


**Please cite the Published Version**

Sullivan, MJP , Newson, SE and Pearce-Higgins, JW (2015) Using habitat-specific population trends to evaluate the consistency of the effect of species traits on bird population change. *Biological Conservation*, 192. pp. 343-352. ISSN 0006-3207

**DOI:** <https://doi.org/10.1016/j.biocon.2015.10.009>

**Publisher:** Elsevier

**Version:** Accepted Version

**Downloaded from:** <https://e-space.mmu.ac.uk/624028/>

**Additional Information:** This is an Author Accepted Manuscript of a paper accepted for publication in *Biological Conservation*, published by and copyright Elsevier.

**Enquiries:**

If you have questions about this document, contact [openresearch@mmu.ac.uk](mailto:openresearch@mmu.ac.uk). Please include the URL of the record in e-space. If you believe that your, or a third party's rights have been compromised through this document please see our Take Down policy (available from <https://www.mmu.ac.uk/library/using-the-library/policies-and-guidelines>)

1 **Using habitat-specific population trends to evaluate the consistency of the effect of species traits**  
2 **on bird population change**

3 Martin J. P. Sullivan<sup>1,2</sup>, Stuart E. Newson<sup>1</sup> \* and James W. Pearce-Higgins<sup>1</sup>

4 <sup>1</sup>British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK.

5 <sup>2</sup>School of Geography, University of Leeds, Leeds, LS2 9JT, UK.

6 \*Author for correspondence: [stuart.newson@bto.org](mailto:stuart.newson@bto.org).

7

8

9

10

11

12

13

14

15

16

17

18

19

20 Many species are undergoing rapid population declines, while other species have increased.  
21 Previous work has related population change to species traits to elucidate the drivers of population  
22 change. However, this assumes that these drivers operate consistently across habitats. We use  
23 national-scale monitoring data on UK bird abundance from 1994-2012 to calculate habitat-specific  
24 population trends, allowing us to evaluate whether the effect of species traits was consistent  
25 between habitats. Although we found significant interactions with habitat for traits relating to  
26 migratory behaviour, diet, nest site, body mass and habitat specialisation, the direction of these trait  
27 effects were generally consistent between habitats. This suggests that large-scale processes  
28 operating across habitats are responsible for many changes in bird populations, although processes  
29 operating within habitats can modulate the effect of these drivers. Despite this, differences in  
30 population trends between habitats remain when variation in population trends due to species  
31 identity is accounted for, indicating that some habitat effects do occur. By identifying the scale at  
32 which drivers of population change operate, it is possible to target conservation actions more  
33 directly. Population declines were most evident in woodland and urban habitats, and we suggest  
34 these habitats should be the focus of increased research and conservation effort if declines evident  
35 in many bird species are to be reversed.

36

37

38 Keywords: population decline; traits, habitat change; citizen science; breeding bird survey

39

40

41

42

43 **1. Introduction**

44 Large-scale biodiversity monitoring programmes, often utilising the participation of citizen scientists,  
45 have revealed rapid population changes in multiple taxa (Jiguet et al. 2012; Powney and Isaac 2015)  
46 These include declines in common moth species (Conrad et al. 2006) and climate induced changes in  
47 bird and butterfly populations (Devictor et al. 2012). Population declines are especially evident in  
48 certain habitats. In Europe, for example, widespread declines in farmland birds and more localised  
49 declines in woodland birds have been well documented (Donald et al. 2001; Hewson and Noble  
50 2009). These declines could result from a general reduction in habitat quality (i.e. be a property of a  
51 habitat), but could also be driven by the responses of certain species typical of a habitat to broad-  
52 scale environmental drivers (i.e. be a property of species), or some interaction between these  
53 habitat and species effects.

54 Understanding the extent to which habitat versus species effects drive population trends is  
55 important for directing conservation strategies. If population declines are primarily driven by habitat  
56 effects, then this supports the use of conservation interventions targeted in particular habitats to  
57 address specific changes in quality, while if population declines are primarily driven by species  
58 effects then species-specific conservation responses or landscape-scale measures that operate  
59 across habitats may be more appropriate to halt declines.

60 Investigations to date have tended to focus on either habitat effects or species effects, so  
61 understanding of their relative importance and interactions is limited. Whilst some studies have  
62 identified contrasting population trends between habitats, others have examined how bird  
63 population trends vary with species' characteristics, described by a range of ecological traits. Studies  
64 of European birds have revealed consistent associations with habitat specialism, with generalists  
65 having more positive population trends than specialists (Julliard et al. 2004; Le Viol et al. 2012; Salido  
66 et al. 2012; Shultz et al. 2005; Van Turnhout et al. 2010), and highlighted declines in populations of  
67 Afro-Palearctic migrants migrants (Ockendon et al. 2012; Salido et al. 2012; Sanderson et al. 2006;

68 Van Turnhout et al. 2010), particularly of species wintering in the humid bioclimatic zone (Thaxter et  
69 al. 2010). However, these studies look at national population trends, so do not allow the consistency  
70 of these trait effects to be evaluated between habitats. For example, the importance of traits such as  
71 migratory strategy for driving population trends varies spatially (Morrison et al. 2013), part of which  
72 may be associated with spatial variation in habitat cover. Given strong contrasts in population trends  
73 between habitats, it is therefore important to assess the extent to which the ecological traits  
74 associated with population trend may also vary between habitats to inform conservation action. If  
75 the importance of different traits varied strongly between habitats, this would indicate that the  
76 drivers of population trend are likely to differ between them.

77 Analysing habitat-specific population trends of species potentially allows the importance of habitat-  
78 level and species-level drivers of population change to be evaluated. We extend the methods  
79 developed by Newson et al. (2009) to calculate habitat-specific population trends for 89 bird species  
80 in the UK. Analysis of this dataset has shown that the broad pattern of these habitat-specific trends  
81 is consistent with the widespread operation of the buffer effect, where declining species retreat to  
82 high quality habitats while increasing species spread into lower quality habitats (Sullivan et al. 2015).  
83 However, the high degree of variation around this broad pattern suggests that other processes are  
84 also important in driving variation in population trends between habitats. In this study, we analyse  
85 these habitat-specific population trends with the aim of (1) identifying habitats where bird  
86 population trends are especially negative, (2) evaluating the relative importance of habitat- and  
87 species-effects in driving trends, and (3) assessing the consistency of trait effects between habitats.

## 88 **2. Materials and methods**

### 89 2.1 Habitat specific population trends

90 We calculated species' population trends using data from the Breeding Bird Survey (BBS), which  
91 since its inception in 1994 has been the principal monitoring scheme for populations of widespread

92 breeding birds in the UK. The BBS uses a stratified random sampling design, ensuring representative  
93 coverage of habitats throughout the UK (Baillie et al. 2014). BBS squares are also stratified by region  
94 to ensure maximum utilisation of available volunteers; BBS squares are weighted in later analyses to  
95 correct for biases in sampling effort introduced by this. Each BBS square is visited twice during the  
96 breeding season (mid-March to late-June), with the visits separated by at least four weeks. In each  
97 square, volunteers walk two 1 km transects (as close to parallel as possible), and record all bird  
98 species seen or heard within 200m transect sections. We used the maximum count of the two visits,  
99 and excluded flying birds except for aerial feeders, displaying skylarks *Alauda arvensis* and hovering  
100 common kestrels *Falco tinnunculus*.

101 Volunteers record up to two habitat classes for each 200m transect section following a hierarchical  
102 coding system described by Crick (1992). Following Newson *et al.*(2009), we reclassified habitats into  
103 12 habitat classes given in Table A1 (see Table A2 for number of BBS squares and transect sections  
104 surveyed in each year). These were deciduous woodland (abbreviated to DECID), mixed woodland  
105 (MIXW), coniferous woodland (CONIF), upland semi-natural open habitats (UPSN), lowland semi-  
106 natural open habitats (LOSN), arable farmland (ARAB), pasture (PAST), mixed farming (MIXF), rural  
107 settlements (RURA), urban settlements (URBA), wetlands (WETL) and flowing water (FLOW).

108 Separate population trends were calculated for each habitat. To do this, data were subset by habitat  
109 types so that only transect sections of a particular habitat contributed to the calculation of that  
110 habitat's trends. Log-linear generalised linear models with Poisson error terms were constructed  
111 using the GENMOD procedure in SAS 9.2 (SAS Institute 2008), with bird count modelled as a function  
112 of site (i.e. BBS square) and categorical year to give population indices in each year, with a dispersion  
113 parameter (deviance divided by the degrees of freedom) to account for overdispersion. Subsetting  
114 data in this way by habitat meant that the number of transect sections per site varied. To control for  
115 this we included the log of the number of transect sections containing the given habitat type as an  
116 offset variable (Newson et al. 2009).

