over fitted model relying on a
285 large number of parameters. The response of bird richness to individual trees also produced
286 a relatively high R^2 value for the linear model; however, the fitted *knn* model better
287 explained the FC distribution. One of the most interesting results of the study was that the
288 responses to the rest of the EH variables were clearly non-linear, with R^2 values of below
289 0.38; these responses were however relatively well explained by the *knn* models.

290

291 *3.3 Predictive models*

292 RF models predicted the values for each of the six top-ranked EH variables, based on the
293 LCM2000 land-cover percentages and ITE Land classes in CS2000 squares. The accuracies
294 for these models varied from 81·6% (habitat diversity) to 21·6% (boundary habitat). The
295 accuracies for hedges, lines of trees, plant richness and individual trees models were,
296 respectively, 61·3, 44·0, 43·0 and 38·0%. The EH variables were then up-scaled to the
297 whole of GB, based on land class and land cover. In turn, these were used to create
298 predictive models of bird richness for different scenarios of ash tree abundance (from 100 to
299 0% of current abundance) in these features. At current levels of ash abundance, maps of the
300 modelled variables showed important differences in bird richness (Fig. 4a), with all of the
301 predicted values varying between seven and 43 species in total and with 55% of richness
302 variance explained (estimated using a 7-fold cross validation). Areas of lower bird richness
303 were found in northern regions, as well as upland areas in Wales and Northern England.
304 Higher richness was found in the lowlands. A total loss of ash trees from these features was
305 associated with a loss of one or more species for 21% of all GB squares and a loss of three
306 or more species for 3% of squares (especially in regions situated at Eastern Scotland and in
307 lowlands of Central England, Fig. 4b). As expected, the most affected regions were

308 associated with land classes that contain significant amounts of ash trees as components of
309 lines of trees or hedges (such as arable-dominated lowland).

310 Rather than a steady decline in bird richness with decreasing proportions of ash trees, an
311 abrupt decrease in bird richness occurred for a presence of between 10 and 0% of ash trees
312 (Fig.5). This abrupt change was especially noticeable for squares with already relatively
313 low species numbers which had large decreases in bird richness (Fig. 5c and 5d).

314

315 **4. Discussion**

316 *4.1 EH effects on British bird richness*

317 Our analysis of 335 1-km squares across GB indicated that components of EH have strong
318 positive effects on bird richness, and that the strength of the effect is dependent on the
319 measurement in question. This positive EH-richness relationship on a 1-km scale may be
320 attributed to an increased number of bird niches. Our results reflect the predominance of
321 positive EH-diversity relationships found in studies in different regions of the world and
322 with different taxa (Stein *et al.*, 2014). Data rich in spatial detail, such as those collected by
323 the CS2000, are likely to provide increased potential for the detection of high EH variability
324 and related EH-diversity relationships (Van Rensburg *et al.*, 2002).

325 Biotic factors related to the structural properties of the landscape were the best predictors
326 of bird richness in GB. Two linear features and one point feature related to habitat structure
327 (i.e. lines of trees, hedges and individual trees) were identified as key components of EH in
328 our models. This supports the hypothesis that bird diversity is strongly regulated by the
329 structural diversity of the vegetation (Kissling *et al.*, 2008; Ferger *et al.*, 2014). Our study
330 indicates that hedges and individual trees are acting as keystone structures (Tews *et al.*,
331 2004) in the promotion of bird diversity in British ecosystems. Measurements of vegetation
332 and habitat diversity were also important predictors of British bird richness, and may be
333 associated with an increase in the diversity of nesting sites and food resources via plant or
334 animal prey species richness.

335

336 *4.2 EH-diversity non-linear relationships*

337 Previous studies have discussed the shape of EH-diversity relationships (Kadmon and
338 Allouche, 2007; Seiferling *et al.*, 2014; Marini *et al.*, 2008, 2011). Here we note that, with
339 the exception of habitat diversity, the responses of bird species richness to EH components
340 were all non-linear, most of them showing saturating relationships. Had we used traditional
341 linear modelling techniques instead of RF this would have been overlooked. Some EH
342 components showed moderate correlations with each other, but the analysis of responses,
343 based on feature contribution (FC) techniques, helped to isolate the effect of each variable.

