



Deposited via The University of Leeds.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/id/eprint/96802/>

Version: Accepted Version

Article:

Sullivan, MJP, Newson, SE and Pearce-Higgins, JW (2016) Changing densities of generalist species underlie apparent homogenization of UK bird communities. *Ibis*, 158 (3). pp. 645-655. ISSN: 0019-1019

<https://doi.org/10.1111/ibi.12370>

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

1 **Running head:** *Community specialisation*

2

3 **Changing densities of generalist species underlie apparent homogenization of UK**

4 **bird communities**

5

6 MARTIN J. P. SULLIVAN,^{1,2} STUART E. NEWSON^{1*} & JAMES W. PEARCE-HIGGINS¹

7

8 ¹ *British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK.*

9 ² *School of Geography, University of Leeds, Leeds, LS2 9JT, UK.*

10

11 * Corresponding author.

12 Email: stuart.newson@bto.org

13

14 Generalist species are becoming increasingly dominant in European bird communities. This has been

15 taken as evidence of biotic homogenization, where generalist ‘winners’ systematically replace

16 specialist ‘losers’. We test this by relating changes in the average specialisation of UK bird

17 communities to changes in the density of species with different degrees of habitat-specialisation.

18 Although we find the expected continued decline in community specialisation, this was driven by a

19 combination of a strong increase in the density of the most generalist quartile of species and declines

20 in the density of moderately generalist species. Contrary to expectation, specialist species increased

21 slightly over the 18 year study period, but had little effect on the overall trend in community

22 specialisation. Our results indicate that the apparent homogenization of UK bird communities is not

23 driven by the replacement of specialists by generalists, but instead by the changing fortunes of

24 generalist species.

25

26 **Keywords:** biotic homogenization, Breeding Bird Survey, community specialisation index,

27 monitoring.

28 Changes to the environment, such as climate change and land-use intensification, do not affect all
29 species equally (Rader *et al.* 2014). Habitat specialists may be more vulnerable to environmental
30 change than habitat generalists, due to their more restricted habitat requirements and potentially lower
31 ability to exploit new opportunities (Shultz *et al.* 2005). Environmental change could therefore lead to
32 a loss of differentiation in species composition between habitats, as a few generalist ‘winners’ replace
33 specialist ‘losers’ (McGill *et al.* 2015). This is supported by negative relationships between
34 population growth rate and specialisation in a wide range of taxa (Munday 2004, Matthews *et al.*
35 2014, Timmermann *et al.*, 2015), including birds (Julliard *et al.* 2004, Jiguet *et al.* 2007, Salido *et al.*
36 2012), and by observations of communities becoming increasingly composed of individuals of
37 generalist species (Davey *et al.* 2012, Timmermann *et al.* 2015).

38 However, while individuals of generalist species make up an increasing proportion of
39 European bird communities (Davey *et al.* 2012, Le Viol *et al.* 2012), it is unclear whether these
40 changes are being driven by increases in populations of generalist species, declines in populations of
41 specialist species or some combination of both. The nature of the processes driving changes in
42 community specialisation has important consequences, as a reduction in community specialisation
43 through population declines may be of greater conservation concern than if it is driven by population
44 increases in generalists, whilst large changes in populations of widespread generalists may have
45 implications for ecosystem function.

46 We follow changes in UK bird communities over 18 years (2598 ± 597 SD 1 km squares
47 monitored each year). Our aims are to (1) quantify changes in community specialisation and (2) assess
48 the extent to which these changes reflect changes in the populations of specialist and generalist
49 species.

50

51 **METHODS**

52

53 **Bird density data**

54 Data from the UK Breeding Bird Survey (BBS), a national scale survey designed to monitor changes
55 in bird populations in the UK, were used to track changes in community structure. The survey started
56 in 1994, and we used data from this point up to 2012. Survey squares of 1 km² in area were selected
57 for the BBS using a stratified random sampling design, with more squares in areas with a higher
58 human population density to maximise utilisation of available volunteers. In each BBS square, a
59 volunteer walks two 1 km line-transects across the square on two visits during the breeding season
60 (April to June), with the visits separated by at least four weeks. Each transect is divided into 200 m
61 long transect sections, and the birds seen in each transect section are recorded in three distance bands
62 (<25 m, 25 – 100 m and >100 m), or as flying. Volunteers also record the habitat in each transect
63 section according to a hierarchical coding system (Crick 1992). Data from 2001 were excluded from
64 analyses as access to the countryside was restricted in that year due to foot-and-mouth disease. In the
65 other years, 1570 to 3718 squares were surveyed each year, with a total of 5155 squares surveyed
66 during the study period.

67 In this study, we used records in the first two bounded distance bands, and excluded records
68 of flying birds, with the exception of swifts, hirundines and raptors, as these species either are aerial
69 feeders or hunt from the air, so flying birds of these species are likely to be using resources within the
70 BBS square. Feral forms of Rock Dove *Columba livia*, Mallard *Anas platyrhynchos* and Greylag
71 Goose *Anser anser* were recorded separately to wild forms by volunteers and are treated separately
72 here. We removed birds that were likely to be transient migrants or lingering winter visitors, with the
73 aim of ensuring the bird community recorded consisted of the species likely to be using the square for
74 breeding. To do this, we removed unusually high counts of waders, indicating flocks away from
75 breeding areas, records of European Golden Plovers *Pluvialis apricaria* from unsuitable lowland
76 habitat, species that are regular passage migrants or winter visitors to the UK, but that have fewer than
77 ten breeding pairs, and species with fewer than ten records in the entire BBS dataset. Following
78 application of these filters, our dataset consisted of approximately 1.2 million records of 195 bird
79 species (see Table S1 for a list of species).

80 In order to turn raw abundances into estimates of density, we estimated detection probabilities
81 for each species in each BBS square. For each species, the distance band in which each observation

82 was recorded was modelled as a function of visit date (i.e. early or late) and the primary habitat class
83 (the 12 habitat classes are defined in Table S2) in the transect section in which the bird was recorded
84 using a half-normal distance model in the R package MRDS (Laake *et al.* 2015). If there were fewer
85 than 20 observations in a habitat class, the habitat class was combined with similar habitats to form a
86 broader habitat class to be used as a covariate (for example, if there were fewer than 20 observations
87 in flowing water, that habitat would be grouped with wetlands and standing water to form a broader
88 wetland habitat class; see Table S2 for other broader habitat classes). These covariates allow variation
89 in detectability over the breeding season and between habitats to be modelled. These models were
90 used to predict the probability of individuals of a species being detected in each transect section, and
91 these were averaged per species to obtain the predicted detection probability for that visit to a BBS
92 square. The density of each species in a BBS square was then calculated by dividing the raw count by
93 the detection probability. Detection functions could not be calculated for ten species, so for these
94 species we estimated detection probabilities using models fitted to observations of similar surrogate
95 species (Table S3). Raw counts were used for swifts, hirundines and raptors, as the majority of
96 records of these species related to flying individuals for which distance data were not available. We
97 obtained similar results to those reported in the main paper when we repeated the analysis using raw
98 counts for all species (Fig. S1, Fig. S2).

99

100 **Quantifying species specialisation**

101 For each species, we calculated a species specialisation index (SSI) as the coefficient of variation of
102 the density of a species across the 12 habitat classes across all BBS squares, with values close to zero
103 indicating little variation in density between habitats (i.e. generalist species), and high values
104 indicating considerable variation between habitats (i.e. specialist species). We grouped species into
105 four habitat specialisation groups based on the quartiles of SSI values; species with SSI values in the
106 first quartile (Q1, $SSI < 0.81$) can be considered very generalist, species in the second quartile (Q2,
107 $SSI \geq 0.81$ and < 1.29) moderately generalist, species in the third quartile (Q3, $SSI \geq 1.29$ and < 1.82)
108 moderately specialist, and species in the fourth quartile (Q4, $SSI \geq 1.82$) very specialist. Changes in

109 the total density of species in each quartile give an indication of differences in general population
110 trends of specialist and generalist species. The total density of birds across all species in a given
111 quartile was calculated by subsetting the dataset so that it only contained species in a given habitat
112 specialisation quartile, and then summing the density of those birds in each BBS square-year
113 combination. Densities were natural log transformed prior to analysis, with a constant of one added
114 prior to transformation as some densities were equal to zero. For each quartile, we modelled the total
115 density across all species in that quartile as a function of year (treated as a continuous variable), with
116 BBS square identity as a random effect, using linear mixed effects models implemented in the R
117 package lme4 (Bates *et al.* 2014). We also calculated the number of increasing and declining species
118 in each quartile, using national BBS trends from Risely *et al.* (2013) to identify which species were
119 increasing and declining, to give an indication of how variable population trends were within SSI
120 quartiles. SSI was calculated using data from all years (i.e. 1994 – 2012); however, habitat
121 specialisation may have changed during the study period. To ensure this did not affect our results, we
122 also calculated SSI only using data from the start of the study period (1994 – 1997). Both measures of
123 SSI were strongly positively correlated ($r = 0.847$, $df = 193$, $P < 0.001$), and changes in the density of
124 birds in each quartile showed similar patterns using both measures of SSI (Fig. S1, Fig. S2). Only SSI
125 values calculated across all years are presented in the main paper.

126 The community specialisation index (CSI) of each BBS square in each year was calculated as
127 the density weighted mean of SSI values of the bird community in that BBS square. As an alternative,
128 CSI was also calculated as an unweighted mean of SSI values, so that values are only sensitive to the
129 composition of the bird community and not to abundances. A negative trend in CSI is indicative of a
130 reduction in the relative contribution of specialists to generalists, i.e. homogenization.

131

132 **Quantifying the contribution of species and groups of species to CSI**

133 Following Davey *et al.* (2013), a jackknife approach was used to quantify the contribution of species to
134 temporal trends in CSI. To estimate the overall trend in CSI over the study period, we used a linear
135 mixed effects model of CSI (natural log transformed prior to analysis) as a function of year (treated as

136 a continuous variable), with BBS square identity as a random effect. The coefficient of the year term
137 indicates the rate of change in CSI. We restricted models to linear effects because our primary intent
138 was to quantify the rate of change in CSI over time, and to investigate the impact of removing species
139 on this rate of change. To quantify the contribution of species/ groups of species, individual species
140 or groups of species were removed from the dataset as appropriate, CSI was recalculated, and the
141 model re-fitted. The percentage change in the year coefficient (Δ_{β}) was calculated as $\Delta_{\beta} = (\beta_2 - \beta_1) /$
142 $|\beta_1| \times 100$, where β_1 is the year coefficient when all species were included in the calculation of CSI
143 and β_2 is the year coefficient when CSI was calculated with a species or group of species removed.
144 Positive values indicate that the slope of the relationship was less negative when the species was
145 omitted and therefore that the trend of the species was contributing to homogenisation. Negative
146 values show that the slope of the relationship was more negative when the species was omitted,
147 indicating that the species was reducing the slope of the relationship so countering homogenisation. In
148 order to understand the drivers of any change in community specialisation, these percentage change
149 values were calculated when each individual species and each SSI quartile species group was
150 removed from the dataset, as well as when non-native species were removed.

151 We used a linear model to model individual species' influence on the trend in CSI (Δ_{β}) as a
152 function of their SSI and national BBS trend, and the interaction between SSI and BBS trend. We
153 square-root transformed the response variable (percentage change in CSI trend) to meet model
154 assumptions, and also square-root transformed the explanatory variables, which were strongly
155 positively skewed, in order to improve our sampling of parameter space. Both percentage change in
156 CSI trend and national BBS trend could be negative, so we square-root transformed the absolute
157 values before applying the original sign. This analysis could only be conducted using species for
158 which national BBS trends were available ($n = 127$). Removing species without BBS trends could
159 mean that we missed the influence of rare species on CSI trend. However, this is unlikely as we
160 found that individual species' influence on the trend in CSI did not vary significantly between species
161 with and without a national BBS trend (Wilcoxon test, $W = 3937$, $P = 0.310$). All analyses were
162 carried out using R (R Core Team 2014). R code used for statistical analysis is provided in Appendix

163 S1. Marginal and conditional R^2 values for mixed-effects models were calculated following Nakagawa
164 and Schielzeth (2013), implemented in the MuMIn R package (Barton *et al.* 2014).