117 We did not analyse change in annual population indices directly, as they are sensitive to yearly  
118 fluctuations. Instead, we fitted a post-hoc smoothed trend through the annual indices using non-  
119 parametric thin-plate splines, constraining the degrees of freedom to be the nearest integer to  $0.3 \times$   
120 length of time-series (Baillie et al. 2014). We calculated the population trend for each species  
121 between 1995 and 2011 as  $(\text{smoothed population index}_{2011} - \text{smoothed population index}_{1995}) /$   
122  $\text{smoothed population index}_{1995}$ . The first and last years of our dataset (1994 and 2012) were  
123 excluded from this calculation as they have a large influence of the direction of trends so may bias  
124 population changes (Baillie et al. 2014). For each species we repeated this procedure of calculating  
125 annual indices and then fitting post-hoc smooths on 199 bootstraps (Baillie et al. 2014), sampling  
126 with replacement each time. We calculated standard errors and confidence intervals around  
127 population trends from these bootstraps. Species were classed as increasing or declining if the 95%  
128 confidence limits of the population trend did not overlap zero. Habitat-specific population trends for  
129 all species are presented in Appendix B.

## 130 2.2 Ecological variables

131 We collated trait data on breeding season diet, nest site, mass, habitat specialisation, winter  
132 bioclimatic zone and thermal niche in order to test for trait – habitat interactions. Data on diet, mass  
133 and nest site were obtained from Snow and Perrins (2004), with the former two traits previously  
134 collated by Robinson (2005). Breeding season diet was categorised into the following mutually  
135 exclusive categories: herbivorous, granivorous, carnivorous – vertebrates (hereafter referred to as  
136 carnivorous), carnivorous – invertivorous (hereafter insectivorous) and omnivorous. Nest site was  
137 classified as into the following mutually exclusive categories: requiring low vegetation to nest (i.e.  
138 species nesting in shrubs < 2m above the ground, species nesting in low vegetation, and ground  
139 nesting species that nest in long grass or under other low vegetation (e.g. winchat *Saxicola rubetra*)),  
140 other ground nesting species (hereafter ground nesting), nesting in tree cavities, and nesting in  
141 trees. Species that did not fit into these categories, for example species nesting in buildings or on

142 water, were classed as other. Mass was taken as the mean mass of males and females. We obtained  
143 an index of species habitat specialisation (SSI) from Davey et al. (2012). This was calculated as the  
144 coefficient of variation of species densities across the 12 habitat classes (Table A1), with higher  
145 values indicating increasing habitat specialisation. Data on the wintering bioclimatic zone of species  
146 were obtained from Ockendon et al. (2012), Thaxter et al. (2010) and Morrison et al. (2013). Species  
147 were classified as resident, partial or short-distance (i.e. wintering north of the Sahara) migrant, or  
148 for trans-Saharan migrants wintering in either the arid, humid or southern bioclimatic zones. Only  
149 two species wintered in the southern bioclimatic zone, so these were combined with species  
150 wintering in the arid zone in subsequent analyses (humid zone species were treated separately as  
151 previous work has found they have contrasting population trends to other sub-Saharan migrants  
152 (Thaxter et al. 2010). An index of species thermal niche (STI), representing the mean breeding  
153 season temperature in a species' European distribution, was obtained from Devictor et al. (2008).

### 154 2.3 Statistical analysis

155 Analysis of population trends was performed in R (R Core Team 2014). We conducted analyses to (1)  
156 partition variation in habitat-specific population trends between species and habitats, (2) test for  
157 differences in population trends between habitats and (3) examine how consistent the effects of  
158 species traits were among habitats (details below). We used the natural log of population trend + 1  
159 in order to homogenize variances and ensure normality of residuals. Previous studies of population  
160 trends have restricted analyses to species that are on average recorded in more than 30 BBS squares  
161 each year as there may be insufficient power to detect declines in less well recorded species (Joys et  
162 al. 2003). This may lead to rare and declining species being excluded (Renwick et al. 2012). Instead,  
163 we used a more lenient threshold and included species-habitat combinations where a species was  
164 recorded on an average of 10 or more BBS squares per habitat type each year, but then down-  
165 weighted the importance of trends with high degrees of uncertainty in subsequent modelling by  
166 specifying case weights as the reciprocal of population trend standard error, which was also logged



167 to reflect our treatment of the population trend data. This approach allows infrequently recorded  
168 species with clear population trends to contribute to models, so maximises the number of species  
169 that can be included in the study, while reducing the influence of species with highly uncertain  
170 population trends. Despite the use of a more lenient threshold, a number of rare species were  
171 recorded too infrequently to be included in this study. In addition, we excluded common gull *Larus*  
172 *canus*, lesser black-backed gull *Larus fuscus*, herring gull *Larus argentatus*, black-headed gull  
173 *Chroicocephalus ridibundus* and grey heron *Ardea cinerea* from analyses, as the BBS survey design is  
174 not appropriate for assessing population trends of these colonial species (Baillie et al. 2014). In total  
175 there were 746 habitat-specific population trends of 89 species used in analysis.

176 We followed the method of Reino et al. (2005), adapted from Legendre and Legendre (2012), to  
177 partition the proportion of variation in population trends attributable to species and habitat. We  
178 fitted a linear model with population trend as a function of habitat and species (M1), as well as  
179 models with just habitat (M2) or species (M3) as explanatory variables. Explained variation in the full  
180 additive model consists of variation attributable to habitat, variation attributable to species, and  
181 shared variation due to correlations between species and habitat, while explained variation in the  
182 two constituent models consists of variation attributable to the target variable (species or habitat)  
183 and shared variation. This shared variation can be isolated by subtracting explained variation in the  
184 full model from the sum of explained variation in the two constituent models (i.e. shared variation =  
185  $M2 + M3 - M1$ ). This shared variation can then be subtracted from the constituent models (M2 and  
186 M3) to give the proportion of variation attributable to species and habitat. Unexplained variation in  
187 the full additive model (M1) is attributable to species-habitat interactions, as adding a species-  
188 habitat interaction term leads to a saturated model with no unexplained variation.

189 To test whether population trends differed between habitats, we used a mixed effects model with  
190 species as a random effect to model population trend as a function of habitat. Mixed effects models  
191 were constructed in lme4 (Bates et al. 2014). The purpose of the species random effect was to

192 account for the expected correlation of population trends of the same species. We repeated this  
193 analysis on a subset of species that occurred in all habitats, to test whether differences in population  
194 trends between habitats were a consequence of differences in species composition, or due to  
195 differing trends between habitats for the same species. Differences in population trends across all  
196 species between habitats could be driven by increasing species increasing more or less than the  
197 national average or declining species decreasing more or less than the national average. We  
198 explored this by repeating the modelling procedure described above separately for a subset of  
199 increasing species and a subset of declining species assessed from national population trends  
200 between 1995 and 2011 (Risely et al. 2013). We tested whether population trends in each habitat  
201 were significantly different from the overall mean population trend across all habitats and species  
202 (using the Satterthwaite approximation of degrees of freedom), and also used simultaneous tests of  
203 generalised linear hypotheses implemented in multcomp (Hothorn et al. 2008) to test for significant  
204 differences between habitat types. This analysis was repeated using a broader categorisation of five  
205 functional habitat classes (woodland – BROAD, CONIF and MIXW, semi-natural open – UPSN and  
206 LOSN, farmland – ARAB, PAST and MIXF, human – RURA and URBA and wetland – WETL and FLOW).  
207 To investigate whether population trends of specialist species varied between habitats, we first  
208 assessed whether species selected a habitat more frequently than expected given its availability by  
209 calculating Jacobs index,  $J_{h,s} = (u_{h,s} - a_{h,s}) / (u_{h,s} + a_{h,s} - 2 u_{h,s} a_{h,s})$ , where  $u_{h,s}$  is the proportion of  
210 observations of species  $s$  in habitat  $h$  and  $a_{h,s}$  is the proportion of transect sections in BBS squares  
211 where species  $s$  was recorded that contained habitat  $h$ . Jacobs index ranges from -1 to 1, with values  
212  $>0$  indicating more frequent selection of a habitat than expected given availability. We then used  
213 mixed effects models to model population trend as a function of habitat, restricting this analysis to  
214 species with Jacobs index values greater than 0. We repeated this with species where  $J > 0.25$ ,  
215 focusing the analysis further onto habitat specialists.

