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1 **Evidence for the buffer effect operating in multiple species at a national scale**

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5 Keywords: density-dependence, population regulation, population trend, breeding bird survey,  
6 habitat selection

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8 A long-standing aim of ecologists is to understand the processes involved in regulating populations.  
9 One such mechanism is the buffer effect, where lower quality habitats are increasingly used as a  
10 species reaches higher population densities, with a resultant average reduction in fecundity and  
11 survival limiting population growth. Although the buffer effect has been demonstrated in  
12 populations of a number of species, a test of its importance influencing population growth rates of  
13 multiple species across large-spatial scales is lacking. Here we use habitat-specific population trends  
14 for 85 bird species from long-term national monitoring data (the UK Breeding Bird Survey) to  
15 examine its generality. We find that both patterns of population change and changes in habitat  
16 preference are consistent with the predictions of the buffer effect, providing support for its  
17 widespread operation.

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## 23 **Introduction**

24 Understanding how populations are regulated has been a key challenge for ecologists [1,2]. As well  
25 as being of considerable theoretical interest, this is highly relevant for understanding how to  
26 conserve species in a changing world [3]. One mechanism for population regulation is the buffer  
27 effect [4]. The predictions of the buffer effect are founded on the assumption of density-dependent  
28 habitat selection. As population densities increase, higher quality habitats become saturated, so  
29 individuals move into lower quality ones. Therefore, species whose populations are increasing  
30 should increase most rapidly in low quality habitats. This shift into poorer quality habitats has the  
31 potential to regulate population growth if poorer quality habitats incur fitness costs [5]. At lower  
32 population densities higher quality habitats are preferred, reflecting density independent habitat  
33 preferences, so population declines are predicted to be more rapid in poorer quality habitats.

34 The buffer effect has been documented in several taxa [4,6,7] and shown to regulate populations of  
35 individual species at large spatial scales [5,8]. However, it is unclear how general the buffer effect is  
36 across species [9,10]. We used long-term national monitoring data on UK birds to examine whether  
37 variation in bird population trends between habitats is consistent with expectations from the buffer  
38 effect operating across a national avifauna. If the buffer effect is operating, we hypothesise that  
39 nationally declining species will show the least negative habitat-specific population trends in their  
40 preferred (assumed high quality) habitats, while species showing strong national population  
41 increases will have the most positive habitat-specific population trends in avoided (assumed lower  
42 quality) habitats. Density-dependent shifts in habitat preference should also mean that as species  
43 increase, the differences in preference between their most and least preferred habitats should  
44 reduce (Table 1).

## 45 **Materials and methods**

46 National and habitat-specific population trends were calculated using data from the UK breeding  
47 bird survey (BBS, further details in Appendix S1) between 1994 and 2012. This survey involves all  
48 adult birds being counted from two 1-km line transects, divided into five 200m sections, and located  
49 within 1km grid squares (the BBS sampling units) across the UK by stratified random sampling.  
50 Annual abundance indices were produced using Poisson generalized linear models, modelling count  
51 as a function of square identity and year. Indices were smoothed using a post-hoc thin-plate spline  
52 smooth and final trends calculated as  $(\text{smooth population index}_{2011} - \text{smoothed population index}_{1995})$   
53  $/ \text{smoothed population index}_{1995}$ , with the first and last years removed as these have an excessive  
54 influence on trend.

55 Observers record up to two habitat-types in each transect section, which following [10], were  
56 aggregated into 12 broad habitat-types for analysis (see Appendix S1). Habitat-specific population  
57 trends were generated using only BBS transect sections in a given habitat-type, with transect length  
58 incorporated as an offset to account for resultant differences in transect length. This procedure was  
59 repeated on 199 bootstraps (sampling data with replacement) to generate the standard errors for  
60 each trend (see Appendix S1 for more details).