165

166 RESULTS

167

168 The total density of Q1 (very generalist) and Q4 (very specialist) species in BBS squares increased
169 (Q1: $\beta = 0.018 \pm < 0.001$, $\chi^2_1 = 1397.6$, $P < 0.0001$, marginal $R^2 = 0.005$, conditional $R^2 = 0.881$; Q4:
170 $\beta = 0.009 \pm 0.001$, $\chi^2_1 = 84.2$, $P < 0.0001$, marginal $R^2 = 0.001$, conditional $R^2 = 0.607$), while the total
171 density of Q2 (moderately generalist) species decreased over the study period ($\beta = -0.018 \pm 0.001$, χ^2_1
172 $= 556.7.4$, $P < 0.0001$ marginal $R^2 = 0.006$, conditional $R^2 = 0.632$). There was no significant trend in
173 the density of Q3 (moderately specialist) species ($\chi^2_1 < 0.1$, $P = 0.978$, marginal $R^2 < 0.001$,
174 conditional $R^2 = 0.653$). The low marginal R^2 and high conditional R^2 in these models indicates that
175 spatial variation in bird density (captured by the random site effect) is much greater than temporal
176 variation (captured by the fixed year effect). Changes were most pronounced for the increase in the
177 density of Q1 species and the decrease in the density of Q2 species (Fig. 1), with the total density of
178 Q1 species predicted to have increased by 132 birds.km⁻² and the total density of Q2 species predicted
179 to have declined by 21 birds.km⁻² over the study period. The total density of Q3 and Q4 species were
180 both predicted to have changed by less than 1 bird.km⁻². Within these general trends, there was
181 considerable variation in the direction of individual species trends, with increasing and decreasing
182 species in all quartiles. However, the balance of increasing and decreasing species reflected overall
183 changes in density, with more than half of species in Q2 declining, while more than half of species in
184 the other quartiles were increasing (Fig. S3).

185 CSI declined over the study period ($\beta = -0.004 \pm < 0.001$, $\chi^2_1 = 1255.2$, $P < 0.0001$, marginal
186 $R^2 = 0.004$, conditional $R^2 = 0.885$, Fig. 2a). A similar, although slightly less steep trend in CSI was
187 observed when based on an unweighted mean of SSI values across the species present, and therefore
188 indicative of changes in occupancy rather than abundance ($\beta = -0.001 \pm < 0.001$, $\chi^2_1 = 290.6$, $P <$
189 0.0001 , marginal $R^2 = 0.001$, conditional $R^2 = 0.867$, Fig. 2b). The decrease in CSI has thus been
190 driven by both changes in species abundance and changes in species identity. Changes in the densities

191 of Q1 species were largely responsible for driving these trends; when Q1 species were removed, the
192 overall trend in CSI was weakly positive (Fig. 3b). The trend in CSI remained negative when all other
193 quartiles were removed (Fig. 3), although it was significantly less negative when Q2 species were
194 removed (as indicated by non-overlapping trend confidence intervals, Fig. 3b). This indicates that
195 species in Q1 and to a lesser extent Q2 are responsible for driving the negative trend in CSI. The
196 effect of each quartile on the trend of CSI was similar when CSI was calculated as an unweighted
197 mean of SSI (Fig. S2). Changes in the density of non-native species had little effect on CSI (-4.3 %
198 change in year coefficient when removed), despite an overall increase in the density of non-native
199 species over the study period ($\beta = 0.032 \pm 0.001$, $\chi^2_1 = 1260.4$, $P < 0.0001$, marginal $R^2 = 0.013$,
200 conditional $R^2 = 0.641$, Fig. S4).

201 Removing individual species and recalculating the trend in CSI allowed the contribution of
202 individual species to be assessed. Changes in the abundance of Starling *Sturnus vulgaris* (Q2, 30.0%
203 change when removed), Woodpigeon *Columba palumbus* (Q1, 17.0% change when removed) and
204 Meadow Pipit *Anthus pratensis* (Q3, 8.3% change when removed) had the greatest contribution to the
205 decline in CSI (Table 1). Across all species, there was a significant interaction between SSI and
206 national BBS trend in influencing species' contributions to change in CSI ($F_{1,124} = 15.7$, $P = 0.0001$,
207 model $R^2 = 0.129$), with generalist species reducing homogenization when declining, but increasing
208 homogenization when increasing, while specialist species showed the opposite pattern (Fig. 4).

209

210 **DISCUSSION**

211

212 We documented a continued decline in CSI in UK bird communities, supporting previous studies
213 documenting the increasing dominance of generalist species in the UK and elsewhere in Europe
214 (Davey *et al.* 2012, Le Viol *et al.* 2012). However, we showed that despite strong increases in the
215 density of generalist species, this does not come at the expense of specialist species, as the overall
216 density of the most specialist quartile of species increased over the study period. Instead, changes in
217 CSI largely reflected the changing balance of very generalist species (in Q1, which tended to increase)
218 and moderately generalist species (Q2, which tended to decline).

219 What has driven these patterns? Recent analyses of European bird population trends has
220 shown a similar pattern where common species have tended to decline in abundance, whilst the rarest
221 species have tended to increase (Inger *et al.* 2015). This was partly attributed to long-term population
222 declines in relatively widespread farmland birds (Donald *et al.* 2001), and the potential benefits of
223 conservation management for rare species (e.g. Donald *et al.* 2007, Hoffmann *et al.* 2010). The
224 pattern we have observed has some similarities to this, but suggests that in the UK, the most
225 widespread species (e.g. Woodpigeon, Great Tit *Parus major* and Goldfinch *Carduelis carduelis*)
226 have actually increased in abundance. These are species which occupy the greatest range of habitats,
227 and therefore are potentially most resilient to anthropogenic pressures. The most rapidly declining
228 species were the moderate generalists, which includes many of the farmland birds (e.g.
229 Yellowhammer *Emberiza citrinella*, Grey Partridge *Perdix perdix* and Lapwing *Vanellus vanellus*)
230 that occupy a number of habitat types, but that have declined widely in the UK in response to
231 agricultural intensification (Chamberlain *et al.* 2000, Eglington & Pearce-Higgins 2012). Declines in
232 CSI have been greatest in UK farmland habitats (Davey *et al.* 2012), supporting this explanation.
233 There also appear to be divergent impacts of warming upon habitat generalists and specialists, which
234 may have contributed to this pattern (Davey *et al.* 2012, Pearce-Higgins *et al.* 2015), although it is
235 unclear how the sensitivity of species to climate change varies between the different SSI quartiles, or
236 how the impacts of warming may interact with land-use change to drive these patterns.

237 Our analyses followed Davey *et al.* (2012), and defined habitat specialisation based on
238 associations with 12 habitat categories. The inferences we obtained are sensitive to this definition. SSI
239 values obtained by defining habitat specialisation using four habitat categories (woodland, wetland,
240 urban and open) are uncorrelated with those using 12 habitat categories ($r = 0.14$), and if these SSI
241 values are used, declines are evident in habitat specialists (Q4) and strong generalists (Q1), while the
242 density moderate generalists (Q2) and moderate specialists (Q3) increases (Fig. S1). A consequence
243 of using broader habitat categories is that species primarily associated with one habitat type within a
244 broad habitat will be considered more generalist, while species associated with all habitat-types within
245 a broad habitat will be considered more specialist. For example, Siskins *Carduelis spinus* are strongly
246 associated with coniferous woodland, but not with other woodland habitats (12 habitat SSI = 2.11,

247 Q4), so appear less strongly associated with any habitat type when all woodland types are combined
248 into one category (four habitat SSI = 1.23, Q1). Yellowhammers, on the other hand, are associated
249 with a wide-range of open habitats (12 habitat SSI = 1.04, Q2), so appear strongly associated with the
250 open broad habitat category (four habitat SSI = 1.99, Q4), despite not being strongly associated with
251 any of the 12 habitat categories. Because of this, we consider that using 12 habitat categories to
252 calculate SSI gives a more meaningful representation of habitat specialisation than using four
253 categories, although it is clear that the precision of measurement of habitat-specialisation has a strong
254 impact on community specialisation metrics.

255 Some individual species had large effects on changes in CSI, demonstrating that changes in
256 the populations of individual species can have a large impact on community level metrics. Starling
257 and Woodpigeon contributed most to the decline in CSI. Both of these species are abundant (Newson
258 *et al.* 2005) and found throughout most of the UK (Balmer *et al.* 2013), and show consistent
259 population trends across habitats, with Woodpigeons increasing and Starlings declining in all habitats
260 where population trends could be calculated (Baillie *et al.* 2014). The role of these species in driving
261 changes in CSI contrasts with the small role of most species, with the exclusion of most individual
262 species changing the trend in CSI by <1% (Table S1). Despite this, the effect of excluding any
263 individual species was considerably smaller than the effect of excluding a whole quartile, indicating
264 that our results reflect the cumulative effect of a broad suite of species, rather than just the effects of a
265 few individual species.

266 We calculated SSI using data on habitat associations pooled across the study period, so
267 treated it as a fixed attribute of a species. This means that our results reflect changes in species
268 abundance and community composition. However, SSI can change through time (Barnagaud *et al.*,
269 2011), with species that exhibit density dependent habitat-selection spreading out into less favourable
270 habitats as their populations increase and retreating to favourable habitats as populations decline
271 (Sullivan *et al.* 2015a). This can potentially increase rates of community homogenization (Barnagaud
272 *et al.* 2011), as increasing species become more generalist and declining species become more
273 specialist. In this analysis, our interest was in analysing changes in bird communities rather than
274 changes in the attributes of individual species, so we did not investigate this here, except for showing

275 that similar changes in the density of specialist and generalist species are observed when quartiles are
276 defined based on habitat specialisation in the initial years of the study period as over the whole study
277 period (Fig. S1).

278 Change in CSI was partially attributable to changes in the species composition of bird
279 communities, as well as changes in abundance, as a trend in CSI was evident when it was calculated
280 discounting abundance data. One potential source of change in bird community composition is the
281 spread of non-native species in the UK (Balmer *et al.* 2013). However, the effect of non-native
282 species on change in CSI was limited, with the increase in the density of non-native species over the
283 study period acting to slightly reduce the decline in CSI. This indicates that the observed decline in
284 CSI was due to changes in the abundance and distribution of native species rather than non-native
285 species, as previously found for Europe (Le Viol *et al.* 2012). However, it is important to note that we
286 may have over-estimated the habitat specialism of non-native species, as we derived estimates of SSI
287 from habitat associations in the UK, whereas non-native species may be dispersal-limited, and thus
288 not currently occupy all the habitats that may be suitable for them (Sullivan *et al.* 2012). It is also
289 important to note that the limited effect of non-native species on CSI does not mean that they do not
290 impact native bird communities. Some authors would consider their increased dominance within bird
291 communities evidence of biotic homogenization (Olden *et al.* 2004), and although some studies
292 suggest limited negative impacts on native bird communities (Blackburn *et al.* 2009, Newson *et al.*
293 2011, Grundy *et al.* 2014), negative impacts may be evident when non-native species reach higher
294 population densities.