216 We tested for inter-habitat differences in the effect of species traits on population change by  
217 constructing a general linear mixed effects model (LMM) with habitat, traits and interactions

218 between traits and habitat for traits where we hypothesised *a priori* that the effect of the trait  
219 would vary among habitats (see Table 1 for hypotheses) as explanatory variables. We included SSI,  
220 STI, the natural logarithm of body mass, migratory strategy (resident, short distance or partial  
221 migrant, long-distance migrant wintering in the humid bioclimatic zone, long-distance migrant  
222 wintering elsewhere in sub-Saharan Africa), diet (insectivorous, granivorous, herbivorous,  
223 carnivorous or omnivorous) and nest site (ground, low vegetation, trees, tree cavities or other) as  
224 main effects. Given our hypotheses, interactions with habitat were included for STI, SSI, the humid  
225 and arid/ southern levels of migratory strategy, the insectivorous and granivorous levels of diet, and  
226 the ground, low vegetation and tree cavity levels of nest site. There were at least three species for  
227 each trait-habitat interaction combination (mean =  $15 \pm 10$  SD species, see Table A3 for number of  
228 species in each trait-habitat combination). Species was included as a random effect. This model was  
229 simplified by sequential removal of non-significant terms, followed by aggregation of factor levels  
230 until a minimum adequate model was obtained (Crawley 2007). We calculated variance inflation  
231 factors (VIF) to assess multicollinearity in predictor variables; these were  $< 3$  for all variables expect  
232 for diet, where  $VIF = 4.98$ . Diet was correlated with body mass, with granivorous and insectivorous  
233 species tending to be lighter than other species. Both body mass and diet were retained in our  
234 analysis, however repeating the analysis excluding body mass reduced multicollinearity ( $VIF < 2$ ) but  
235 resulted in the same minimum adequate model. We assessed model fit by plotting residuals against  
236 fitted values, as well as plotting residuals against each explanatory variable. In all cases no patterns  
237 were observed (Fig. A1).

238 We reduced the number of comparisons made during model selection by first assessing the  
239 significance of interactions with habitat as a whole, and only assessing the significance of  
240 interactions with individual habitat classes if the interaction with habitat was significant. Had we  
241 looked at all interactions with habitat classes in the full model then there would have been 124,  
242 giving a high probability of significant results occurring by chance. The Bonferonni adjustment for  
243 this number of tests is  $\alpha = 0.0004$ . However, such corrections have been criticized for being overly

244 conservative as highly significant results may be rejected (Crawley 2007). We therefore take a  
245 pragmatic approach to dealing with multiple testing, interpreting results where  $P < 0.0004$  as strongly  
246 supported, but still considering strongly significant results with larger  $P$  values (i.e.  $P \leq 0.01$  but  $\geq$   
247  $0.0004$ ) as worthy of discussion. Results where  $0.05 > P > 0.01$  are presented and retained in the  
248 minimum adequate model, but interpreted with caution. The significance of main effects that were  
249 also retained in the minimum adequate model as interactions was assessed by likelihood ratio tests  
250 of the model without the main effect and interaction term against the more complicated model just  
251 lacking the interaction term.

252 We repeated this test for inter-habitat differences in trait effects using phylogenetic generalised  
253 least squares (PGLS) to account for correlations between species trends that result from shared  
254 evolutionary history (Felsenstein 1985). We used a phylogenetic tree of British birds obtained from  
255 Thomas (2008). We implemented the model using Pagel's correlation structure (Paradis et al. 2004)  
256 in the gls procedure in nlme (Pinheiro and Bates 2007). The  $\lambda$  parameter in Pagel's correlation  
257 structure determines how similar the covariances are to those in a Brownian motion model of trait  
258 evolution, with values of 1 indicating Brownian motion and 0 indicating random trait evolution.  
259 Following Revell (2010) we parameterised  $\lambda$  simultaneously with coefficient estimation when fitting  
260 the PGLS.

### 261 **3. Results**

#### 262 3.1 Differences in overall population trends between habitats

263 There were significant differences in population trends between habitat classes ( $\chi^2 = 66.1$ ,  $P <$   
264  $0.0001$ ). Trends were significantly more negative in all woodland habitat classes and in urban/  
265 suburban habitats compared to the overall mean population trend across habitats (Fig. 1a).  
266 Population trends were most positive in wetlands and standing water, followed by both upland and  
267 lowland semi-natural grassland/ heath, but were not significantly different from the overall mean

268 across habitats (Fig. 1a). Largely similar patterns were evident when the analysis was restricted to  
269 species selecting a habitat more frequently than expected given availability (Fig. A2), although  
270 population trends were less negative in deciduous woodland, stable instead of negative in mixed  
271 woodland, positive instead of negative in coniferous woodland, and more negative in arable and  
272 mixed farmland (Fig. A2). Trends differed significantly between broad functional habitat classes ( $\chi^2 =$   
273 43.8,  $P < 0.001$ , Fig. 1b), driven by contrasting patterns for rural settlements and urban/ suburban  
274 settlements in the human class and wetlands/ standing water and flowing water in the wetland class  
275 (Fig. 1a).

276 When separating species showing positive national population trends from declining species,  
277 population trends of increasing species were significantly less positive in deciduous and mixed  
278 woodland than in other habitats (Figure 1c), while species that were declining nationally were  
279 declining more strongly in deciduous woodlands and in urban/ suburban areas than other habitats  
280 (Figure 1d). These differences in the magnitude of population trends were reflected in significant  
281 differences in the distribution of population trends between habitats ( $\chi^2 = 147.0$ ,  $P < 0.0001$ , Table  
282 A4). The highest proportion of declining species were found in urban/ suburban areas (32.7% of  
283 species declining), deciduous woodland (33.8%) and mixed woodland (38.3%). Large numbers of  
284 declining species were also found in rural settlements (29.6%) and in farmland habitat classes (23.9%  
285 - 28.2%), but were offset by a high proportion (46.3% - 54.4%) of species with increasing population  
286 trends in those habitats. In most habitats more species were estimated to be increasing in  
287 abundance than declining, with this pattern only reversed in mixed and deciduous woodland.

288

### 289 3.2 Partitioning variation in trend between species and habitats

290 Variation in habitat-specific population trends was largely explained by a strong independent effect  
291 of species (71.5% of variation in saturated model explained). Habitat alone explained 2.6% of

292 variation, with the combined effect of habitat and species explaining a further 0.4%. As this is a  
293 saturated model the remaining 25.5% of variation can be attributed to the interaction between  
294 species and habitats. This can be seen in considerable variation in species trends between habitats,  
295 with 23 species out of the 89 for which trends were calculated showing significant increases in one  
296 habitat and significant declines in another.

297 The importance of species does not mean that the differences in population trend between habitats  
298 (Fig. 1a) are unrelated to habitat. Observed contrasts in habitat-specific trends remained when this  
299 analysis was repeated only including generalist species that occur in all habitats (Fig. A3,  $\chi^2 = 26.9$ ,  $P$   
300 = 0.005).

### 301 3.3 Variation in population trends in relation to species traits

302 Migratory strategy, nest site and diet were retained in the minimum adequate mixed effects model  
303 (Table A5). Species wintering in the humid zone had more negative population trends than other  
304 species ( $\beta = -0.613 \pm 0.152$ ,  $\chi^2 = 15.8$ ,  $P < 0.0001$ ). Population trends of ground nesting species were  
305 more negative than species nesting in other places ( $\beta = -0.420 \pm 0.144$ ,  $\chi^2 = 8.6$ ,  $P = 0.003$ ). Although  
306 both granivore and insectivore factor levels of diet were retained in the minimum adequate model,  
307 neither was statistically significant as a main effect ( $\chi^2 \leq 0.3$ ,  $P \geq 0.608$ ).

308 The above traits were all retained in the minimum adequate phylogenetic model as well. However,  
309 in that analysis ground nesting was not significant as a main effect, while insectivorous species had  
310 more positive population trends than non-insectivorous species ( $\beta = 0.445 \pm 0.171$ ,  $F = 7.0$ ,  $P =$   
311 0.008). Several traits had significant effects in the phylogenetic analysis but not in the mixed effect  
312 model analysis (coefficients of both models in Table A5). Species requiring low vegetation to nest  
313 had more positive population trends ( $\beta = 0.500 \pm 0.138$ ,  $F = 13.5$ ,  $P = 0.0002$ ), while population trend  
314 was negatively related to STI ( $\beta = -0.056 \pm 0.024$ ,  $F = 5.5$ ,  $P = 0.0195$ ). SSI and the Arid/ Southern

315 bioclimatic zone factor level of migratory strategy were included in the minimum adequate  
316 phylogenetic model, but were not significant as main effects ( $F \leq 1.2$ ,  $P \geq 0.188$ ).

317

### 318 3.4 Consistency of trait effects between habitats

319 The effects of ecological traits were often consistent among habitats, with interactions mainly  
320 strengthening or weakening the effect of traits in certain habitats (Table 2). However, the direction  
321 of several trait effects was reversed; in the mixed effects model analysis granivorous and  
322 insectivorous species had more positive population trends than other species in upland semi-natural  
323 habitats but more negative population trends in other habitats, while in the phylogenetic analysis  
324 the direction of STI, SSI and ground nesting trait effects varied between habitats (Table 2).