61 In the absence of measures of habitat quality for all species we use habitat preference as a proxy for  
62 habitat quality. We calculated Jacobs index of habitat preference for each species and habitat,  $J_{h,s} =$   
63  $(u_{h,s} - a_{h,s}) / (u_{h,s} + a_{h,s} - 2u_{h,s}a_{h,s})$ , where  $u_{h,s}$  is the proportion of the BBS registrations for species  $s$  in  
64 habitat  $h$  and  $a_{h,s}$  the proportion of transect sections in BBS squares where the species was recorded  
65 that contained that habitat (see Appendix S1 for further details). We did this using data for each  
66 year, and used the mean value of  $J$  across all years in further analysis, to maximise the number of  
67 records of each species. We also calculated  $J$  at the start (1994 – 1997) and end (2009 – 2012) of the  
68 survey period.

69 We conducted three analyses to test for hypothesised signatures of the buffer effect (Table 1), using  
70 data for 85 species recorded in a minimum of two separate habitats at a threshold of at least ten

71 times per year (see Appendix S1 for more detail, and Appendix 2 for results for different thresholds  
72 for species inclusion). Firstly, habitat-specific trends of species were modelled as a function of  
73 national trend, habitat preference index ( $J$ ) and their interaction, using a linear mixed effects model  
74 with species identity as a random effect (Analysis 1 in Table 1)). In this model, observations were  
75 weighted by  $1/\text{habitat-specific trend SE}$  to account for uncertainty in trend estimation. Secondly, we  
76 used linear regression to model the relationship between habitat-specific trend and  $J$  for all species  
77 recorded in at least five habitats (73 species, see Appendix S2 for results with different threshold  
78 number of habitats), and then looked at the correlation between the estimated coefficient of this  
79 relationship (divided by the standard error of the parameter estimate) with national trend (Analysis  
80 2 in Table 1). Finally, we calculated the range of  $J$  for each species at the start and end of the survey  
81 period, and used linear regression to model changes in this range as a function of national trend  
82 (Analysis 3 in Table 1). These analyses assume normally distributed errors, so we used  $\ln(\text{habitat-}$   
83  $\text{specific trend} + 1)$  to ensure normality of residuals and avoid heteroscedacity of variances. Analyses  
84 were performed in R, using lme4 for mixed-effects models [12].

## 85 **Results**

86 Habitat-specific trends were positively related to both national trend ( $\beta = 0.010 \pm <0.001 \text{ SE}$ ,  $\chi^2 =$   
87  $151.99$ ,  $P < 0.0001$ ) and habitat preference index  $J$  ( $\beta = 0.119 \pm 0.035 \text{ SE}$ ,  $\chi^2 = 7.73$ ,  $P = 0.0054$ ), and  $J$   
88 significantly interacted with national trend ( $\chi^2 = 5.73$ ,  $P = 0.017$ ). For declining species, habitat-  
89 specific trends were positively related to  $J$ , while for strongly increasing species the direction of this  
90 relationship was reversed (Fig. 1a), supporting the predictions of the buffer effect. This was reflected  
91 in a negative correlation between national trend and the standardised coefficient of the relationship  
92 between  $J$  and habitat-specific trend ( $r = -0.333$ ,  $P = 0.004$ , Fig. 1b). This relationship remained  
93 significant when  $J$  was calculated from the beginning of the study period ( $r = -0.268$ ,  $P = 0.022$ ).

94 Values of  $J$  at the start of the study period were strongly correlated with those at the end ( $r = 0.948$ ,  
95  $P < 0.0001$ ), indicating only weak shifts in habitat preference occurred. However, small changes in  $J$

96 were evident. These changes ( $\Delta J_{h,s}$ ) were correlated with changes in proportional habitat use ( $\Delta u_{h,s}$ ;  $r$   
97 = 0.57,  $P < 0.001$ ), but not with changes in habitat availability ( $\Delta a_{h,s}$ ;  $r = -0.03$ ,  $P = 0.21$ ). The range of  $J$   
98 values (i.e. difference in  $J$  between a species most preferred and most avoided habitat) tended to  
99 decrease over the study period for nationally increasing species, but increase over the study period  
100 for nationally declining species (Fig. 1c, linear regression between  $\Delta J$  range and national trend:  $\beta = -$   
101  $0.104 \pm 0.030$  SE,  $t = -3.427$ ,  $P = 0.0009$ ).