295 Community weighted means, such as CSI, are often used as indicators of change in
296 communities in time and space (Devictor *et al.* 2008, Davey *et al.* 2012, Le Viol *et al.* 2012, Vimal &
297 Devictor 2015). However, such metrics have been criticized as they only indicate the balance of (in
298 the case of CSI) specialists and generalists, and do not indicate if these changes are due to increases in
299 generalists or declines in specialists (Gosselin 2012). We showed that changes in CSI in UK birds
300 were primarily driven by increases in very generalist species and declines in moderately generalist
301 species, and little affected by changes in the density of specialist species, supporting this criticism. On
302 average, specialist species were found at lower densities than generalist species (Fig. S5), so are likely

303 to have less influence of community weighted metrics. Our approach of accompanying analysis of
304 CSI with more detailed analysis of changes in the density of specialists and generalists gave greater
305 insight into the mechanisms acting on a bird community than analysis of change in CSI alone, and
306 could be applied to other analyses using community weighted means.

307 Environmental change can act as an environmental filter, with only a subset of the original
308 species pool able to persist in altered conditions (Helmus *et al.* 2010, Mouillot *et al.* 2013). Generalist
309 species are expected to be more likely to be able to pass through a given environmental filter due to
310 their greater niche breadth (Clavel *et al.* 2011). Under this model of biotic homogenisation,
311 environmental change is expected to lead to declines in specialist species, with generalist species
312 increasing to exploit new opportunities. Our results, together with those of Inger *et al.* (2015), contrast
313 with this expectation by showing that the overall abundance of rare and specialised species has not
314 declined, with declines evident instead in abundant, moderately generalist species. How can these
315 results be reconciled with this model of biotic homogenisation? Natural habitats in the UK have been
316 heavily fragmented and modified by humans for > 2,000 years (Rackham 1986), and this long history
317 of human impact is likely to have considerably reduced populations of habitat specialists so that there
318 was a low baseline in terms of population size at the start of the study. Thus, the modest increase in
319 the overall density of the most specialised quartile of species reported in this study is not inconsistent
320 with the expectation that environmental change negatively affects habitat specialists, and instead is
321 likely to reflect remaining populations of habitat specialists benefiting from conservation actions.
322 Drivers of population change that act across habitats appear to be more important in explaining
323 change in UK bird populations than processes operating within particular habitats (Sullivan *et al.*
324 2015b), and these landscape scale drivers are likely to particularly affect widespread generalist
325 species (Gaston & Fuller 2007). Patterns of population change amongst these widespread generalists
326 are consistent with the prediction that generalist species are more resistant to environmental change,
327 with increases in the overall density of the most generalist quartile of species and declines in the
328 density of moderate generalists (Fig. 1).

329 To conclude, despite the continued decline in the habitat specialisation of UK bird
330 communities, the overall density of specialist species has not declined. This apparent homogenization

331 does not therefore appear to have been at the expense of specialist species of the greatest conservation
332 concern. Instead, the decline in CSI was driven by increases in the density of the most generalist
333 quartile of species, and by declines in the density of moderate generalists. These results reflect
334 previous work comparing changes in the populations of abundant and rare species (Inger *et al.* 2015),
335 and collectively indicate that recent changes in bird communities across Europe have been
336 characterized by declines in relatively abundant, moderately generalist species.

337

338 We are grateful to the thousands of volunteers who contributed to the Breeding Bird Survey. The BBS, and this
339 analysis, were jointly funded by the British Trust for Ornithology, the Joint Nature Conservation Committee and
340 the Royal Society for the Protection of Birds. MS is currently funded by the European Research Council grant
341 “Tropical Forests in the Changing Earth System”. We thank Richard Inger, the editor, associate editor and an
342 anonymous reviewer for constructive comments on the manuscript.

343

344

345

346 REFERENCES

347

348 **Baillie, S. R., Marchant, J. H., Leech, D. I., Massimino, D., Sullivan, M. J. P., Eglinton, S. M.,**
349 **Barimore, C., Dadam, D., Downie, I., Harris, S. J., Kew, A. J., Newson, S. E., Noble, D.**
350 **G., Risely, K. & Robinson, R. A.** 2014. BirdTrends 2014: trends in numbers, breeding
351 success and survival of UK breeding birds. Research Report 662. Thetford.

352 **Balmer, D. E., Gillings, S., Caffrey, B., Swann, R., Downie, I. & Fuller, R.** 2013. *Bird Atlas 2007-*
353 *11: the breeding and wintering birds of Britain and Ireland*: BTO Thetford.

354 **Barton, K.** 2014. MuMIn: Multi-Model Inference. R package version 1.12.1. [http://CRAN.R-](http://CRAN.R-project.org/package=MuMIn)
355 [project.org/package=MuMIn](http://CRAN.R-project.org/package=MuMIn)

356 **Barnagaud, J. Y., Devictor, V., Jiguet, F. & Archaux, F.** 2011. When species become generalists:
357 on-going large-scale changes in bird habitat specialization. *Global Ecol Biogeogr.* **20**: 630-
358 640.

- 359 **Bates, D., Maechler, M., Bolker, B. M. & Walker, S.** 2014. lme4: Linear mixed-effects models
360 using Eigen and S4.
- 361 **Blackburn, T., Lockwood, J. & Cassey, P.** 2009. *Avian invasions: the ecology and evolution of*
362 *exotic birds*. Oxford: Oxford University Press.
- 363 **Chamberlain, D. E., Fuller, R. J., Bunce, R. G. H., Duckworth, J. C. & Shrubbs, M.** 2000.
364 Changes in the abundance of farmland birds in relation to the timing of agricultural
365 intensification in England and Wales. *J Appl Ecol* **37**: 771-788.
- 366 **Crick, H. Q. P.** 1992. A bird-habitat coding system for use in Britain and Ireland incorporating
367 aspects of land-management and human activity. *Bird Study* **39**: 1-12.
- 368 **Clavel, J., Julliard, R. & Devictor, V.** 2010. Worldwide decline of specialist species: toward a
369 global functional homogenization? *Frontiers Ecol Environ* **9**: 222-228.
- 370 **Davey, C. M., Chamberlain, D. E., Newson, S. E., Noble, D. G. & Johnston, A.** 2012. Rise of the
371 generalists: evidence for climate driven homogenization in avian communities. *Global Ecol*
372 *Biogeogr* **21**: 568-578.
- 373 **Davey, C. M., Devictor, V., Jonzén, N., Lindström, Å. & Smith, H. G.** 2013. Impact of climate
374 change on communities: revealing species' contribution. *J Anim Ecol* **82**: 551-561.
- 375 **Devictor, V., Julliard, R., Couvet, D. & Jiguet, F.** 2008. Birds are tracking climate warming, but
376 not fast enough. *Proc Royal Soc B* **275**: 2743-2748.
- 377 **Donald, P. F., Green, R. E. & Heath, M. F.** 2001. Agricultural intensification and the collapse of
378 Europe's farmland bird populations. *Proc Royal Soc B* **268**: 25-29.
- 379 **Donald, P. F., Sanderson, F. J., Burfield, I. J., Bierman, S. M., Gregory, R. D. & Waliczky, Z.**
380 2007. International conservation policy delivers benefits for birds in Europe. *Science* **317**:
381 810-813.
- 382 **Eglington, S. M. & Pearce-Higgins, J. W.** 2012. Disentangling the Relative Importance of Changes
383 in Climate and Land-Use Intensity in Driving Recent Bird Population Trends. *PLoS ONE* **7**:
384 e30407.
- 385 **Gaston, K.J. & Fuller, R.A.** 2007. Commonness, population depletion and conservation biology.
386 *Trends Ecol Evol* **23**: 14-19

387 **Gosselin, F.** 2012. Improving approaches to the analysis of functional and taxonomic biotic
388 homogenization: beyond mean specialization. *J Ecol* **100**: 1289-1295.

389 **Grundy, J. P. B., Franco, A. M. A. & Sullivan, M. J. P.** 2014. Testing multiple pathways for
390 impacts of the non-native Black-headed Weaver *Ploceus melanocephalus* on native birds in
391 Iberia in the early phase of invasion. *Ibis* **156**: 355-365.

392 **Helmus, M.R., Keller, W.B., Paterson, M.J., Yan, N.D., Cannon, C.H. & Rusak, J.A.** 2010.
393 Communities contain closely related species during ecosystem disturbance. *Ecol Lett* **13**: 162-
394 174.

395 **Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T. M., Butchart, S. H. M.,**
396 **Carpenter, K. E., Chanson, J., Collen, B., Cox, N. A., Darwall, W. R. T., Dulvy, N. K.,**
397 **Harrison, L. R., Katariya, V., Pollock, C. M., Quader, S., Richman, N. I., Rodrigues, A.**
398 **S. L., Tognelli, M. F., Vié, J.-C., Aguiar, J. M., Allen, D. J., Allen, G. R., Amori, G.,**
399 **Ananjeva, N. B., Andreone, F., Andrew, P., Ortiz, A. L. A., Baillie, J. E. M., Baldi, R.,**
400 **Bell, B. D., Biju, S. D., Bird, J. P., Black-Decima, P., Blanc, J. J., Bolaños, F., Bolivar-G.,**
401 **W., Burfield, I. J., Burton, J. A., Capper, D. R., Castro, F., Catullo, G., Cavanagh, R. D.,**
402 **Channing, A., Chao, N. L., Chenery, A. M., Chiozza, F., Clausnitzer, V., Collar, N. J.,**
403 **Collett, L. C., Collette, B. B., Fernandez, C. F. C., Craig, M. T., Crosby, M. J.,**
404 **Cumberlidge, N., Cuttelod, A., Derocher, A. E., Diesmos, A. C., Donaldson, J. S.,**
405 **Duckworth, J. W., Dutson, G., Dutta, S. K., Emslie, R. H., Farjon, A., Fowler, S.,**
406 **Freyhof, J., Garshelis, D. L., Gerlach, J., Gower, D. J., Grant, T. D., Hammerson, G. A.,**
407 **Harris, R. B., Heaney, L. R., Hedges, S. B., Hero, J.-M., Hughes, B., Hussain, S. A.,**
408 **Icochea M., J., Inger, R. F., Ishii, N., Iskandar, D. T., Jenkins, R. K. B., Kaneko, Y.,**
409 **Kottelat, M., Kovacs, K. M., Kuzmin, S. L., La Marca, E., Lamoreux, J. F., Lau, M. W.**
410 **N., Lavilla, E. O., Leus, K., Lewison, R. L., Lichtenstein, G., Livingstone, S. R.,**
411 **Lukoschek, V., Mallon, D. P., McGowan, P. J. K., McIvor, A., Moehlman, P. D., Molur,**
412 **S., et al.** 2010. The Impact of Conservation on the Status of the World's Vertebrates. *Science*
413 **330**: 1503-1509.

414 **Inger, R., Gregory, R., Duffy, J. P., Stott, I., Voříšek, P. & Gaston, K. J.** 2015. Common
415 European birds are declining rapidly while less abundant species' numbers are rising. *Ecol*
416 *Lett* **18**: 28-36.

417 **Jiguet, F., Gadot, A. S., Julliard, R., Newson, S. E. & Couvet, D.** 2007. Climate envelope, life
418 history traits and the resilience of birds facing global change. *Global Change Biol* **13**: 1672-
419 1684.

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

422 **Laake, J., Borchers, D., Thomas, L., Miller, D. & Bishop, J.** 2015. mrds: Mark-Recapture Distance
423 Sampling. R package version 2.1.12. <http://CRAN.R-project.org/package=mrds>.

424 **Le Viol, I., Jiguet, F., Brotons, L., Herrando, S., Lindström, Å., Pearce-Higgins, J. W., Reif, J.,**
425 **Van Turnhout, C. & Devictor, V.** 2012. More and more generalists: two decades of changes
426 in the European avifauna. *Biol Lett* **8**: 780-782.