344 This modelling approach revealed acute parabolic shapes for the EH components which
345 were linear landscape features. A sharp increase in the effect on bird richness was detected
346 for low values of each linear feature (Fig. 3) indicating that even low amounts of these
347 components of heterogeneity can promote and preserve richness. However, it should be
348 noted that the response of bird abundance to the value of a linear feature might be very
349 different for each species (Thompson *et al.*, 2016); with potential negative effects on some
350 species. This negative effect on some species may explain the stabilisation of the diversity
351 response at higher values of these variables. Similar effects, to those for linear features, were
352 also found for individual trees with predicted richness increasing to a maximum and then
353 stabilising at intermediate numbers of trees. This supports previous studies showing that the
354 presence of trees can regulate the abundance of some species (Tews *et al.*, 2004). A positive
355 linear relationship of bird species richness and habitat diversity has been found for a large
356 number of other studies (Bühning-Gaese, 1997; Hortal *et al.*, 2009). However, due to the
357 scale of the study, processes such as stochastic extinctions might not determine diversity
358 gradients for very high EH (Chocron *et al.*, 2015), and therefore the decreasing section of a
359 possible unimodal relationship would not be detected. In this case, the increase of niches
360 may be the main consequence of habitat diversity and partitioning, and therefore only a
361 linear increase in diversity would be observed.

362

363 *4.3 Ash trees loss scenarios*

364 Models, based on land classes and remotely sensed land-cover data, were used to upscale the
365 six key EH variables to a national scale and to create bird richness maps of GB. These types
366 of medium-high resolution, national-scale diversity maps are useful tools for assessing
367 important geographical differences, including detecting hot and cold spots for biodiversity
368 (Pressey, 2004). In order to predict the impact of ash tree loss on bird richness, the EH
369 predictors were altered to mimic ash loss scenarios over the next decades. Our predictive
370 maps showed very few changes in bird richness on a national scale for simulated ash
371 decreases of less than 90% in the EH components considered. However, significant losses
372 were predicted locally for the hypothetical extinction of ash trees. This result reflects the
373 non-linear effects of the linear and point EH variables on bird richness. In some regions, for
374 a certain level of ash tree decrease, the model predicts a step change in the EH-richness
375 relationship resulting in acute decreases in bird richness. The risk of reaching very low bird
376 species richness might increase for ash tree decreases above 90%. Bird richness levels
377 stayed stable in most regions, primarily because these areas contain very low amounts of
378 linear features and individual trees. However, it should be noted that reductions of ash in
379 woodland, may also have significant impacts on bird numbers for these areas.

380

381 *4.4 Applications for biodiversity prediction and conservation*

382 We provide an example of how the detection of non-linear relationships between EH
383 components and bird richness could help to identify tipping points for biodiversity loss. The

384 identification of non-linear relationships could be especially useful for scenarios that affect
385 the structural diversity of landscapes, such as the loss of ash trees in GB, because
386 components of EH that contribute to structural diversity are key to explaining bird diversity
387 at landscape scales. There are, however, several important limitations to this analysis,
388 including the fact that no account was taken of ash in woodland, that the potential
389 replacement of ash with other species providing similar structural functions was not
390 considered, and that ash trees may play roles within food webs (Mitchell *et al.*, 2014).

391 Prioritising conservation efforts through maintaining appropriate measures of EH can be
392 an effective tool for supporting biodiversity (Londono-Murcia *et al.*, 2010). Our results,
393 showing that diversity responses can vary for different EH components, could help to direct
394 efforts to maintain EH at a landscape level. For example, protecting minimal
395 extents/numbers of linear and point features might be enough to support current levels of
396 bird diversity. However, in upland areas where such features are not currently present,
397 increasing the length of linear features may be unlikely to increase diversity, as species
398 living in the uplands tend to have different ecological requirements to those living in lower
399 areas. Furthermore, previous studies have suggested that linear features are crucial for
400 promoting species diversity in the lowlands, while the quality of ecosystems may be more
401 important in the uplands (Petit *et al.*, 2004). Optimal EH levels might therefore also be
402 dependent on the level of human footprint (Seiferling *et al.*, 2014), with the maintenance of
403 EH for conservation purposes in Britain being strongly dependent on the anthropogenic

404 modification of the region under consideration. In contrast to results for increasing structural
405 components of EH, our results indicate that increasing habitat diversity might steadily
406 enhance bird diversity without arriving at any plateau within the current range of
407 heterogeneity.