325 Of the hypothesised trait-habitat interactions (Table 1), only interactions between migratory  
326 strategy and habitat were supported (Table 2, see Table A5 for coefficients). As hypothesised,  
327 population trends of Afro-Palearctic migrants wintering in the humid bioclimatic zone were less  
328 negative in coniferous woodlands (LMM:  $\chi^2 = 13.0$ ,  $P = 0.0003$ , PGLS:  $F = 10.5$ ,  $P = 0.001$ ) and upland  
329 semi-natural habitats (the latter only in the LMM analysis,  $\chi^2 = 9.8$ ,  $P = 0.0017$ ) and more negative in  
330 arable and mixed farmland (LMM:  $\chi^2 = 22.6$ ,  $P < 0.0001$ , PGLS:  $F = 26.0$ ,  $P < 0.0001$ ). To check this was  
331 not a result of a single-species outlier, this effect remained when the rapidly declining turtle dove  
332 *Streptopelia turtur*, which uses these habitats, was excluded ( $\chi^2 = 20.2$ ,  $P < 0.0001$ ). Migrants  
333 wintering in the arid/ southern bioclimatic zone had positive population trends in upland semi-  
334 natural habitats compared to negative trends elsewhere (PGLS analysis only,  $F = 7.2$ ,  $P = 0.002$ ).

335 Although other hypothesised trait-habitat interactions were not supported, some trait-habitat  
336 interactions that we did not predict *a priori* were statistically significant. Population trends of humid  
337 zone migrants were less negative in lowland semi-natural habitats (LMM:  $\chi^2 = 9.8$ ,  $P = 0.0017$ , PGLS:  
338  $F = 10.5$ ,  $P = 0.001$ ) and flowing water (the latter only in the LMM,  $\chi^2 = 5.5$ ,  $P = 0.019$ ), while

339 population trends of both humid and arid/ southern migrants were more negative in urban  
340 settlements (PGLS only,  $F = 26.0$ ,  $P < 0.0001$  and  $F = 9.7$ ,  $P = 0.002$  respectively). Granivorous species  
341 had more negative population trends in urban settlements (LMM:  $\chi^2 = 17.8$ ,  $P < 0.0001$ , PGLS:  $F =$   
342  $26.1$ ,  $P < 0.0001$ ) and in both wetland habitats than in other habitats ( $\chi^2 = 13.4$ ,  $P = 0.0002$ , PGLS:  $F =$   
343  $26.1$ ,  $P < 0.0001$ ). In the mixed model analysis both granivorous and insectivorous species had more  
344 positive population trends in upland semi-natural habitats ( $\chi^2 = 7.0$ ,  $P = 0.008$  and  $\chi^2 = 9.5$ ,  $P = 0.002$   
345 respectively) and insectivorous species had more negative population trends in urban settlements  
346 ( $\chi^2 = 9.9$ ,  $P = 0.002$ ), while in the phylogenetic analysis granivorous species had more negative  
347 population trends in mixed woodland (Table A5). Ground-nesting species had more negative  
348 population trends in urban settlements than in other habitats (LMM:  $\chi^2 = 15.4$ ,  $P < 0.0001$ , PGLS:  $F =$   
349  $24.5$ ,  $P < 0.0001$ ). In the phylogenetic analysis, STI had a contrasting effect between habitats, with a  
350 positive effect in arable and mixed farmland and rural and urban settlements compared to a  
351 negative effect in other habitats ( $F = 22.5$ ,  $P < 0.0001$ ). SSI had a non-significant negative effect in all  
352 habitats except for lowland semi-natural habitats, where it had a positive effect on population trend  
353 ( $F = 7.5$ ,  $P = 0.006$ ).

354

#### 355 **4. Discussion**

356 Population trends of UK breeding birds varied among habitats, with generally negative population  
357 trends in woodland and urban habitats. Despite these differences, the strongest component of  
358 variation was between species, indicating that many of the drivers of UK bird population trends are  
359 likely to be acting across habitats. However, species-scale effects are not the only driver of  
360 population change, as we found that variation in the strength of trait effects between habitats  
361 accounted for about a quarter of the variation in population trends. Our results are consistent in this  
362 respect with a previous study in The Netherlands investigating variation in the response of bird



363 communities to temperature and land-use change (Kampichler et al. 2012), and suggest that habitat-  
364 level drivers can ameliorate or enhance the effect of broad scale drivers.

#### 365 4.1 Effect of species traits on population trends

366 Many of the effects of species traits reported here are consistent with those found in previous  
367 studies looking at European bird population trends. Thus, as demonstrated previously, long distance  
368 humid zone migrants (Ockendon et al. 2012; Thaxter et al. 2010) and ground nesting species (Van  
369 Turnhout et al. 2010) were the most likely to decline in abundance. Declines of ground nesting  
370 species in the Netherlands have been attributed to increased nitrogen deposition and related  
371 increases in nitrophillous vegetation (Van Turnhout et al. 2010). Our results are consistent with this,  
372 with species requiring low vegetation to nest having more positive population trends in the  
373 phylogenetic analysis, but may also reflect the impact of increasing populations of generalist,  
374 particularly mammalian, predators upon ground-nesting species such as waders (MacDonald and  
375 Bolton 2008).

376 In contrast to previous studies, which have found that bird communities in Europe are becoming  
377 increasingly dominated by warm associated species (Devictor et al. 2008; Devictor et al. 2012;  
378 Kampichler et al. 2012), we find (in the phylogenetic analysis only) population declines in species  
379 associated with warmer regions. There are two potential explanations for this. Firstly, the UK  
380 experienced three successive winters with severe cold spells towards the end of the time series,  
381 including one month (December 2010) where temperatures were 5°C below the 1971-2000 mean  
382 (Met Office 2015), which were likely to have impacted populations of cold sensitive species (Pearce-  
383 Higgins et al. 2015). Excluding data from these three years weakens the overall relationship between  
384 population trend and STI ( $\beta = -0.019 \pm 0.027$ ). Secondly, in our analyses population trends of each  
385 species are weighted equally, so may give a different inference to that from analyses of change using  
386 weighted average community temperature associations in which the contribution of species is  
387 weighted by their abundance (e.g. Devictor et al. 2012; Kampichler et al. 2012). Using our data to

388 estimate changes in the Community Temperature Index (CTI) in a comparable way to these previous  
389 studies replicates the previously observed positive trend ( $\beta = 0.004 \pm 0.001$ ). Thus while we do not  
390 find that warm associated species are more likely to have increased, our data do not contradict  
391 previous studies that have documented increases in community averaged temperature associations,  
392 with differences in results instead due to methodological differences.

393 We did not find a significant relationship between population trend and body mass. Habitat  
394 specialisation was retained in the phylogenetic minimum adequate model due to a significant  
395 interaction with habitat, but was not significant as a main effect. Both traits have been found in be  
396 correlated with population trend in previous studies, with larger species and habitat generalists  
397 having more positive population trends (Salido et al. 2012; Shultz et al. 2005). Despite these traits  
398 not being significant, the direction of these trait effects in this study (positive relationship with mass,  
399 negative relationship with habitat specialisation) were consistent with previous studies.

#### 400 4.2 Consistency of drivers between habitats

401 Previously reported declines in humid zone migrants (Ockendon et al. 2012; Thaxter et al. 2010;  
402 Vickery et al. 2014) were particularly severe relative to other species in rural settlements, arable and  
403 mixed farmland. Such spatial variation is suggestive of a role of breeding season drivers of  
404 population decline (see also Morrison et al. 2013; Ockendon et al. 2012). As detrimental impacts  
405 during the breeding season have been reported in single species studies for the majority of  
406 European long-distance migrants breeding in farmland (Vickery et al. 2014), stronger declines in  
407 agricultural and rural settlement habitats could result from the interacting or additive effects of  
408 reduced resources in the breeding season due to agricultural intensification combined with habitat  
409 degradation and climatic stresses in the wintering grounds (Vickery et al. 2014). However, variation  
410 in habitat-specific trends could also result from density dependent processes. As species decline in  
411 response to a species-scale driver these declines are predicted to be stronger in less preferred  
412 habitats as species retreat to their preferred habitats (Sullivan et al. 2015).