427 **Matthews, T. J., Cottee-Jones, H. E. & Whittaker, R. J.** 2014. Habitat fragmentation and the
428 species–area relationship: a focus on total species richness obscures the impact of habitat loss
429 on habitat specialists. *Divers Distrib* **20**: 1136-1146.

430 **McGill, B. J., Dornelas, M., Gotelli, N. J. & Magurran, A. E.** 2015. Fifteen forms of biodiversity
431 trend in the Anthropocene. *Trends Ecol Evol* **30**: 104-113.

432 **Mouillot, D., Graham, N.A., Villéger, S., Mason, N.W. & Bellwood, D.R.** 2013. A functional
433 approach reveals community responses to disturbances. *Trends Ecol Evol* **28**: 167-177.

434 **Munday, P. L.** 2004. Habitat loss, resource specialization, and extinction on coral reefs. *Global*
435 *Change Biol* **10**: 1642-1647.

436 **Nakagawa, S. & Schielzeth, H.** 2013. A general and simple method for obtaining R^2 from
437 generalized linear mixed-effects models. *Methods Ecol Evol* **4**: 133-142.

438 **Newson, S. E., Johnston, A., Parrott, D. & Leech, D. I.** 2011. Evaluating the population-level
439 impact of an invasive species, Ring-necked Parakeet *Psittacula krameri*, on native avifauna.
440 *Ibis* **153**: 509-516.

441 **Newson, S. E., Woodburn, R. J. W., Noble, D. G., Baillie, S. R. & Gregory, R. D.** 2005.
442 Evaluating the Breeding Bird Survey for producing national population size and density
443 estimates. *Bird Study* **52**: 42-54.

444 **Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E. & Fausch, K. D.** 2004. Ecological and
445 evolutionary consequences of biotic homogenization. *Trends Ecol Evol* **19**: 18-24.

446 **Pearce-Higgins, J. W., Eglington, S. M., Martay, B. & Chamberlain, D. E.** 2015. Drivers of
447 climate change impacts on bird communities. *J Anim Ecol* **84**: 943-954.

448 **R Core Team.** 2014. R: A language and environment for statistical computing. Vienna, Austria: R
449 Foundation for Statistical Computing.

450 **Rackham, O.** 1986. *The History of the Countryside*. London: J.M. Dent.

451 **Rader, R., Bartomeus, I., Tylianakis, J. M. & Laliberté, E.** 2014. The winners and losers of land
452 use intensification: pollinator community disassembly is non-random and alters functional
453 diversity. *Divers Distrib* **20**: 908-917.

454 **Risely, K., Massimino, D., Newson, S.E., Eaton, M.A., Musgrove, A.J., Noble, D.G., Procter, D.**
455 **& Baillie, S.R.** 2013. The Breeding Bird Survey 2012. BTO Research Report 645. British
456 Trust for Ornithology, Thetford

457 **Salido, L., Purse, B. V., Marrs, R., Chamberlain, D. E. & Shultz, S.** 2012. Flexibility in phenology
458 and habitat use act as buffers to long-term population declines in UK passerines. *Ecography*
459 **35**: 604-613.

460 **Shultz, S., Bradbury, R. B., Evans, K. L., Gregory, R. D. & Blackburn, T. M.** 2005. Brain size
461 and resource specialization predict long-term population trends in British birds. *Proc Royal*
462 *Soc B* **272**: 2305-2311.

463 **Sullivan, M. J. P., Davies, R. G., Reino, L. & Franco, A. M. A.** 2012. Using dispersal information
464 to model the species–environment relationship of spreading non-native species. *Methods Ecol*
465 *Evol* **3**: 870-879.

466 **Sullivan, M. J. P., Newson, S. E. & Pearce-Higgins, J. W.** 2015a. Evidence for the buffer effect
467 operating in multiple species at a national scale. *Biol Lett* **11**: 20140930.

468 **Sullivan, M.J.P., Newson, S.E. & Pearce-Higgins, J.W.** 2015b. Using habitat-specific population
469 trends to evaluate the consistency of the effect of species traits on bird population change.
470 *Biol Conserv* **192**: 343-352.

471 **Timmermann, A., Damgaard, C., Strandberg, M. T. & Svenning, J. C.** 2015. Pervasive early
472 21st-century vegetation changes across Danish semi-natural ecosystems: more losers than
473 winners and a shift towards competitive, tall-growing species. *J Appl Ecol* **52**: 21-30.

474 **Vimal, R. & Devictor, V.** 2015. Building relevant ecological indicators with basic data: Species and
475 community specialization indices derived from atlas data. *Ecological Indicators* **50**: 1-7.

476

477

478 **Supporting material**

479 **Table S1.** Species included in this study, and change in trend in CSI when individual species are
480 removed.

481 **Table S2.** Definition of habitat classes

482 **Table S3.** Surrogate species used for species where distance models failed to estimate detection
483 functions.

484 **Figure S1.** Sensitivity of changes in density of each quartile to different treatment of data.

485 **Figure S2.** Relationship between population trend and degree of habitat specialization.

486 **Figure S3.** Sensitivity of effect of each quartile on CSI trend to different treatment of data.

487 **Figure S4.** Change in density of non-native species.

488 **Figure S5.** Relationship between population density and habitat specialization.

489 **Appendix S1.** R code used in statistical analysis.

490

491

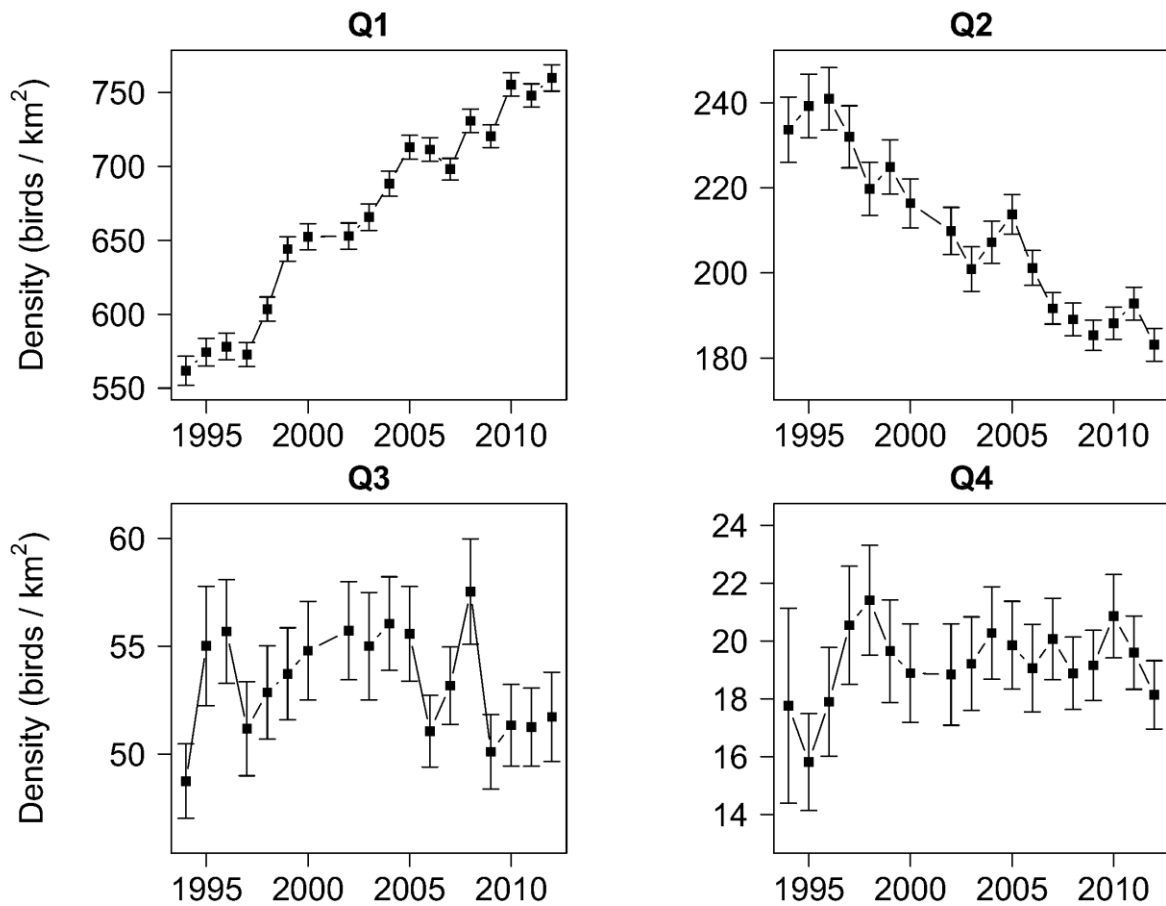
492

493

494 **Table 1.** Ten species contributing most to driving the decline in CSI over the study period. % change
 495 is the percentage change in the trend in CSI when a species is removed, SSI is the species
 496 specialisation index for a species, while BBS trend is the national population trend for a species over
 497 the study period.

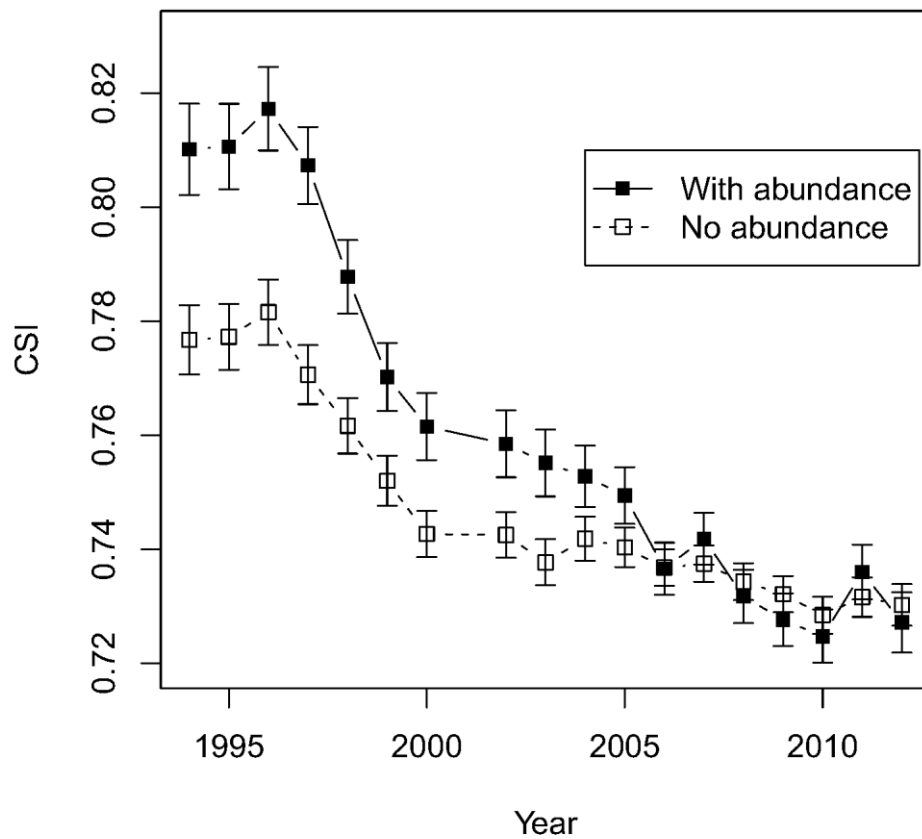
Species	Scientific name	Trend in CSI when omitted	% change	SSI (quartile)	BBS trend (1995 – 2011)
Starling	<i>Sturnus vulgaris</i>	-0.0027	30.0	1.23 (Q2)	-52
Woodpigeon	<i>Columba palumbus</i>	-0.0032	17.0	0.38 (Q1)	40
Meadow Pipit	<i>Anthus pratensis</i>	-0.0035	8.3	1.80 (Q3)	-23
Great Tit	<i>Parus major</i>	-0.0037	4.9	0.38 (Q1)	45
Yellowhammer	<i>Emberiza citrinella</i>	-0.0037	3.4	1.04 (Q2)	-13
Swift	<i>Apus apus</i>	-0.0038	1.5	0.89 (Q2)	-39
Goldcrest	<i>Regulus regulus</i>	-0.0038	1.3	1.46 (Q3)	-7
Goldfinch	<i>Carduelis carduelis</i>	-0.0038	1.0	0.60 (Q1)	109
Yellow Wagtail	<i>Motacilla flava</i>	-0.0038	0.96	1.45 (Q3)	-45
Corn Bunting	<i>Emberiza calandra</i>	-0.0038	0.95	1.65 (Q3)	-34