408 An important element of the discussion on biodiversity conservation is the scale at which
409 diversity is measured. Our study uses nationally representative but highly resolved
410 information from a sample of 1-km squares to model relationships between EH components
411 and bird diversity at a national scale. Our results show that the presence/extent of EH
412 components is linked to overall measures of bird richness at 1km scales. However, whilst it
413 is important to preserve biodiversity at regional, national and global levels (Convention on
414 Biological Diversity, 2014), attempts to increase bird diversity by indiscriminately
415 increasing components of EH across Britain could be detrimental to national scale diversity,
416 as discussed above.

417 In summary, our analysis of British breeding birds indicates that the shapes of
418 relationships between EH components and bird richness were unique to each component and
419 generally non-linear. Separately studying the effects of each component, and using
420 methodological approaches that consider non-linear effects on diversity may help
421 conservationists to prioritise their management interventions, as well as help them to create
422 and interpret diversity projections in future environmental scenarios.

423

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429 Welsh Governments.

430

431 **Data references and access**

432 Countryside Survey 2000 data are deposited at the CEH Environmental Information Data
433 Centre as an aggregate of datasets; broad habitats: <https://doi.org/10.5285/acbb0f9c-f2a5-4cbd-97c3-84e786f2e479> (Barr *et al.*, 2016a), vegetation data:
434 <https://doi.org/10.5285/07896bb2-7078-468c-b56d-fb8b41d47065> (Barr *et al.*, 2016b),
435 landscape area features: <https://doi.org/10.5285/1e050028-5c55-42f4-a0ea-c895d827b824>
436 (Barr *et al.*, 2016c), linear features: <https://doi.org/10.5285/8aaf6f8c-c245-46bb-8a2a-f0db012b2643> (Barr *et al.*, 2016d), and point features: <https://doi.org/10.5285/ed10944f-40c8-4913-b3f5-13c8e844e153> (Barr *et al.*, 2016e). The LCM2000 data are deposited at:

440 <https://doi.org/10.5285/d5ee5360-12c5-448c-9d2b-f5c941fe3948> (Fuller *et al.*, 2002). The
441 ITE land classification data are deposited at: <https://doi.org/10.5285/5f0605e4-aa2a-48ab->
442 [b47c-bf5510823e8f](https://doi.org/10.5285/5f0605e4-aa2a-48ab-b47c-bf5510823e8f) (Bunce *et al.*, 2007).

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- 570

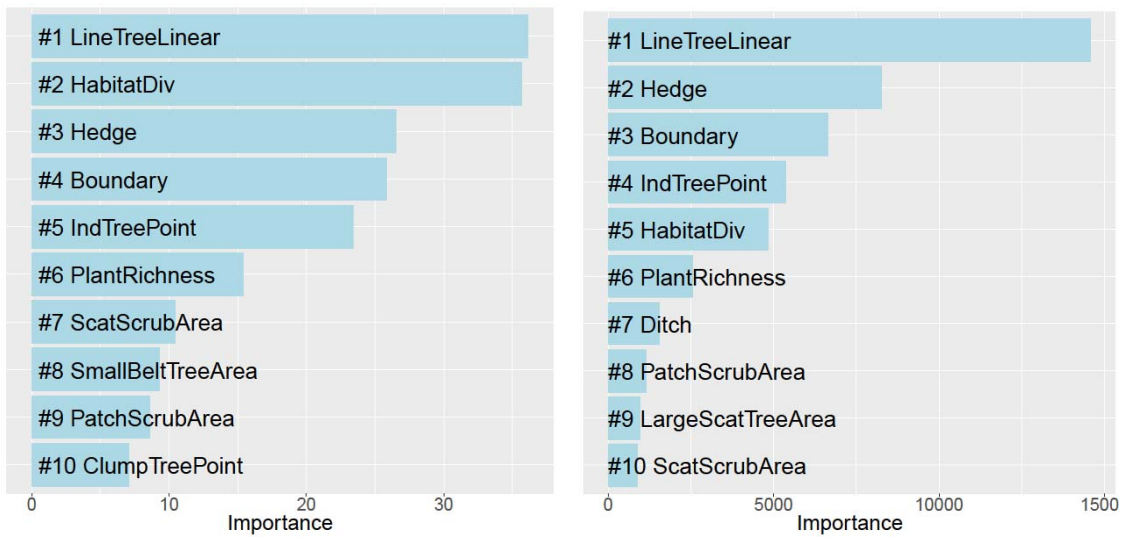
Table 1. Top ranked environmental heterogeneity variables by the random forests variable importance analysis. These variables were selected to study the bird richness responses to the variability of EH components.