## 102 Discussion

103 Our results are consistent with the operation of the buffer effect at a national level across multiple  
104 species, and suggest that it is an important driver of local population trends. While the buffer effect  
105 has been demonstrated previously in studies considering a small number of species [7,8], we  
106 demonstrate here for the first time its generality across species and locations. However, the fact that  
107 there was considerable variation in the change in the range of  $J$  for species with stable population  
108 trends, which would not be predicted by the buffer effect, suggests that habitat-specific  
109 environmental changes are also an important driver of population trends. Two previous studies of  
110 British bird populations have failed to find evidence of the buffer effect [9,10], including one that  
111 also analysed BBS data. Unlike these, our study included a much greater number of species (85  
112 versus 19- 23), and considered population trends of both increasing and declining species, giving  
113 greater statistical power. Additionally, the time-period covered by this study was longer than that  
114 used in [10], which also used BBS data.

115 Not all species responded in a manner consistent with the buffer effect. Most notably, five nationally  
116 declining species declined most strongly in their preferred habitat. Known habitat-specific drivers  
117 account for two of these. Greenfinches *Carduelis chloris* preferentially selected rural and urban/  
118 suburban areas, but their populations have undergone declines in gardens due to disease [13], while  
119 goldcrests *Regulus regulus* have declined following recent cold winters in the UK, and populations in  
120 preferred but northerly distributed coniferous woodlands are likely to have been especially affected.

121 We did not find that the strength of the buffer effect varied between species in relation to their  
122 degree of habitat specialisation (Appendix S4), suggesting our findings are relevant to both  
123 generalists and specialists.

124 As robust measures of habitat quality do not exist for an entire avifauna, we necessarily quantified  
125 habitat preference rather than quality, assuming that preferred habitats were of higher quality. A  
126 danger with this is that we expect habitat preference to vary with population density and trend, as  
127 supported by our analyses (Fig. 1c). This means that by looking at their habitat preference over a  
128 window of time we could underestimate preference for the higher quality habitat and overestimate  
129 preference for the lower quality habitat. However, the implications of this for our conclusions are  
130 limited. Firstly, this bias reduces rather than enhances our chances of finding relationships  
131 supporting the predictions of the buffer effect. Secondly, the strong correlation between habitat  
132 preference at the start and end of the study period indicates that changes in habitat preference over  
133 the study period were relatively minor. Thirdly, repeating the analyses using only the habitat  
134 preferences at the start of the study period did not significantly alter our results. We note that  
135 relationships between habitat preference and demographic parameters are not necessarily linear,  
136 and in some cases preferred habitats may be lower quality (i.e. when a habitat is an ecological trap).  
137 Another caveat is that we have assumed that the strength of density-dependence increases with  
138 population growth, when it is possible that strongly increasing species are starting from small  
139 population sizes and so are largely free from density-dependent effects. Again, this is likely to have  
140 reduced our chances of finding relationships supporting our hypotheses by adding random noise to  
141 the data.

142 Processes other than density-dependent habitat selection can buffer populations in high quality  
143 habitats. For example, high quality habitats may have more non-breeding individuals (floaters) that  
144 take the place of breeding individuals as populations decline [14]. This could lead to more stable  
145 breeding populations in high quality habitats, but total populations (breeders + floaters) could still

146 fluctuate. Our results reflect changes in total populations (as surveyors recorded all adult birds  
147 observed), so they are unlikely to be explained by buffering by floaters, although this remains  
148 possible if floaters have lower detectability. Site-dependent population regulation is an alternative  
149 that differs slightly from the buffer effect in that individuals shift to better quality sites as they  
150 become available rather than in response to territoriality [15]. Further work is needed to explore  
151 how widespread different buffering mechanisms are, for example through analysis of demographic  
152 data and settlement decisions. Understanding the relative importance of density-dependent  
153 processes like the buffer effect in regulating populations, and investigating potential their  
154 interactions with drivers of environmental change, is likely to allow the responses of species to  
155 environmental change to be predicted with greater accuracy.