498
 499
 500
 501
 502
 503



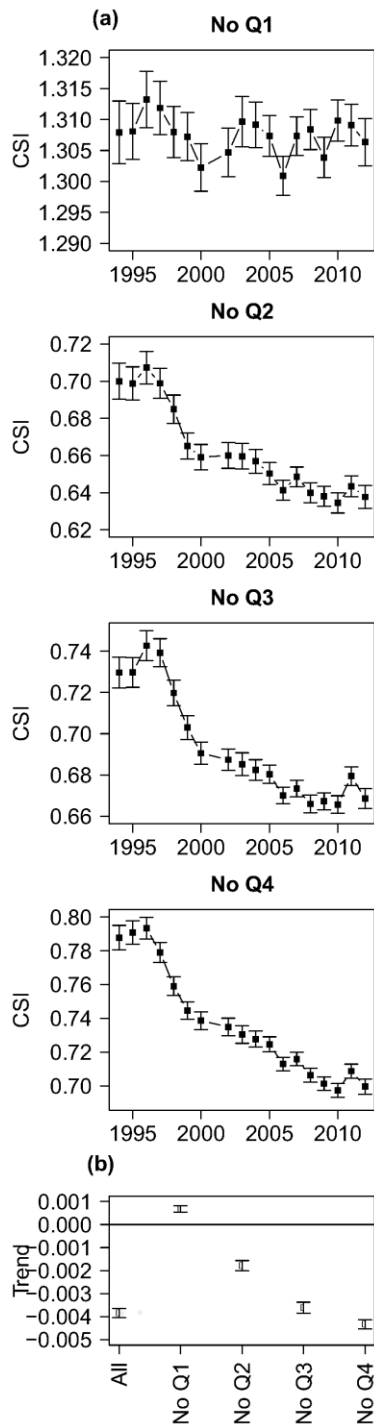
504

505 **Figure 1.** Change in density of birds in each quartile of habitat specialisation (SSI). Species in the
 506 first quartile (Q1) had SSI values < 0.81 , species in the second quartile (Q2) had SSI values ≥ 0.81 and
 507 < 1.29 , species in the third quartile (Q3) had SSI values ≥ 1.29 and < 1.82 , species in the fourth quartile
 508 had SSI values ≥ 1.82 . Points show the mean density of all birds in a given quartile in BBS squares,
 509 with error bars showing standard errors.



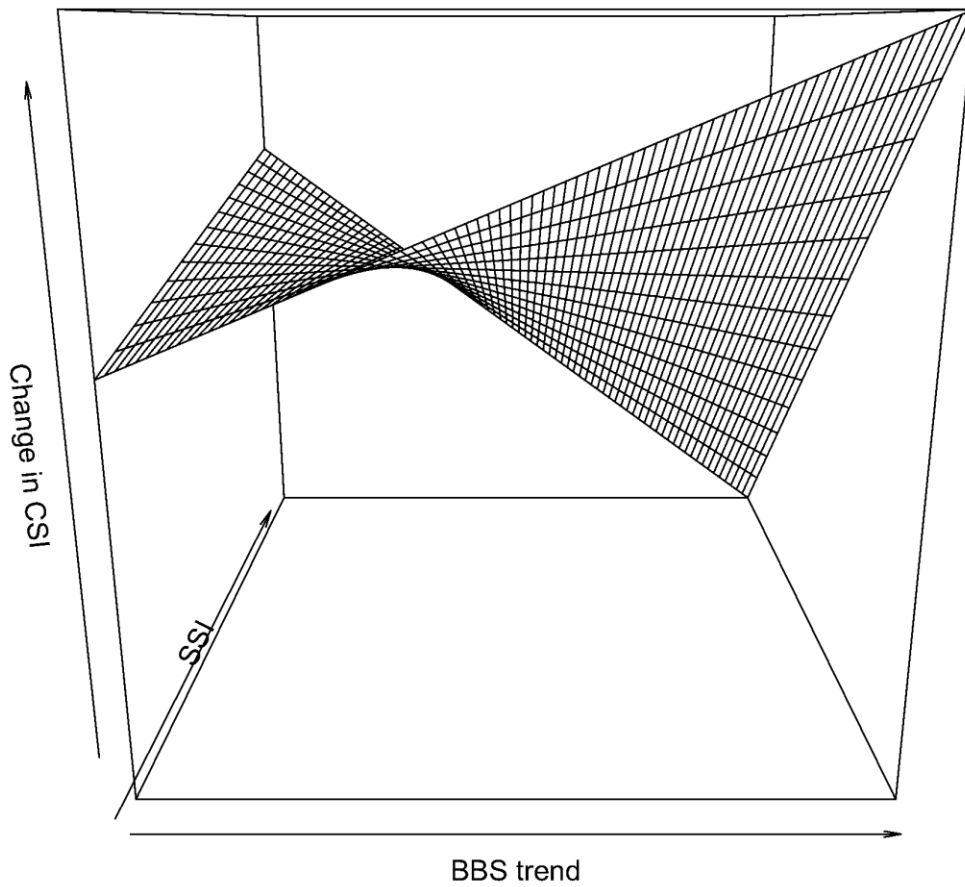
510

511 **Figure 2.** Change in the community specialisation index (CSI) of UK bird communities. CSI has been
 512 calculated as the community weighted mean of species specialisation index (SSI), thus incorporating
 513 the effect of species abundance (filled squares, solid line), and the unweighted mean of SSI, thus only
 514 including the effect of species occurrence (open squares, dashed line). Points show the mean CSI
 515 across BBS squares in a given year, with error bars showing standard errors.



516

517 **Figure 3.** Effect of removing quartiles of species with different degrees of habitat specialisation on
 518 the overall trend in CSI. In (a) points show the mean CSI across BBS squares in a given year, with
 519 error bars showing standard errors. In (b) the mean and 95% confidence intervals of trend in CSI over
 520 time are shown. Removing Q1 species (most generalist) and Q2 species reduced rates of
 521 homogenization (118.0% and 35.9% change in CSI trend when removed), while removing Q3 and Q4
 522 (most specialist) species had little effect (-6.5% and -12.9% change in CSI trend when removed).



523

524 **Figure 4.** Modelled surface showing the interaction between SSI and BBS trend in influencing the
 525 change in CSI trend when species were removed in a jackknife procedure. The modelled surface
 526 shows predicted change in CSI trend when a species is removed from the dataset, with predictions
 527 from a linear model where the change in CSI trend when a species was removed from the dataset was
 528 modelled as a function of that species' SSI, BBS trend and their interaction. Response and
 529 explanatory variables have been square-root transformed while preserving their original sign (see
 530 methods), and transformed values have been plotted.

531

532

533

534

535 **Supporting materials**

536 **Table S1.** Species included in this study, and change in trend in CSI when individual species are
 537 removed.

Scientific Name	Common Name	Trend in CSI when omitted	% change	SSI	Quartile
<i>Sturnus vulgaris</i>	Starling	-0.0027	30.03	1.23	Q2
<i>Columba palumbus</i>	Woodpigeon	-0.0032	17.04	0.38	Q1
<i>Anthus pratensis</i>	Meadow Pipit	-0.0035	8.26	1.80	Q3
<i>Parus major</i>	Great Tit	-0.0037	4.85	0.38	Q1
<i>Emberiza citrinella</i>	Yellowhammer	-0.0037	3.44	1.04	Q2
<i>Apus apus</i>	Swift	-0.0038	1.49	0.89	Q2
<i>Regulus regulus</i>	Goldcrest	-0.0038	1.34	1.46	Q3
<i>Carduelis carduelis</i>	Goldfinch	-0.0038	1.02	0.60	Q1
<i>Motacilla flava</i>	Yellow Wagtail	-0.0038	0.96	1.45	Q3
<i>Miliaria calandra</i>	Corn Bunting	-0.0038	0.95	1.65	Q3
<i>Aegithalos caudatus</i>	Long-tailed Tit	-0.0038	0.91	0.43	Q1
<i>Perdix perdix</i>	Grey Partridge	-0.0038	0.89	1.01	Q2
<i>Sylvia atricapilla</i>	Blackcap	-0.0038	0.81	0.53	Q1
<i>Phylloscopus trochilus</i>	Willow Warbler	-0.0038	0.67	0.69	Q1
<i>Buteo buteo</i>	Buzzard	-0.0038	0.53	0.42	Q1
<i>Acrocephalus schoenobaenus</i>	Sedge Warbler	-0.0038	0.49	1.46	Q3
<i>Numenius arquata</i>	Curlew	-0.0038	0.49	1.28	Q2
<i>Parus palustris</i>	Marsh Tit	-0.0038	0.48	1.07	Q2
<i>Phylloscopus collybita</i>	Chiffchaff	-0.0038	0.46	0.54	Q1

<i>Ficedula hypoleuca</i>	Pied Flycatcher	-0.0038	0.32	1.06	Q2
<i>Saxicola rubetra</i>	Whinchat	-0.0038	0.27	1.31	Q3
<i>Phylloscopus</i>	Wood Warbler	-0.0038	0.24	1.10	Q2
<i>sibilatrix</i>					
<i>Tringa totanus</i>	Redshank	-0.0038	0.23	1.75	Q3
<i>Actitis hypoleucos</i>	Common Sandpiper	-0.0038	0.20	1.50	Q3
<i>Certhia familiaris</i>	Treecreeper	-0.0038	0.17	0.82	Q2
<i>Dendrocopos major</i>	Great Spotted Woodpecker	-0.0038	0.17	0.56	Q1
<i>Gallinago gallinago</i>	Snipe	-0.0038	0.16	1.61	Q3
<i>Anthus trivialis</i>	Tree Pipit	-0.0038	0.15	1.35	Q3
<i>Gallinula chloropus</i>	Moorhen	-0.0038	0.12	1.31	Q3
<i>Vanellus vanellus</i>	Lapwing	-0.0038	0.11	0.89	Q2
<i>Oxyura jamaicensis</i>	Ruddy Duck*	-0.0038	0.10	2.42	Q4
<i>Haematopus</i>	Oystercatcher	-0.0038	0.10	0.99	Q2
<i>ostralegus</i>					
<i>Picus viridis</i>	Green Woodpecker	-0.0038	0.10	0.45	Q1
<i>Motacilla cinerea</i>	Grey Wagtail	-0.0038	0.09	1.05	Q2
<i>Carduelis flavirostris</i>	Twite	-0.0038	0.09	1.40	Q3
<i>Tadorna tadorna</i>	Shelduck	-0.0038	0.09	1.36	Q3
<i>Calidris alpina</i>	Dunlin	-0.0038	0.07	2.02	Q4
<i>Catharacta skua</i>	Great Skua	-0.0038	0.07	2.86	Q4
<i>Prunella modularis</i>	Dunnock	-0.0038	0.07	0.44	Q1
<i>Sylvia undata</i>	Dartford Warbler	-0.0038	0.07	2.37	Q4
<i>Luscinia</i>	Nightingale	-0.0038	0.06	1.16	Q2
<i>megarhynchos</i>					
<i>Parus montanus</i>	Willow Tit	-0.0038	0.06	0.68	Q1