EH Type	EH Component	EH Variable Name
Vegetation	Plant species richness	PlantRichness
Land cover	Land cover Shannon diversity	HabitatDiv
	Boundary habitat	Boundary
Structure	Lines of trees	LineTreeLinear
	Individual trees	IndTreePoint
	Hedges	Hedge

Table 2. R^2 values for the feature contribution plots (Fig. 3), estimated from the fitted k-nearest neighbor (*knn*) regression and linear models. The *knn* cross validation mean square errors were used to calculate an R^2 .

EH Variable	R^2	
	<i>knn</i>	linear
LineTreeLinear	0·93	0·37
Hedge	0·95	0·36
IndTreePoint	0·86	0·60
HabitatDiv	0·78	0·76
Boundary	0·87	0·37
PlantRichness	0·60	0·23

573



574

a) Mean decrease index

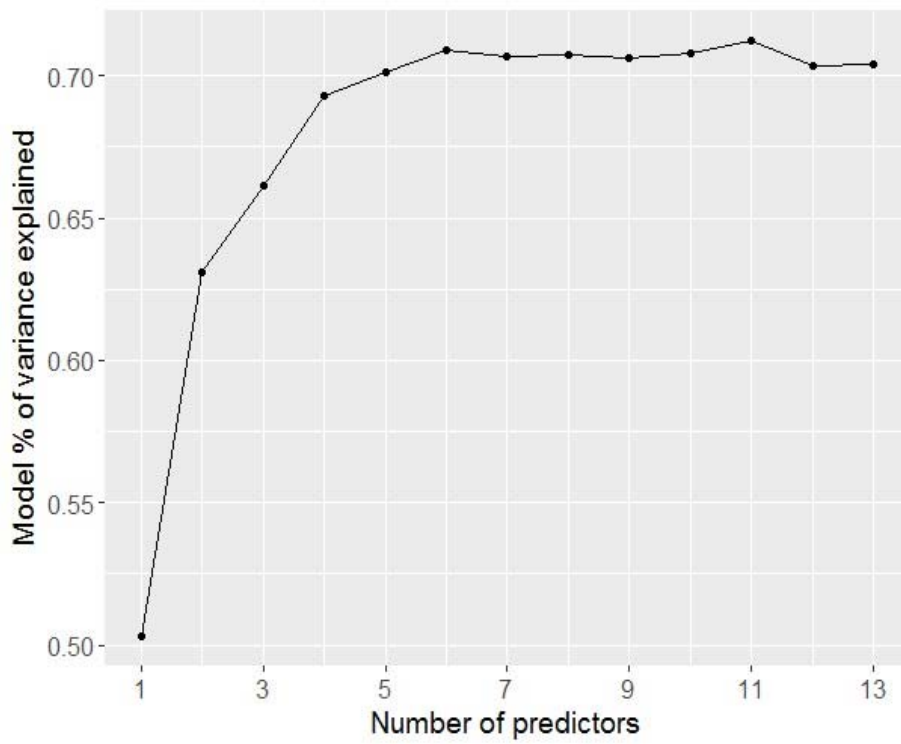
b) Gini

576

577 **Fig. 1.** Importance of the top ten ranked variables measured with two indices: mean decrease

578 in accuracy (a) and Gini (b).