413 One potential mechanism causing variation in habitat-specific trends of humid zone migrants could  
414 be that the arrival times of humid zone migrants may be constrained by their reliance on resource  
415 pulses following early spring rains prior to migration, potentially leading to phenological mismatch in  
416 their breeding grounds (Ockendon et al. 2012). The effect of this upon breeding success and  
417 population trends is likely to be less severe in habitats, such as coniferous woodland, where  
418 resources are less seasonal in abundance than in other habitats, such as deciduous woodland (Both  
419 et al. 2010). We found that declines in humid zone migrants were less severe in coniferous  
420 woodland, and to a lesser extent semi-natural grassland and heath, than in other habitats, providing  
421 some support for humid zone migrant declines being less negative in habitats with stable resources  
422 or relatively late phenologies. However, the less negative population trend of humid zone migrants  
423 in coniferous woodland was also at least partly due to such habitats being distributed further north  
424 (Fig. A5; see also Morrison et al. 2013; Ockendon et al. 2012), potentially because they have later  
425 phenologies or greater prey abundance than in the south (Conrad et al. 2006; Smith et al. 2011). This  
426 may also explain the steeper declines of humid zone migrants in rural areas and arable and mixed  
427 farmland, as these have a southerly distribution in the UK, so experience earlier springs and hence  
428 greater potential for phenological mismatch (Morrison et al. 2013). We note that the effect of  
429 phenological mismatch on habitat-specific population trends is further complicated by variation in  
430 migratory species' ability to change their arrival time (Møller et al. 2008) and by the potential for  
431 increased post-fledging survival to offset negative effects of phenological mismatch on productivity  
432 (Reed et al. 2013).

433 The weak negative relationship between habitat specialisation and population trend in most habitats  
434 in the phylogenetic analysis is consistent with the increasing domination of bird communities by  
435 generalist species reported previously in the UK (Davey et al. 2012), Sweden (Davey et al. 2013) and  
436 across Europe (Le Viol et al. 2012). The significant contrast between semi-natural open habitats,  
437 where this relationship was more positive than in other habits, was only apparent in the  
438 phylogenetic analysis and was not significant at the Bonferoni adjusted alpha level, but is consistent

439 with a previous assessment of rates of change in community specialisation in UK birds (Davey et al.  
440 2012) and on Dutch heath compared to farmland (Kampichler et al. 2012).

441 The effect of species thermal niche on population trends varied between habitats in the  
442 phylogenetic analysis, with a positive effect in more anthropogenic habitats (arable and mixed  
443 farmland, rural and urban settlements) and a negative effect in other habitats. A similar division in  
444 the direction of the effect of species thermal niche between more anthropogenic and more natural  
445 habitats has been reported by Kampichler et al. (2012), however in that study warm associated  
446 species increased in more natural habitats and became less dominant in farmland. The reasons for  
447 variation between habitats in the effect of temperature on bird communities in both studies are  
448 unclear, and warrant further investigation, but could reflect differences in the importance of climate  
449 and non-climate drivers of bird populations in different habitats (Eglington and Pearce-Higgins  
450 2012), or variation in the thermal association of species between habitats (e.g. Clavero et al. 2011;  
451 Kampichler et al. 2012).

452 We did not find support for the hypothesised interactions between diet and habitat (Table 1),  
453 although several others were identified. The hypothesis that granivorous species were declining  
454 more strongly in farmland was not supported, however, the more negative population trends of  
455 granivorous species in urban settlements and the two wetland habitats was highly statistically  
456 significant in both modelling approaches. The more negative trends of granivorous species in  
457 wetlands was not driven by a single species, as it remained significant when the wetland associated  
458 reed bunting *Emberiza schoeniclus* was removed ( $\chi^2 = 14.9$ ,  $P = 0.0001$ ), so the mechanisms behind  
459 this pattern need further exploration. The more negative population trends of granivorous and  
460 ground nesting birds in urban areas are discussed below.

461 4.3 Reasons for declines in woodlands and urban areas

462 Although our results suggest that species effects are more important than habitat effects, we do find  
463 support for consistent variation in trends between habitats. Declines were particularly evident in  
464 woodland habitats and urban/ suburban settlements, the latter contrasting with more positive  
465 trends in rural settlements. These differences were not due to differences in species composition  
466 between habitats, as these patterns remained when the analysis was repeated only including species  
467 found in all habitats (Fig. A3).

468 While declines in woodland bird populations have been noted previously (Hewson and Noble 2009),  
469 the strong negative population trends of birds in urban/ suburban areas contrasts with trends in  
470 rural settlements, and is the first time that such a difference has been documented in UK bird  
471 populations, but reflects wider evidence that urbanisation is associated with negative impacts on  
472 biodiversity (Aronson et al. 2014). Interestingly, despite negative overall population trends, large  
473 numbers of species were increasing in urban/ suburban areas, suggesting that environmental change  
474 there is creating both winners and losers. Indeed, population trends of nationally increasing species  
475 were comparable to the average across all habitats, with the overall negative trend instead driven by  
476 nationally declining species having more negative population trends in urban settlements than in  
477 other habitats (Fig 1d). Population declines were most evident in strong urban specialists (Jacobs  
478 index > 0.25) and species not positively associated with urban settlements (Jacobs index  $\leq 0$ ), while  
479 declines were not evident in species moderately associated with urban settlements (Jacobs index >0  
480 and  $\leq 0.25$ ).

481 Population trends of granivorous and ground nesting birds were more negative in urban areas in  
482 both mixed and phylogenetic models. A number of granivorous and/ or ground-nesting species  
483 typical of open farmland, such as linnet *Carduelis cannabina*, skylark *Alauda arvensis*, meadow pipit  
484 *Anthus pratensis* and yellowhammer *Emberiza citrinella*, were declining especially strongly in urban  
485 areas (Appendix B). These changes could be due to loss of urban wastelands for brownfield  
486 development, decline in the quality of open habitats in and bordering urban/ suburban areas, or a

487 density dependent shift in habitat preferences towards higher quality habitats outside urban areas  
488 as national populations decline (Sullivan et al. 2015). Although we did not specifically examine  
489 population trends of species nesting in cavities in buildings, house sparrows *Passer domesticus* and  
490 common swifts *Apus apus*, which both nest in or on buildings, were both declining more strongly in  
491 urban and suburban areas compared to other habitats. Both these species may be affected by  
492 renovations to buildings reducing the availability of cavities (Shaw et al. 2008).

493 General drivers that could be operating in urban and suburban areas include increased infilling of  
494 green space with houses (Evans et al. 2009), predation by cats (Beckerman et al. 2007), disease  
495 transmission at garden bird feeders (Robinson et al. 2010) and increased noise and light pollution  
496 (Francis et al. 2009). Similar drivers are likely to be operating in urban areas across Europe, so  
497 declines in urban bird populations may be evident in other countries. Further work will be important  
498 to evaluate the role of these habitat-level drivers in urban and suburban areas.

499 Apart from the main patterns apparent across all habitats, population trends in woodland did not  
500 vary strongly with species traits. For example, species associated with both the shrub layer (e.g.  
501 common whitethroat *Sylvia communis*, European robin *Erithacus rubecula*) and with mature trees  
502 (e.g. nuthatch *Sitta europaea*, great spotted woodpecker *Dendrocopos major*) had less positive  
503 population trends in deciduous woodlands than other habitats. Populations of both nationally  
504 increasing and nationally declining species tended to be more negative in woodlands than in other  
505 habitats, supporting the importance of general drivers of declines in woodland. However, declines  
506 were more severe in species that did not positively select woodland (Jacobs index  $\leq 0$ ), meaning that  
507 declines in woodland were stronger for generalist species and specialist species associated with  
508 other habitats than for woodland specialists. This may indicate that declining non-woodland  
509 specialists are retracting to their preferred habitats (Sullivan et al. 2015). However, population  
510 trends of deciduous woodland specialists were still negative, and may be more severe than indicated  
511 by this study as populations of woodland specialists underwent large declines prior to the start of

512 the BBS (Defra 2013). Candidate drivers include increased deer browsing (Newson et al. 2012),  
513 eutrophication, canopy shading, and reduction in the shrub layer, with associated taxonomic  
514 homogenisation of woodland floor plant communities (Keith et al. 2009) and increases in grass  
515 species at the expense of herbs (Corney et al. 2008). These changes may be responsible for declines  
516 in species using the understory and shrub layer of woodlands (Hewson and Noble 2009), with  
517 changes in canopy shading hinting at changes in woodland structure that may have influenced  
518 arboreal species. Population trends of woodland birds, as revealed by the woodland birds indicator,  
519 are similar in many parts of Europe (Gregory et al. 2007), so the declines noted here may be evident  
520 in other European countries. However, trends of woodland birds in central and eastern Europe are  
521 stable in contrast to a declining indicator elsewhere (Gregory et al. 2007). Two differences between  
522 these areas and the UK are lower densities of deer in continental Europe (Burbaité and Csányi 2010)  
523 and a higher nitrogen inputs in farming (and thus potentially greater eutrophication of woodland) in  
524 western Europe compared to eastern Europe (Liu et al. 2010).

525 Population trends in farmland were more positive than those in some other habitats. However, the  
526 trends produced here are relative to a baseline of the beginning of the BBS in 1994, when farmland  
527 bird populations were already low following steep declines between the mid-1970s and mid 1980s  
528 (Defra 2013). Ongoing declines in some species are evident, however, with 1/4<sup>th</sup> of species declining  
529 in farmland. Indeed, the generally positive population trends of species in farmland is likely to be  
530 driven by generalist species, as restricting the analysis to species with a strong preference for  
531 farmland (i.e. Jacobs index > 0.25) resulted in a negative overall population trend in mixed farmland  
532 and a stable overall population trend in arable farmland.