<i>Turdus torquatus</i>	Ring Ouzel	-0.0038	0.05	2.00	Q4
<i>Strix aluco</i>	Tawny Owl	-0.0038	0.05	0.87	Q2
<i>Turdus philomelos</i>	Song Thrush	-0.0038	0.04	0.36	Q1
<i>Charadrius dubius</i>	Little Ringed Plover	-0.0038	0.03	2.23	Q4
<i>Aythya ferina</i>	Pochard	-0.0038	0.03	2.51	Q4
<i>Sterna sandvicensis</i>	Sandwich Tern	-0.0038	0.03	1.49	Q3
<i>Bucephala clangula</i>	Goldeneye	-0.0038	0.03	1.87	Q4
<i>Lagopus mutus</i>	Ptarmigan	-0.0038	0.03	3.18	Q4
<i>Corvus cornix</i>	Hooded Crow	-0.0038	0.03	0.77	Q1
<i>Fulmarus glacialis</i>	Fulmar	-0.0038	0.03	1.05	Q2
<i>Stercorarius parasiticus</i>	Arctic Skua	-0.0038	0.02	2.13	Q4
<i>Charadrius hiaticula</i>	Ringed Plover	-0.0038	0.02	1.33	Q3
<i>Locustella naevia</i>	Grasshopper Warbler	-0.0038	0.02	0.93	Q2
<i>Chrysolophus pictus</i>	Golden Pheasant*	-0.0038	0.02	1.41	Q3
<i>Athene noctua</i>	Little Owl*	-0.0038	0.02	0.72	Q1
<i>Corvus corax</i>	Raven	-0.0038	0.02	0.72	Q1
<i>Netta rufina</i>	Red-crested Pochard*	-0.0038	0.02	2.02	Q4
<i>Coccothraustes coccothraustes</i>	Hawfinch	-0.0038	0.02	1.37	Q3
<i>Podiceps cristatus</i>	Great Crested Grebe	-0.0038	0.02	1.82	Q4
<i>Caprimulgus europaeus</i>	Nightjar	-0.0038	0.02	1.95	Q4
<i>Phalacrocorax aristotelis</i>	Shag	-0.0038	0.02	1.81	Q3
<i>Cygnus cygnus</i>	Whooper Swan	-0.0038	0.02	1.43	Q3
<i>Asio otus</i>	Long-eared Owl	-0.0038	0.01	1.42	Q3

<i>Rallus aquaticus</i>	Water Rail	-0.0038	0.01	2.11	Q4
<i>Mergus serrator</i>	Red-breasted Merganser	-0.0038	0.01	1.13	Q2
<i>Tyto alba</i>	Barn Owl	-0.0038	0.01	0.63	Q1
<i>Anthus petrosus</i>	Rock Pipit	-0.0038	0.01	1.02	Q2
<i>Coturnix coturnix</i>	Quail	-0.0038	0.01	0.94	Q2
<i>Dendrocopos minor</i>	Lesser Spotted Woodpecker	-0.0038	0.01	0.71	Q1
<i>Falco peregrinus</i>	Peregrine	-0.0038	0.01	1.06	Q2
<i>Hirundo rustica</i>	Swallow	-0.0038	0.01	0.55	Q1
<i>Falco columbarius</i>	Merlin	-0.0038	0.01	1.88	Q4
<i>Arenaria interpres</i>	Turnstone	-0.0038	0.00	1.01	Q2
<i>Certhia brachydactyla</i>	Short-toed Treecreeper	-0.0038	0.00	1.39	Q3
<i>Charadrius morinellus</i>	Dotterel	-0.0038	0.00	2.72	Q4
<i>Scolopax rusticola</i>	Woodcock	-0.0038	0.00	1.21	Q2
<i>Alcedo atthis</i>	Kingfisher	-0.0038	0.00	1.45	Q3
<i>Anas penelope</i>	Wigeon	-0.0038	0.00	1.83	Q4
<i>Anas clypeata</i>	Shoveler	-0.0038	0.00	2.27	Q4
<i>Turdus iliacus</i>	Redwing	-0.0038	0.00	0.95	Q2
<i>Burhinus oediconemus</i>	Stone-curlew	-0.0038	0.00	1.24	Q2
<i>Pandion haliaetus</i>	Osprey	-0.0038	0.00	1.92	Q4
<i>Cygnus atratus</i>	Black Swan*	-0.0038	0.00	1.60	Q3
<i>Cairina moschata</i>	Muscovy Duck*	-0.0038	0.00	1.10	Q2
<i>Anser caerulescens</i>	Snow Goose*	-0.0038	0.00	1.30	Q3
<i>Aix sponsa</i>	Wood Duck*	-0.0038	0.00	0.81	Q2

<i>Numenius phaeopus</i>	Whimbrel	-0.0038	0.00	1.07	Q2
<i>Cinclus cinclus</i>	Dipper	-0.0038	0.00	1.42	Q3
<i>Anas querquedula</i>	Garganey	-0.0038	0.00	2.24	Q4
<i>Panurus biarmicus</i>	Bearded Tit	-0.0038	0.00	2.59	Q4
<i>Phoenicurus</i>	Black Redstart	-0.0038	0.00	1.10	Q2
<i>ochruros</i>					
<i>Asio flammeus</i>	Short-eared Owl	-0.0038	0.00	1.37	Q3
<i>Larus</i>	Mediterranean Gull	-0.0038	0.00	0.89	Q2
<i>melanocephalus</i>					
<i>Crex crex</i>	Corncrake	-0.0038	0.00	1.60	Q3
<i>Pluvialis squatarola</i>	Grey Plover	-0.0038	0.00	1.42	Q3
<i>Tringa ochropus</i>	Green Sandpiper	-0.0038	0.00	1.76	Q3
<i>Tringa nebularia</i>	Greenshank	-0.0038	0.00	1.93	Q4
<i>Tetrao tetrix</i>	Black Grouse	-0.0038	0.00	1.52	Q3
<i>Phoenicurus</i>	Redstart	-0.0038	0.00	0.71	Q1
<i>phoenicurus</i>					
<i>Limosa limosa</i>	Black-tailed Godwit	-0.0038	-0.01	2.03	Q4
<i>Falco subbuteo</i>	Hobby	-0.0038	-0.01	0.89	Q2
<i>Sterna hirundo</i>	Common Tern	-0.0038	-0.01	1.89	Q4
<i>Podiceps nigricollis</i>	Black-necked Grebe	-0.0038	-0.01	3.16	Q4
<i>Numida meleagris</i>	Helmeted Guineafowl*	-0.0039	-0.01	0.65	Q1
<i>Accipiter gentilis</i>	Goshawk	-0.0039	-0.01	1.95	Q4
<i>Columba livia</i>	Rock Dove	-0.0039	-0.01	1.35	Q3
<i>Gavia stellata</i>	Red-throated Diver	-0.0039	-0.01	2.07	Q4
<i>Loxia scotica</i>	Scottish Crossbill	-0.0039	-0.01	2.78	Q4
<i>Circus cyaneus</i>	Hen Harrier	-0.0039	-0.01	1.83	Q4

<i>Gavia arctica</i>	Black-throated Diver	-0.0039	-0.01	2.18	Q4
<i>Sterna albifrons</i>	Little Tern	-0.0039	-0.02	2.25	Q4
<i>Recurvirostra avosetta</i>	Avocet	-0.0039	-0.02	2.14	Q4
<i>Mergus merganser</i>	Goosander	-0.0039	-0.02	1.27	Q2
<i>Pyrrhula pyrrhula</i>	Bullfinch	-0.0039	-0.02	0.38	Q1
<i>Pyrrhocorax pyrrhocorax</i>	Chough	-0.0039	-0.02	1.40	Q3
<i>Emberiza cirrus</i>	Cirl Bunting	-0.0039	-0.02	0.83	Q2
<i>Garrulus glandarius</i>	Jay	-0.0039	-0.02	0.56	Q1
<i>Circus aeruginosus</i>	Marsh Harrier	-0.0039	-0.03	1.82	Q3
<i>Cephus grylle</i>	Black Guillemot	-0.0039	-0.03	3.23	Q4
<i>Larus canus</i>	Common Gull	-0.0039	-0.03	0.92	Q2
<i>Parus cristatus</i>	Crested Tit	-0.0039	-0.03	3.09	Q4
<i>Tachybaptus ruficollis</i>	Little Grebe	-0.0039	-0.03	1.96	Q4
<i>Lullula arborea</i>	Woodlark	-0.0039	-0.03	1.58	Q3
<i>Erithacus rubecula</i>	Robin	-0.0039	-0.03	0.39	Q1
<i>Larus marinus</i>	Great Black-backed Gull	-0.0039	-0.03	0.93	Q2
<i>Milvus milvus</i>	Red Kite	-0.0039	-0.04	0.68	Q1
<i>Calidris alba</i>	Sanderling	-0.0039	-0.04	3.23	Q4
<i>Phalacrocorax carbo</i>	Cormorant	-0.0039	-0.05	1.53	Q3
<i>Pavo cristatus</i>	Indian Peafowl*	-0.0039	-0.07	1.04	Q2
<i>Alopochen aegyptiacus</i>	Egyptian Goose*	-0.0039	-0.07	1.35	Q3
<i>Larus ridibundus</i>	Black-headed Gull	-0.0039	-0.07	0.92	Q2

<i>Ardea cinerea</i>	Grey Heron	-0.0039	-0.07	1.17	Q2
<i>Egretta garzetta</i>	Little Egret	-0.0039	-0.08	1.28	Q2
<i>Delichon urbica</i>	House Martin	-0.0039	-0.09	0.66	Q1
<i>Riparia riparia</i>	Sand Martin	-0.0039	-0.10	1.21	Q2
<i>Corvus corone</i>	Carrion Crow	-0.0039	-0.10	0.35	Q1
<i>Branta leucopsis</i>	Barnacle Goose*	-0.0039	-0.11	1.87	Q4
<i>Regulus ignicapillus</i>	Firecrest	-0.0039	-0.11	1.30	Q3
<i>Aythya fuligula</i>	Tufted Duck	-0.0039	-0.12	1.79	Q3
<i>Anas strepera</i>	Gadwall	-0.0039	-0.13	1.93	Q4
<i>Streptopelia turtur</i>	Turtle Dove	-0.0039	-0.13	0.62	Q1
<i>Columba oenas</i>	Stock Dove	-0.0039	-0.13	0.50	Q1
<i>Passer montanus</i>	Tree Sparrow	-0.0039	-0.14	0.80	Q1
<i>Anas crecca</i>	Teal	-0.0039	-0.15	2.09	Q4
<i>Sylvia borin</i>	Garden Warbler	-0.0039	-0.16	0.57	Q1
<i>Somateria mollissima</i>	Eider	-0.0039	-0.16	2.13	Q4
<i>Sylvia curruca</i>	Lesser Whitethroat	-0.0039	-0.17	0.70	Q1
<i>Sterna paradisaea</i>	Arctic Tern	-0.0039	-0.17	2.60	Q4
<i>Muscicapa striata</i>	Spotted Flycatcher	-0.0039	-0.18	0.56	Q1
<i>Aix galericulata</i>	Mandarin*	-0.0039	-0.18	1.19	Q2
<i>Anser anser</i>	Greylag Goose (feral)	-0.0039	-0.19	1.89	Q4
<i>Cuculus canorus</i>	Cuckoo	-0.0039	-0.20	0.40	Q1
<i>Oenanthe oenanthe</i>	Wheatear	-0.0039	-0.21	1.25	Q2
<i>Larus fuscus</i>	Lesser Black-backed Gull	-0.0039	-0.22	1.06	Q2
<i>Lagopus lagopus</i>	Red Grouse	-0.0039	-0.25	2.82	Q4
<i>Carduelis cabaret</i>	Lesser Redpoll	-0.0039	-0.26	1.25	Q2