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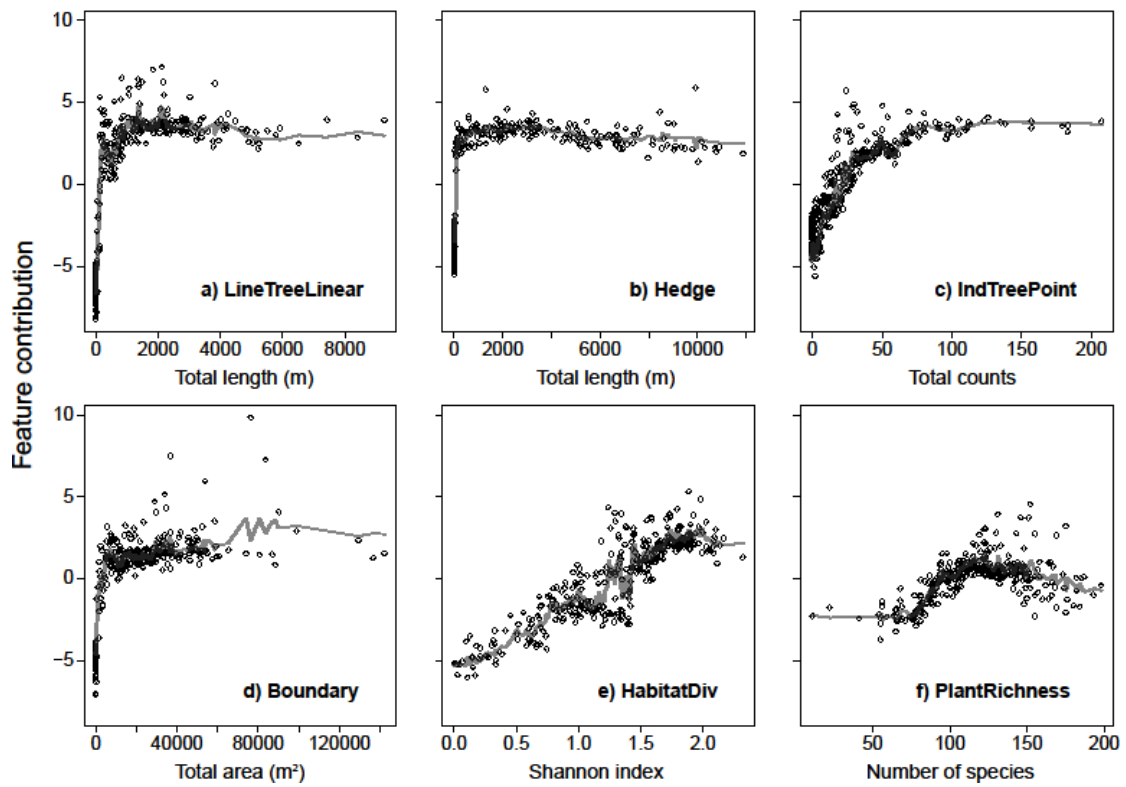
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582 **Fig. 2.** Variance explained (%) for the models including different number of predictors (by
583 ranking).

584

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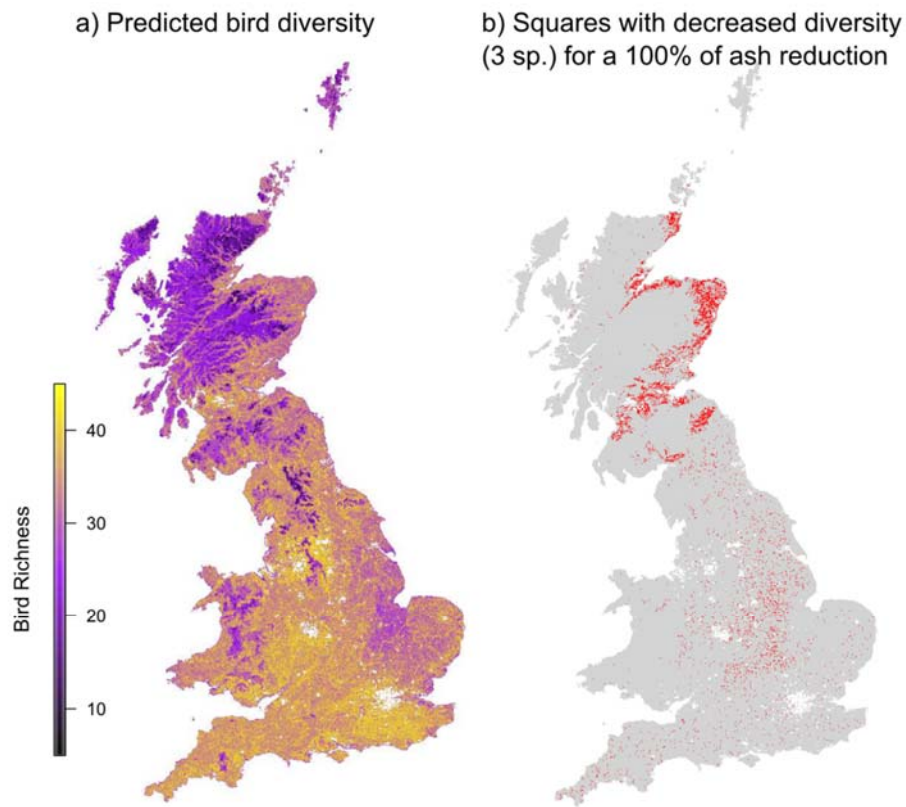