#### 533 4.4 Comparison with indicators

534 Different patterns were revealed by analysing habitat-specific population trends compared to  
535 species-based indicators. Although there has been a long term decline, the woodland bird indicator  
536 has largely been stable since the beginning of the BBS in 1994 (Defra 2013), although this national

537 assessment masks declines in woodland specialists, particularly in southern Britain, which are largely  
538 offset by increases further north (Massimino et al. 2015). However, habitat-specific trends of  
539 woodland birds have declined in this period. In contrast, both the farmland and wetland bird  
540 indicator trends have decreased over the BBS period (Defra 2013), while habitat-specific trends have  
541 been positive over this period. A key difference between indicators and habitat-specific trends is  
542 that the former contains habitat specialists (Renwick et al. 2012), while the latter also includes  
543 populations of generalists using that habitat. While many farmland specialists are declining, many  
544 generalist species associated with farmland are increasing (Massimino et al. 2015). Therefore, while  
545 around 1/4<sup>th</sup> of species for which farmland-specific population trends were calculated were  
546 declining, these were offset by increases in other species. Restricting our analysis to habitat  
547 specialists resulted in habitat-specific trends of woodland species being less negative or even  
548 positive, while trends in farmland became less positive or even negative (Fig. A2), supporting this  
549 explanation for differences between our results and wild bird indicators. For many applications  
550 indicators will be more relevant, as they focus on population trends of habitat specialists that are  
551 likely to be greater conservation priorities than generalists. However, analysis of habitat-specific  
552 trends sheds light onto the differing fortunes of a wider suite of species in different habitats and  
553 may therefore indicate previously undescribed patterns of environmental change. They are also  
554 likely to be particularly useful to monitor habitats with few specialists.

#### 555 4.5 Conclusions and conservation implications

556 Producing habitat-specific trends for birds in the UK has revealed considerable differences in  
557 population trends between habitats, with notable declines in birds in woodland and in urban/  
558 suburban areas. Population trends were largely driven by species-scale effects, particularly related  
559 to migratory strategy, with consistent declines in species that winter in the humid zone of Africa.  
560 However, variation in the strength of trait effects between habitats suggests that processes  
561 operating in certain habitats can enhance or reduce the effects of larger-scale drivers operating



562 across habitats. For example, reduced declines in humid-zone migrants in northern and less seasonal  
563 habitats was consistent with potential impacts of phenological mismatch. Importantly, the general  
564 consistency in the direction of trait effects indicates that while declines of certain groups of species  
565 were less severe in certain habitats, populations were still declining in these habitats, so they are  
566 unlikely to provide a refuge for these species.

567 It is important to assess whether large-scale drivers of population decline are also dominant in other  
568 taxa, as our results are from highly mobile species living in fragmented landscapes, where large-scale  
569 drivers may be more important. Indeed, our results contrast with two previous studies that suggest  
570 habitat-level effects are more important than species-level effects in explaining population declines  
571 in mammals (Cowlshaw et al. 2009; Fisher et al. 2003). However, our results may be used to infer  
572 that, for UK birds at least, habitat-specific conservation solutions to large-scale population declines  
573 may have only limited success. Certainly devising conservation strategies to address large-scale  
574 drivers of population change acting across habitats, such as the impacts of climate change or  
575 declines in long-distance migrants, will be challenging, but research in this area is of utmost  
576 importance. However, given strong declines in woodland and urban birds, there is an urgent need  
577 for further work to understand their causes. Whilst our findings for woodland birds are not novel  
578 (Hewson and Noble 2009), we believe that the negative trends we have identified for urban  
579 populations of species are, and should be urgently examined and addressed as an emerging signal of  
580 environmental degradation, particularly as it is in such environments that the greatest proportion of  
581 people encounter biodiversity.

## 582 **Acknowledgements**

583 We thank the many fieldworkers who collected data for the Breeding Bird Survey. The BBS is jointly  
584 funded by the Joint Nature Conservation Committee, the British Trust for Ornithology and the Royal  
585 Society for the Protection of Birds. This analysis was jointly funded by JNCC, BTO and RSPB. MS is

586 currently supported by ERC grant “Tropical Forests in the Changing Earth System”. We are grateful to  
587 the editor and three anonymous reviewers for commenting on this manuscript.

## 588 **References**

- 589 Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A., Warren, P.S.,  
590 Williams, N.S.G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J.L.,  
591 Kühn, I., MacGregor-Fors, I., McDonnell, M., Mörtberg, U., Pyšek, P., Siebert, S., Sushinsky, J.,  
592 Werner, P., Winter, M., 2014. A global analysis of the impacts of urbanization on bird and plant  
593 diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*  
594 281.
- 595 Baillie, S.R., Marchant, J.H., Leech, D.I., Massimino, D., Sullivan, M.J.P., Eglinton, S.M., Barimore, C.,  
596 Dadam, D., Downie, I., Harris, S.J., Kew, A.J., Newson, S.E., Noble, D.G., Risely, K., Robinson, R.A.,  
597 2014. *BirdTrends 2014: trends in numbers, breeding success and survival of UK breeding birds.*  
598 *Research Report 662, Thetford.*
- 599 Bates, D., Maechler, M., Bolker, B.M., Walker, S., 2014. *lme4: Linear mixed-effects models using*  
600 *Eigen and S4.*
- 601 Beckerman, A.P., Boots, M., Gaston, K.J., 2007. Urban bird declines and the fear of cats. *Animal*  
602 *Conservation* 10, 320-325.
- 603 Both, C., Van Turnhout, C.A.M., Bijlsma, R.G., Siepel, H., Van Strien, A.J., Foppen, R.P.B., 2010. Avian  
604 population consequences of climate change are most severe for long-distance migrants in seasonal  
605 habitats. *Proceedings of the Royal Society B: Biological Sciences* 277, 1259-1266.
- 606 Burbaitė, L., Csányi, S., 2010. Red deer population and harvest changes in Europe. *Acta Zoologica*  
607 *Lituanica* 20, 179-188.
- 608 Clavero, M., Villero, D., Brotons, L., 2011. Climate Change or Land Use Dynamics: Do We Know What  
609 Climate Change Indicators Indicate? *PLoS ONE* 6, e18581.
- 610 Conrad, K.F., Warren, M.S., Fox, R., Parsons, M.S., Woiwod, I.P., 2006. Rapid declines of common,  
611 widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*  
612 132, 279-291.
- 613 Corney, P.M., Kirby, K.J., Le Duc, M.G., Smart, S.M., McAllister, H.A., Marrs, R.H., 2008. Changes in  
614 the field-layer of Wytham Woods - assessment of the impacts of a range of environmental factors  
615 controlling change. *Journal of Vegetation Science* 19, 287-298.
- 616 Cowlshaw, G., Pettifor, R.A., Isaac, N.J.B., 2009. High variability in patterns of population decline: the  
617 importance of local processes in species extinctions. *Proceedings of the Royal Society B: Biological*  
618 *Sciences* 276, 63-69.
- 619 Crawley, M., 2007. *The R Book.* Wiley, Oxford.
- 620 Crick, H.Q.P., 1992. A bird-habitat coding system for use in Britain and Ireland incorporating aspects  
621 of land-management and human activity. *Bird Study* 39, 1-12.
- 622 Davey, C.M., Chamberlain, D.E., Newson, S.E., Noble, D.G., Johnston, A., 2012. Rise of the  
623 generalists: evidence for climate driven homogenization in avian communities. *Global Ecology and*  
624 *Biogeography* 21, 568-578.
- 625 Davey, C.M., Devictor, V., Jonzén, N., Lindström, Å., Smith, H.G., 2013. Impact of climate change on  
626 communities: revealing species' contribution. *Journal of Animal Ecology* 82, 551-561.
- 627 Defra, 2013. *Wild bird populations in the UK, 1972 to 2012.* Department for Environment, Food and  
628 *Rural Affairs, London.*
- 629 Devictor, V., Julliard, R., Couvet, D., Jiguet, F., 2008. Birds are tracking climate warming, but not fast  
630 enough. *Proceedings of the Royal Society B: Biological Sciences* 275, 2743-2748.
- 631 Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliola, J., Herrando, S.,  
632 Julliard, R., Kuussaari, M., Lindstrom, A., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C.,  
633 Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., Wynhoff, I., Jiguet, F., 2012.

634 Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Clim. Change*  
635 *2*, 121-124.

636 Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's  
637 farmland bird populations. *Proceedings of the Royal Society B: Biological Sciences* *268*, 25-29.