<i>Phasianus colchicus</i>	Pheasant*	-0.0039	-0.26	0.58	Q1
<i>Alauda arvensis</i>	Skylark	-0.0039	-0.28	0.93	Q2
<i>Cygnus olor</i>	Mute Swan	-0.0039	-0.29	1.68	Q3
<i>Cettia cetti</i>	Cetti's Warbler	-0.0039	-0.29	2.28	Q4
<i>Saxicola torquata</i>	Stonechat	-0.0039	-0.33	1.42	Q3
<i>Pluvialis apricaria</i>	Golden Plover	-0.0039	-0.37	2.13	Q4
<i>Fulica atra</i>	Coot	-0.0039	-0.51	1.78	Q3
<i>Anas platyrhynchos</i>	Mallard (feral)	-0.0039	-0.52	1.38	Q3
<i>Psittacula krameri</i>	Ring-necked Parakeet*	-0.0039	-0.55	1.38	Q3
<i>Accipiter nisus</i>	Sparrowhawk	-0.0039	-0.60	0.36	Q1
<i>Emberiza</i>	Reed Bunting	-0.0039	-0.73	1.28	Q2
<i>schoeniclus</i>					
<i>Acrocephalus</i>	Reed Warbler	-0.0039	-0.81	1.53	Q3
<i>scirpaceus</i>					
<i>Sitta europaea</i>	Nuthatch	-0.0039	-0.83	0.83	Q2
<i>Carduelis chloris</i>	Greenfinch	-0.0039	-1.10	0.78	Q1
<i>Motacilla alba</i>	Pied Wagtail	-0.0039	-1.20	0.50	Q1
<i>Pica pica</i>	Magpie	-0.0039	-1.25	0.70	Q1
<i>Falco tinnunculus</i>	Kestrel	-0.0039	-1.26	0.27	Q1
<i>Fringilla coelebs</i>	Chaffinch	-0.0039	-1.37	0.35	Q1
<i>Branta canadensis</i>	Canada Goose*	-0.0039	-1.49	1.63	Q3
<i>Anser anser</i>	Greylag Goose	-0.0039	-1.52	2.26	Q4
<i>Larus argentatus</i>	Herring Gull	-0.0039	-1.57	1.41	Q3
<i>Turdus viscivorus</i>	Mistle Thrush	-0.0039	-1.58	0.29	Q1
<i>Loxia curvirostra</i>	Crossbill	-0.0039	-1.60	2.32	Q4
<i>Alectoris rufa</i>	Red-legged Partridge*	-0.0039	-1.60	1.02	Q2
<i>Carduelis cannabina</i>	Linnet	-0.0039	-1.92	0.64	Q1

<i>Corvus monedula</i>	Jackdaw	-0.0039	-1.95	0.66	Q1
<i>Parus ater</i>	Coal Tit	-0.0039	-2.02	1.39	Q3
<i>Sylvia communis</i>	Whitethroat	-0.0039	-2.53	0.75	Q1
<i>Carduelis spinus</i>	Siskin	-0.0039	-2.55	2.11	Q4
<i>Corvus frugilegus</i>	Rook	-0.0040	-2.66	0.51	Q1
<i>Turdus merula</i>	Blackbird	-0.0040	-3.38	0.54	Q1
<i>Streptopelia</i>	Collared Dove	-0.0040	-3.87	1.29	Q3
<i>decaocto</i>					
<i>Anas platyrhynchos</i>	Mallard	-0.0040	-4.13	1.29	Q3
<i>Columba livia</i>	Feral Pigeon	-0.0040	-4.22	1.96	Q4
<i>Troglodytes</i>	Wren	-0.0040	-4.26	0.34	Q1
<i>troglodytes</i>					
<i>Parus caeruleus</i>	Blue Tit	-0.0040	-4.40	0.41	Q1
<i>Passer domesticus</i>	House Sparrow	-0.0041	-7.30	1.29	Q3

538 * Non-native species.

539

540

541

542

543

544

545

546

547

548

549

550

551

552 **Table S2.** Definition of habitat classes

Habitat class	Constituent habitat classes from Crick (1992)
Broadleaved woodland	Broadleaved, broadleaved water-logged, regenerating natural or semi-natural wood ¹ , young coppice ¹ , new plantation ¹ , clear-felled woodland ¹
Coniferous woodland	Coniferous, coniferous water-logged, regenerating natural or semi-natural wood ¹ , young coppice ¹ , new plantation ¹ , clear-felled woodland ¹
Mixed woodland	Mixed (10% of each), mixed water-logged, regenerating natural or semi-natural wood ¹ , young coppice ¹ , new plantation ¹ , clear-felled woodland ¹
Semi-natural grass, heath and bog	Chalk downland, downland chalk scrub, grass moor
Upland if mean altitude of BBS square $\geq 300\text{m}$	(unenclosed), grass moor mixed with heather (unenclosed), other dry grassland, dry heath, wet heath, mixed heath, bog,
Lowland if $< 300\text{m}$	breckland, drained bog, bare peat, heath scrub,
Arable farmland	Tilled land
Pastoral farmland	Improved grassland, unimproved grassland
Mixed farmland	Mixed grassland / tilled land, orchard other farming
Rural settlement	Rural settlement
Urban and suburban settlement	Urban settlement, suburban settlement
Wetlands and standing water	Pond (less than 50 m^2), small water-body ($50\text{--}450\text{ m}^2$), lake/unlined reservoir, lined reservoir, gravel pit, sand pit, water-meadow/grazing marsh, reed swamp, other open marsh
Flowing water	Stream (less than 3 m wide), river (more than 3 m wide), ditch with water (less than 2 m wide), small canal ($2\text{--}5\text{ m}$ wide), large canal (more than 5 m wide)

553 ¹ Of the appropriate habitat type (i.e. broadleaved, coniferous or mixed)

554 For the habitat covariate in detection models, upland and lowland semi-natural grassland, heath and
555 bog were treated as a single habitat class. Where there were fewer than 20 observations in a habitat,
556 habitat classes were grouped with similar habitat classes to form broader classes. These broader
557 classes were woodland (consisting of the broadleaved, mixed and coniferous woodland classes),
558 farmland (arable, pastoral and mixed farmland), human settlement (urban and rural settlement) and
559 wetland (wetlands and standing water and flowing water).

560

561 **Table S3.** Surrogate species used for species where distance models failed to estimate detection
 562 functions. Surrogate species were chosen based on the authors' field experience with these species.

Species		Surrogate species	
Goldeneye	<i>Bucephala clangula</i>	Goosander	<i>Mergus merganser</i>
Ptarmigan	<i>Lagopus mutus</i>	Red Grouse	<i>Lagopus lagopus</i>
Dotterel	<i>Charadrius morinellus</i>	Golden Plover	<i>Pluvialis apricaria</i>
Green Sandpiper	<i>Tringa ochropus</i>	Common Sandpiper	<i>Actitis hypoleucos</i>
Stone-curlew ¹	<i>Burhinus oediconemus</i>	Curlew	<i>Numenius arquata</i>
Little Tern	<i>Sterna albifrons</i>	Arctic Tern ²	<i>Sterna paradisaea</i>
Sandwich Tern	<i>Sterna sandvicensis</i>	Arctic Tern ²	<i>Sterna paradisaea</i>
Long-eared Owl ¹	<i>Asio otus</i>	Tawny Owl	<i>Strix aluco</i>
Black Redstart	<i>Phoenicurus ochruros</i>	Common Redstart	<i>Phoenicurus phoenicurus</i>
Hawfinch ¹	<i>Coccothraustes</i> <i>coccothraustes</i>	Bullfinch	<i>Pyrrhula pyrrhula</i>

563 ¹ We note that these species are likely to be harder to detect than their surrogates.

564 ² Common Tern *Sterna hirundo* was not selected due to their association with inland waterbodies.

565

566

567

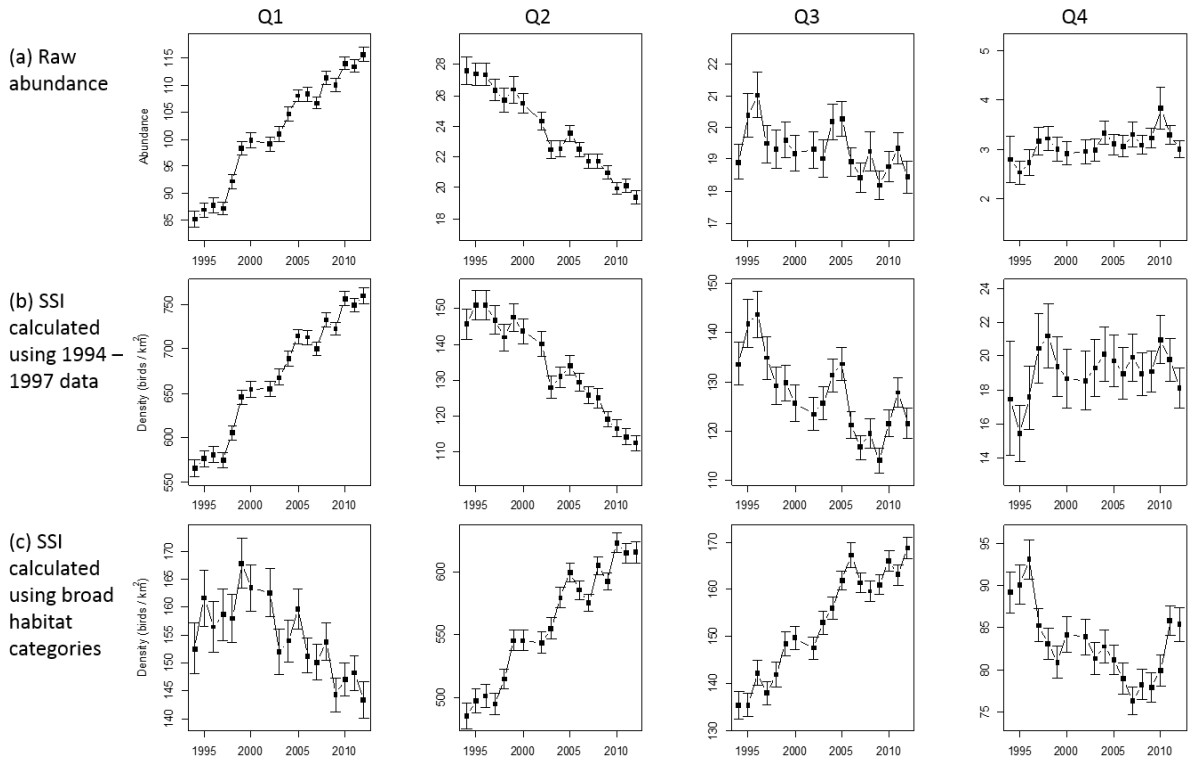
568

569

570

571

572



573

574 **Figure S1.** Sensitivity of changes in density of each quartile (Fig. 1) to different treatment of data. In