586

587 **Fig. 3.** Feature contributions plot. The y axis represents the change of predicted bird richness
588 for a given variable value, measured with the cross-validated feature contribution. The x axis
589 represents the value of the studied variable. The fitted line is based on k-nearest neighbor
590 (*knn*) estimations.

591

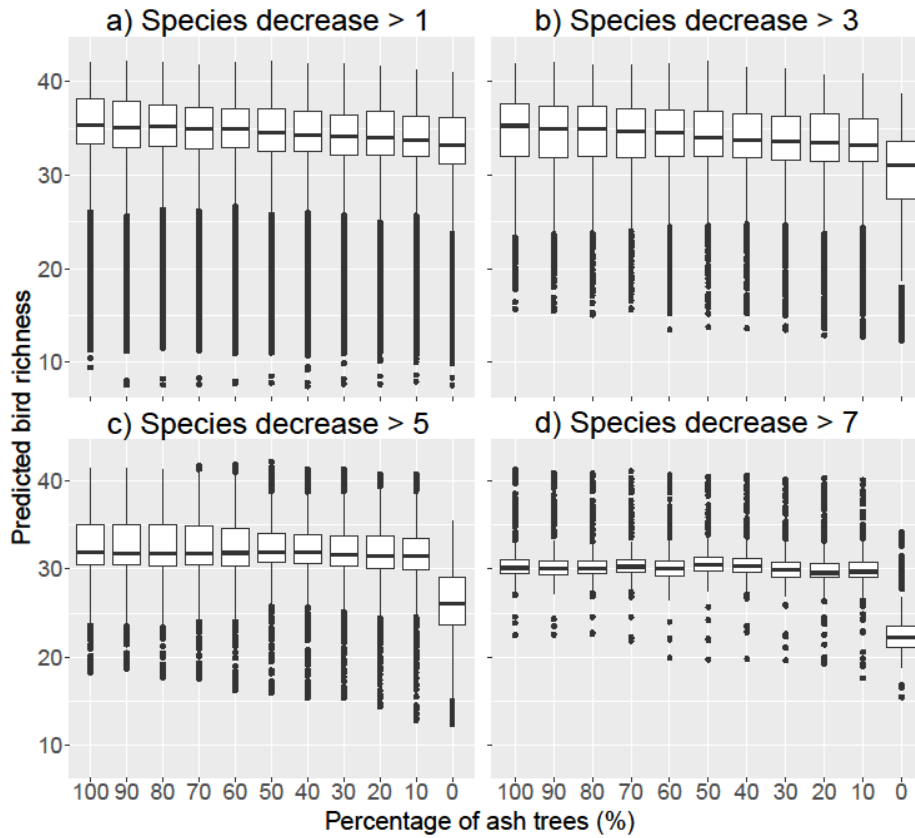
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593

594 **Fig. 4.** Predictive bird diversity maps. a) Predicted bird richness at 1-km scale for current
595 amounts of ash trees; b) 1-km squares (in red) with a decrease on bird diversity of at least 3
596 species, for an ash trees reduction of 100%.

597



598

599 **Fig. 5.** Tukey boxplots for predicted bird richness at 1-km² squares for different ash trees
 600 percentages. Each boxplot was created with a subset of squares presenting different total
 601 number of species decrease for the 11 scenarios of ash tree loss: a) 1 species (n = 49,888), b)
 602 3 species (n = 8,435), c) 5 species (n= 2,570), and d) 7 species (n = 697).