638 Eglinton, S.M., Pearce-Higgins, J.W., 2012. Disentangling the Relative Importance of Changes in  
639 Climate and Land-Use Intensity in Driving Recent Bird Population Trends. *PLoS ONE* *7*, e30407.

640 Evans, K.L., Newson, S.E., Gaston, K.J., 2009. Habitat influences on urban avian assemblages. *Ibis*  
641 *151*, 19-39.

642 Felsenstein, J., 1985. Phylogenies and the comparative method. *American Naturalist*, 1-15.

643 Fisher, D.O., Blomberg, S.P., Owens, I.P.F., 2003. Extrinsic versus intrinsic factors in the decline and  
644 extinction of Australian marsupials. *Proceedings of the Royal Society B: Biological Sciences* *270*,  
645 1801-1808.

646 Francis, C.D., Ortega, C.P., Cruz, A., 2009. Noise pollution changes avian communities and species  
647 interactions. *Curr Biol* *19*, 1415-1419.

648 Gregory, R.D., Vorisek, P., Van Strien, A., Gmelig Meyling, A.W., Jiguet, F., Fornasari, L., Reif, J.,  
649 Chylarecki, P., Burfield, I.J., 2007. Population trends of widespread woodland birds in Europe. *Ibis*  
650 *149*, 78-97.

651 Hallmann, C.A., Foppen, R.P.B., van Turnhout, C.A.M., de Kroon, H., Jongejans, E., 2014. Declines in  
652 insectivorous birds are associated with high neonicotinoid concentrations. *Nature* *511*, 341-343.

653 Hewson, C.M., Noble, D.G., 2009. Population trends of breeding birds in British woodlands over a 32-  
654 year period: relationships with food, habitat use and migratory behaviour. *Ibis* *151*, 464-486.

655 Holt, C.A., Fuller, R.J., Dolman, P.M., 2010. Experimental evidence that deer browsing reduces  
656 habitat suitability for breeding Common Nightingales *Luscinia megarhynchos*. *Ibis* *152*, 335-346.

657 Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous Inference in General Parametric Models.  
658 *Biometrical Journal* *50*, 346-363.

659 Jiguet, F., Devictor, V., Julliard, R., Couvet, D., 2012. French citizens monitoring ordinary birds  
660 provide tools for conservation and ecological sciences. *Acta Oecologica* *44*, 58-66.

661 Joys, A., Noble, D.G., Baillie, S.R., 2003. Evaluation of species coverage and precision using the BBS  
662 indexing method. British Trust for Ornithology, Thetford.

663 Julliard, R., Jiguet, F., Couvet, D., 2004. Common birds facing global changes: what makes a species  
664 at risk? *Global Change Biology* *10*, 148-154.

665 Kampichler, C., van Turnhout, C.A.M., Devictor, V., van der Jeugd, H.P., 2012. Large-Scale Changes in  
666 Community Composition: Determining Land Use and Climate Change Signals. *PLoS ONE* *7*, e35272.

667 Keith, S.A., Newton, A.C., Morecroft, M.D., Bealey, C.E., Bullock, J.M., 2009. Taxonomic  
668 homogenization of woodland plant communities over 70 years. *Proceedings of the Royal Society B:*  
669 *Biological Sciences*.

670 Le Viol, I., Jiguet, F., Brotons, L., Herrando, S., Lindström, Å., Pearce-Higgins, J.W., Reif, J., Van  
671 Turnhout, C., Devictor, V., 2012. More and more generalists: two decades of changes in the  
672 European avifauna. *Biology Letters* *8*, 780-782.

673 Legendre, P., Legendre, L.F., 2012. *Numerical ecology*. Elsevier.

674 Liu, J., You, L., Amini, M., Obersteiner, M., Herrero, M., Zehnder, A.J.B., Yang, H., 2010. A high-  
675 resolution assessment on global nitrogen flows in cropland. *Proceedings of the National Academy of*  
676 *Sciences* *107*, 8035-8040.

677 MacDonald, M.A., Bolton, M., 2008. Predation on wader nests in Europe. *Ibis* *150*, 54-73.

678 Massimino, D., Johnston, A., Noble, D.G., Pearce-Higgins, J.W., 2015. Multi-species spatially-explicit  
679 indicators reveal spatially structured trends in bird communities. *Ecological Indicators* *58*, 277-285.

680 Met Office, 2015. *UK Climate Summaries*.

681 Møller, A.P., Rubolini, D., Lehikoinen, E. 2008. Populations of migratory bird species that did not  
682 show a phenological response to climate change are declining. *PNAS* *105*, 16195-16200.

683 Morrison, C.A., Robinson, R.A., Clark, J.A., Risely, K., Gill, J.A., 2013. Recent population declines in  
684 Afro-Palaeartic migratory birds: the influence of breeding and non-breeding seasons. *Diversity and*  
685 *Distributions* 19, 1051-1058.

686 Newson, S.E., Johnston, A., Renwick, A.R., Baillie, S.R., Fuller, R.J., 2012. Modelling large-scale  
687 relationships between changes in woodland deer and bird populations. *Journal of Applied Ecology*  
688 49, 278-286.

689 Newson, S.E., Ockendon, N., Joys, A., Noble, D.G., Baillie, S.R., 2009. Comparison of habitat-specific  
690 trends in the abundance of breeding birds in the UK. *Bird Study* 56, 233-243.

691 Newton, I., 1998. Population limitation in birds. Academic Press, London.

692 Ockendon, N., Hewson, C.M., Johnston, A., Atkinson, P.W., 2012. Declines in British-breeding  
693 populations of Afro-Palaeartic migrant birds are linked to bioclimatic wintering zone in Africa,  
694 possibly via constraints on arrival time advancement. *Bird Study* 59, 111-125.

695 Paradis, E., Claude, J., Strimmer, K., 2004. APE: Analyses of Phylogenetics and Evolution in R  
696 language. *Bioinformatics* 20, 289-290.

697 Pearce-Higgins, J.W., Eglinton, S.M., Martay, B., Chamberlain, D.E., 2015. Drivers of climate change  
698 impacts on bird communities. *Journal of Animal Ecology* 84, 943-954.

699 Pinheiro, J., Bates, D., 2007. Linear and nonlinear mixed effects models.

700 Powney, G.D., Isaac, N.J., 2015. Beyond maps: a review of the applications of biological records.  
701 *Biological Journal of the Linnean Society*.

702 R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for  
703 Statistical Computing, Vienna, Austria.

704 Reed, T.E., Jenouvrier S., Visser, M.E. 2013. Phenological mismatch strongly affects individual fitness  
705 but not population demography in a woodland passerine. *Journal of Animal Ecology* 82, 131-144.

706 Reino, L., 2005. Variation partitioning for range expansion of an introduced species: the common  
707 waxbill *Estrilda astrild* in Portugal. *Journal of Ornithology* 146, 377-382.

708 Renwick, A.R., Johnston, A., Joys, A., Newson, S.E., Noble, D.G., Pearce-Higgins, J.W., 2012.  
709 Composite bird indicators robust to variation in species selection and habitat specificity. *Ecological*  
710 *Indicators* 18, 200-207.

711 Revell, L.J., 2010. Phylogenetic signal and linear regression on species data. *Methods in Ecology and*  
712 *Evolution* 1, 319-329.

713 Risely, K., Massimino, D., Newson, S.E., Eaton, M.A., Musgrove, A.J., Noble, D.G., Procter, D., Baillie,  
714 S.R., 2013. The Breeding Bird Survey 2012. British Trust for Ornithology, Thetford.

715 Robinson, R.A., 2005. BirdFacts: profiles of brds occuring in Britain & Ireland. British Trust for  
716 Ornithology, Thetford.

717 Robinson, R.A., Lawson, B., Toms, M.P., Peck, K.M., Kirkwood, J.K., Chantrey, J., Clatworthy, I.R.,  
718 Evans, A.D., Hughes, L.A., Hutchinson, O.C., John, S.K., Pennycott, T.W., Perkins, M.W., Rowley, P.S.,  
719 Simpson, V.R., Tyler, K.M., Cunningham, A.A., 2010. Emerging Infectious Disease Leads to Rapid  
720 Population Declines of Common British Birds. *PLoS ONE* 5, e12215.

721 Salido, L., Purse, B.V., Marrs, R., Chamberlain, D.E., Shultz, S., 2012. Flexibility in phenology and  
722 habitat use act as buffers to long-term population declines in UK passerines. *Ecography* 35, 604-613.

723 Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J., van Bommel, F.P.J., 2006. Long-term population  
724 declines in Afro-Palaeartic migrant birds. *Biological Conservation* 131, 93-105.

725 SAS Institute, 2008. SAS 9.2. Statistical Analysis System Institute Inc., Cary, North Carolina.

726 Shaw, L., Chamberlain, D., Evans, M., 2008. The House Sparrow *Passer domesticus* in urban areas:  
727 reviewing a possible link between post-decline distribution and human socioeconomic status.  
728 *Journal of Ornithology* 149, 293-299.