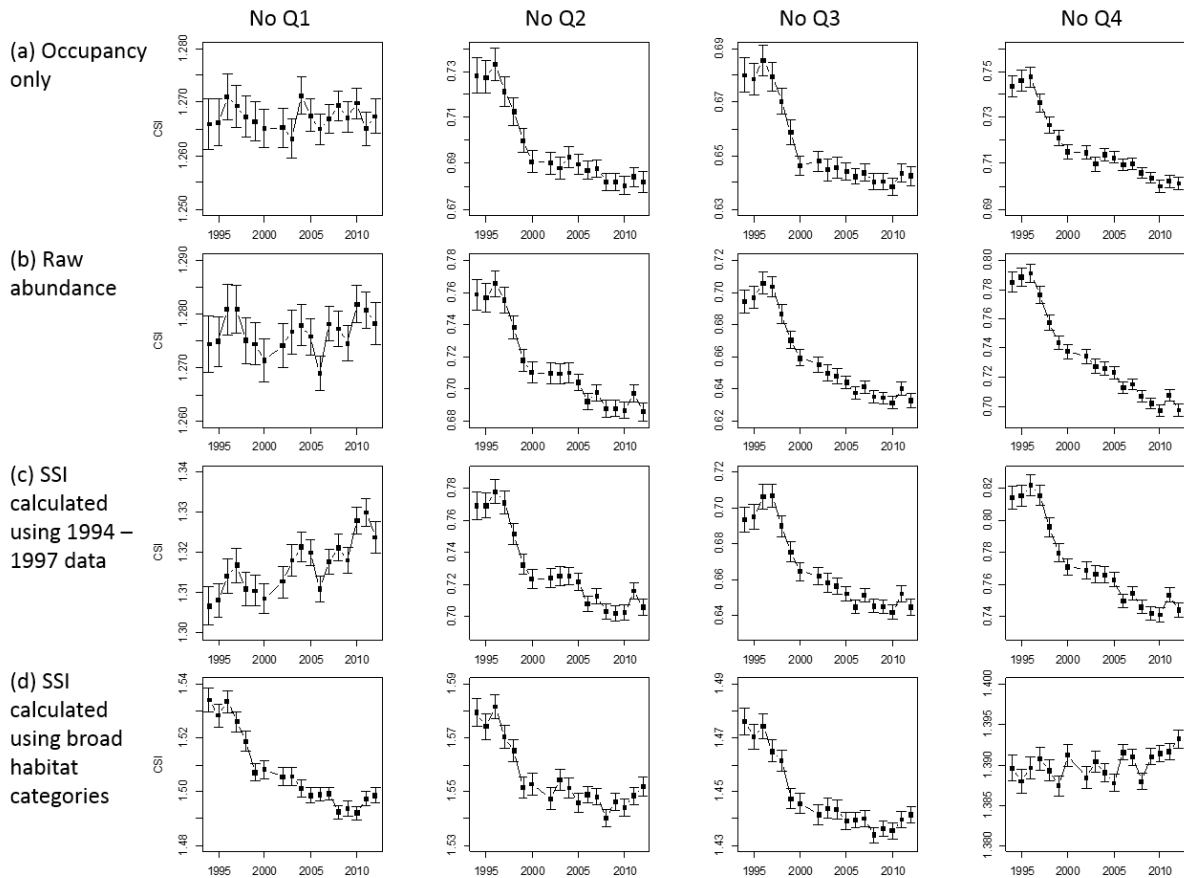
575 (a), observed abundances of all species have been used rather than converting these to density

576 estimates using detection probabilities. In (b), species have been divided into quartiles based on SSI

577 values calculated using data from 1994-1997. In (c), species have been divided into quartiles based on

578 SSI values calculated based on species' associations with four broad habitat types.

579



580

581 **Figure S2.** Sensitivity of effect of each quartile on CSI trend (Fig. 3) to different treatment of data. In

582 (a), CSI was calculated as the unweighted mean of SSI across species found in each community, so

583 reflects occupancy rather than abundance. In (b), observed abundances of all species have been used

584 rather than converting these to density estimates using detection probabilities. In (c), SSI values have

585 been calculated using data from 1994-1997. In (d), SSI values have been calculated based on species'

586 associations with four broad habitat types.

587

588

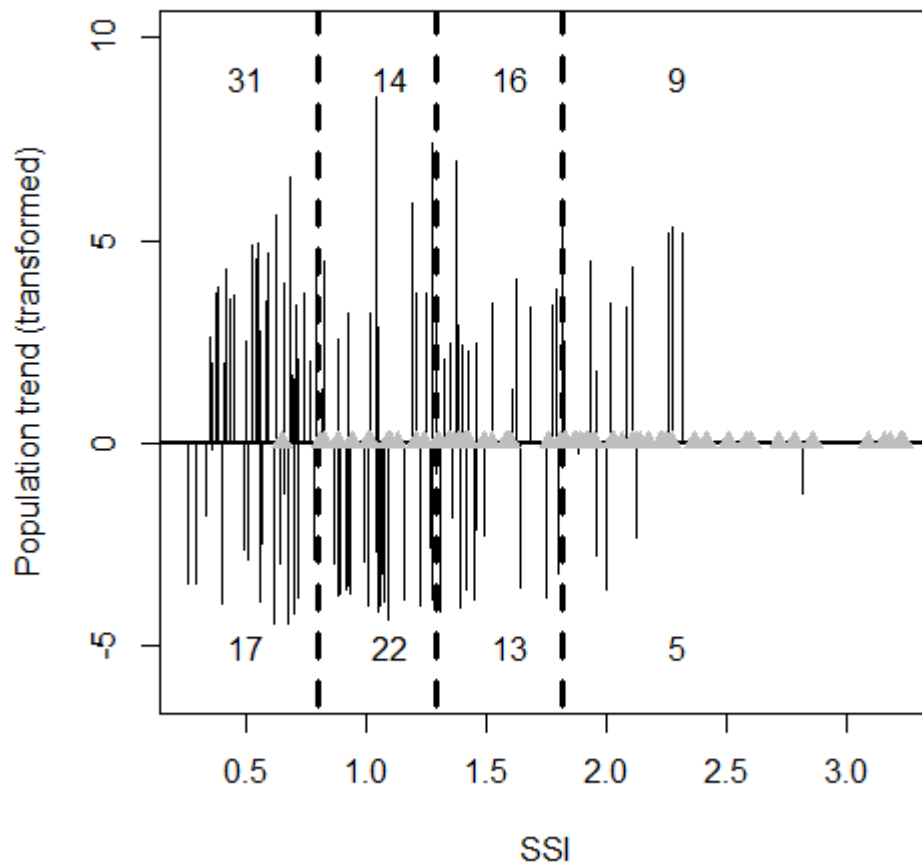
589

590

591

592

593

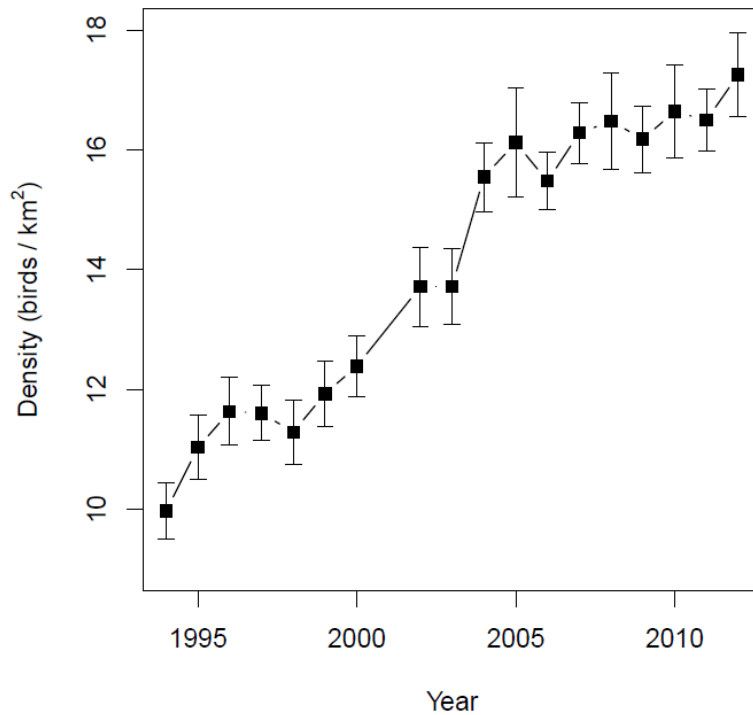


594

595 **Figure S3.** Relationship between population trend and degree of habitat specialization (SSI). Lines
 596 show the population trend of each species from the BBS, with values obtained from Risely et al.
 597 (2013). Grey triangles show species that were recorded too infrequently to calculate robust population
 598 trends. Species are positioned along the x-axis according to their SSI value. Population trends have
 599 been transformed to aid presentation. For positive population trends, $\ln(\text{population trend} + 1)$ have
 600 been shown, while for negative population trends $-\ln(\text{population trend} - 1)$ have been shown. Dashed
 601 lines show quartile boundaries, with text in each quartile indicating the total number of increasing and
 602 declining species in that quartile.

603

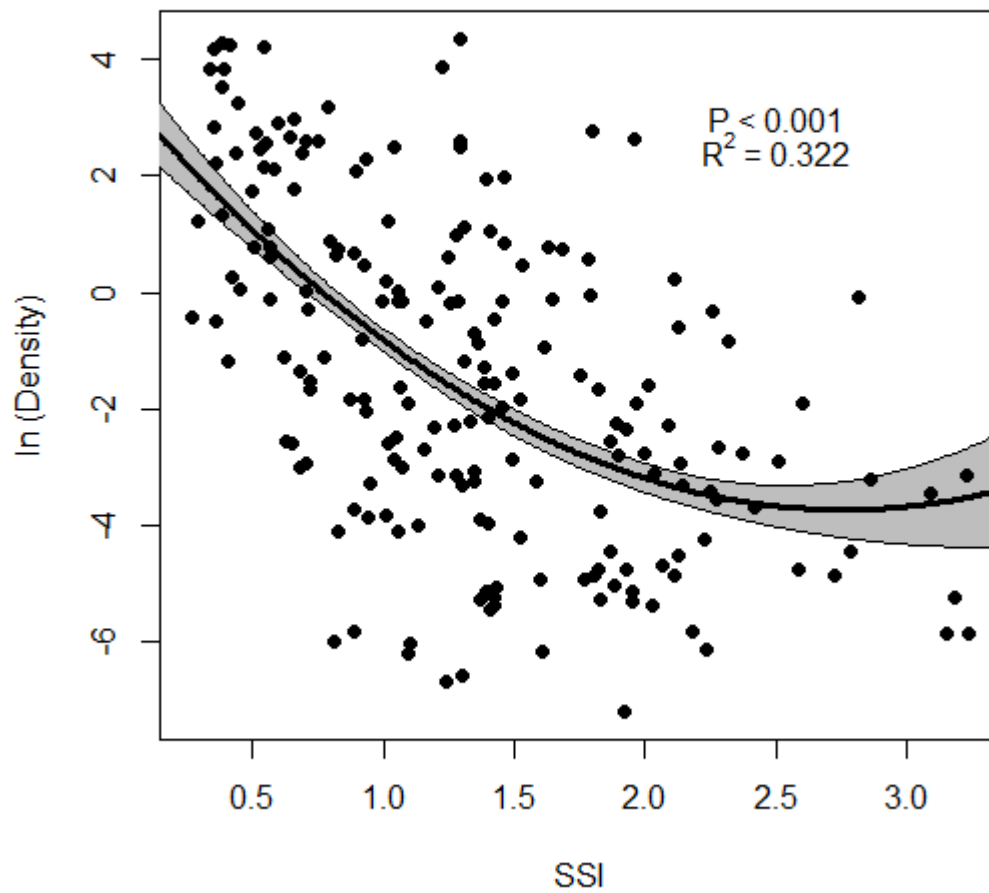
604



605

606 **Figure S4.** Change in density of non-native species. Points show the mean density of non-native
 607 species in BBS squares in a given year, with error bars showing standard errors. Densities were
 608 calculated by subsetting the BBS data to only include non-native species, and then summing the
 609 density of non-native birds in each BBS square-year combination. BBS square-year combinations
 610 where no non-native species was recorded were assigned a density value of zero.

611



612

613 **Figure S5.** Relationship between species' population density and habitat specialization (SSI). Density
 614 (birds.km⁻²) was calculated as the mean density of a species across all BBS square – year
 615 combinations. The polynomial fit shown was better supported than the nested linear fit ($F = 10.2$, $P =$
 616 0.002).

617

618