729 Shultz, S., Bradbury, R.B., Evans, K.L., Gregory, R.D., Blackburn, T.M., 2005. Brain size and resource  
730 specialization predict long-term population trends in British birds. *Proceedings of the Royal Society*  
731 *B: Biological Sciences* 272, 2305-2311.

732 Siriwardena, G.M., Calbrade, N.A., Vickery, J.A., 2008. Farmland birds and late winter food: does  
733 seed supply fail to meet demand? *Ibis* 150, 585-595.

734 Smith, K.W., Smith, L., Charman, E., Briggs, K., Burgess, M., Dennis, C., Harding, M., Isherwood, C.,  
735 Isherwood, I., Mallord, J., 2011. Large-scale variation in the temporal patterns of the frass fall of  
736 defoliating caterpillars in oak woodlands in Britain: implications for nesting woodland birds. *Bird  
737 Study* 58, 506-511.

738 Snow, D., Perrins, C., 2004. *The Birds of the Western Palearctic Interactive*. Oxford University Press,  
739 Oxford.

740 Sullivan, M.J.P., Newson, S.E., Pearce-Higgins, J.W., 2015. Evidence for the buffer effect operating in  
741 multiple species at a national scale. *Biology Letters* 11.

742 Thaxter, C.B., Joys, A.C., Gregory, R.D., Baillie, S.R., Noble, D.G., 2010. Hypotheses to explain patterns  
743 of population change among breeding bird species in England. *Biological Conservation* 143, 2006-  
744 2019.

745 Thomas, G.H., 2008. Phylogenetic distributions of British birds of conservation concern. *Proceedings  
746 of the Royal Society B: Biological Sciences* 275, 2077-2083.

747 Van Turnhout, C.A.M., Foppen, R.P.B., Leuven, R.S.E.W., Van Strien, A., Siepel, H., 2010. Life-history  
748 and ecological correlates of population change in Dutch breeding birds. *Biological Conservation* 143,  
749 173-181.

750 Vickery, J.A., Ewing, S.R., Smith, K.W., Pain, D.J., Bairlein, F., Škorpilová, J., Gregory, R.D., 2014. The  
751 decline of Afro-Palaeartic migrants and an assessment of potential causes. *Ibis* 156, 1-22.

752

753

754

755

756

757

758

759

760

761

762

763

764

765 **Tables**

766 **Table 1.** Hypothesised trait-habitat interactions. Predictions that were found to be supported are  
767 shown in bold.

Trait	Mechanism leading to interaction	Predicted interactions
Migratory	(1) Consequences of phenological mismatch less	<b>(1.1) Declines of long-distance</b>

strategy	severe in habitats with more stable resource environments (Both et al. 2010) or in cooler habitats where spring arrives later.	<b>migrants stronger in deciduous woodland than coniferous woodland.</b>
	(2) Interaction between processes in the breeding and non-breeding grounds lead to stronger declines in long-distance migrants in habitats with the greatest human influence (Vickery et al. 2014).	<b>(1.2) Declines of long-distance migrants weaker in uplands.</b>  <b>(2) Declines of long-distance migrants stronger in farmland.</b>
Nest site	(3) Ground nesting species sensitive to agricultural activity in breeding season (Van Turnhout et al. 2010).	(3) Population trends of ground nesting birds more negative in farmland.
	(4) Eutrophication and subsequent scrub encroachment into grasslands and changes in woodland ground cover favours species nesting in low vegetation over ground nesting species (Corney et al. 2008; Van Turnhout et al. 2010).	(4) Population trends of ground nesting birds more negative in semi-natural grassland and woodland
	(5) Loss of understory vegetation in woodland due to deer browsing (Holt et al. 2010).	(5) Population trends of species nesting in low vegetation more negative in woodland.
	(6) Availability of tree cavities limiting populations of cavity nesting species (Newton 1998).	(6) More negative population trends of cavity nesting species in woodland.
Diet	(7) Shortage of seeds in farmland reduces winter survival of granivorous species (Siriwardena et al. 2008).	(7) More negative population trends of granivorous species in arable farmland.
	(8) Agricultural intensification, including pesticide use, reduces the abundance of invertebrates in agricultural areas, reducing food availability of insectivorous species (Hallmann et al. 2014).	(8) More negative population trends of insectivorous species in farmland.
SSI	(9) Adaptable generalist species better able to exploit resources in human-modified habitats (Davey et al. 2012; Shultz et al. 2005).	(9) Relationship between habitat specialisation and population trend more negative in farmland and human settlements.

STI (10) Greater impact of climate change relative to other environmental change in semi-natural habitats (Eglington and Pearce-Higgins 2012; Kampichler et al. 2012). (10) Positive effect of STI on population trend less evident in farmland and human settlements.

768  
769  
770  
771  
772  
773  
774  
775  
776  
777  
778  
779  
780

781 **Table 2.** Consistency of trait effects among habitats.

Model	Habitat	Migratory strategy		Diet		Nest Ground	STI	SSI
		Humid	Arid/southern	Granivore	Insectivore			
LMM	DECID	↓	NS	(↓)	(↓)	↓	NS	NS
	CONIF	↘ ***	NS	(↓)	(↓)	↓	NS	NS
	MIXW	↓	NS	(↓)	(↓)	↓	NS	NS
	UPGR	↘ **	NS	↑ **	↑ **	↓	NS	NS
	LOGR	↘ **	NS	(↓)	(↓)	↓	NS	NS
	ARAB	↓↓ ***	NS	(↓)	(↓)	↓	NS	NS
	PAST	↓	NS	(↓)	(↓)	↓	NS	NS

	MIXF	↓↓ ***	NS	(↓)	(↓)	↓	NS	NS
	RURA	↓↓ ***	NS	(↓)	(↓)	↓	NS	NS
	URBA	↓	NS	↓↓ ***	↓↓ **	↓↓ ***	NS	NS
	WETL	↓	NS	↓↓ ***	(↓)	↓	NS	NS
	FLOW	↘ *	NS	↓↓ ***	(↓)	↓	NS	NS
PGLS	DECID	↓	(↓)	↑	↑	(↓)	↓	(↓)
	CONIF	↘ **	(↓)	↑	↑	(↓)	↓	(↓)
	MIXW	↓	(↓)	↗ ***	↑	(↓)	↓	(↓)
	UPGR	↓	↑ **	↑	↑	↑ ***	↓	(↓)
	LOGR	↘ **	(↓)	↑	↑	(↓)	↓	↑ **
	ARAB	↓↓ ***	(↓)	↑	↑	(↓)	↑ ***	(↓)
	PAST	↓	(↓)	↑	↑	(↓)	↓	(↓)
	MIXF	↓↓ ***	(↓)	↑	↑	(↓)	↑ ***	(↓)
	RURA	↓↓ ***	(↓)	↑	↑	(↓)	↑ ***	(↓)
	URBA	↓↓ ***	↓↓ **	↗ ***	↑	↓↓ ***	↑ ***	(↓)
	WETL	↓	(↓)	↗ ***	↑	(↓)	↓	(↓)
	FLOW	↓	(↓)	↗ ***	↑	(↓)	↓	(↓)

782 Arrows show the direction of trait effects, with arrows in parentheses denoting non-significant  
783 effects. Asterisks show the significance of trait habitat interactions; \*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ , \*  $P$   
784  $< 0.05$ . Double arrows show a strengthening of a trait effect in a habitat, while angled arrows denote  
785 a weakening of trait effects. Traits that were not significant and thus removed from the minimum  
786 model are marked NS. Traits that were not significant in either modelling approach are not shown.  
787 Model coefficients are given in Table A5.

788

789

790

791

792

793



794 **Figures**

795

796 **Figure 1.** Variation in population trend between habitats. (a) Mean population trends in each habitat  
797 estimated from a LMM modelling log (population trend +1) as a function of habitat, with species as a  
798 random effect. Error bars show standard errors. (b) Modelled mean population trends in aggregated  
799 functional habitat classes. See Table 1 for definition of habitat abbreviations. (c) As (a), but only  
800 including species with nationally increasing population trends. (d) As (a), but only including species  
801 with nationally declining population trends. The dashed line shows the grand mean of population  
802 trends across all habitats; asterisks show significant and near-significant differences from this (\*  $P <$   
803 0.05, \*\*  $P <$  0.01, \*\*\*  $P <$  0.001). Population trends that are significantly different from zero ( $P <$   
804 0.05) are marked with + if they are greater than zero and – if they are less than zero. Lower-case  
805 letters written above bars show results of pairwise tests for differences between habitats – habitats  
806 with different letters had significantly different population trends. Sample sizes (number of species)  
807 are given in parentheses after each habitat name. Differences in population trends after controlling  
808 for significant trait main effects are similar and are shown in Fig. A4.

809

810