#### 156 **Data accessibility**

157 The input data used in the analyses in this paper are provided in Appendix S5. BBS data are available  
158 through the BTO's standard data request procedure (see [http://www.bto.org/research-data-](http://www.bto.org/research-data-services/data-services/data-and-information-policy)  
159 [services/data-services/data-and-information-policy](http://www.bto.org/research-data-services/data-services/data-and-information-policy)).

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#### 166 **Competing interests**

167 We have no competing interests.

#### 168 **Author contributions**



169 MS, SN and JP designed the study, carried out the analysis and wrote the paper.

170

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204 **Table 1.** Hypothesised signatures of the buffer effect.

Facet of buffer effect	Analysis	Hypothesised relationship if buffer effect is operating
Population changes greatest in poorer quality habitats, but more stable in high quality habitats.	Analysis 1: Modelling habitat-specific population trends as a function of habitat preference (proxy for habitat quality), national population trend and their interaction.	Significant interaction, with positive relationship between population trend and habitat preference for nationally declining species reversing direction to become negative for nationally increasing species.
	Analysis 2: Correlation between coefficient of habitat-preference habitat-trend relationship and national population trend.	Negative correlation.
Increasing populations become increasingly equally distributed across habitats, while decreasing populations become more unequally distributed.	Analysis 3: Modelling change in difference in preference between most and least preferred habitats as a function of national population trend.	Negative relationship

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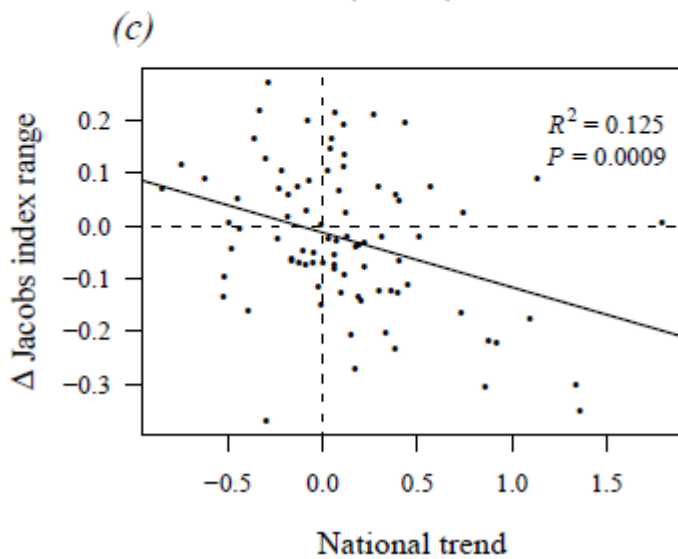
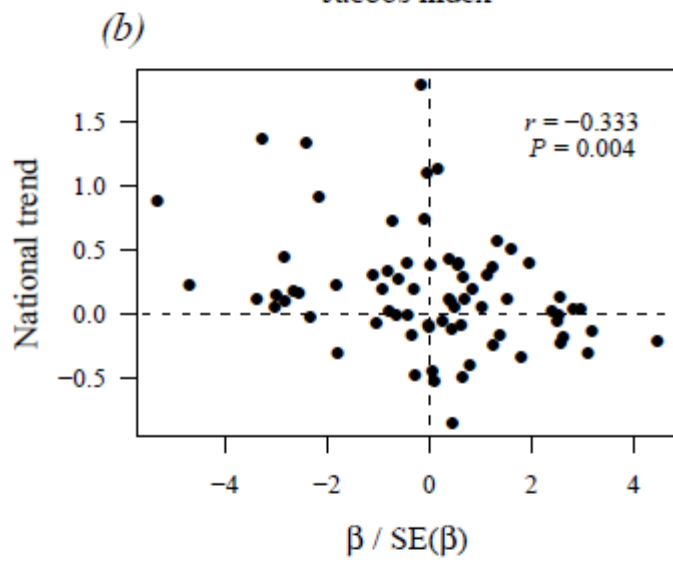
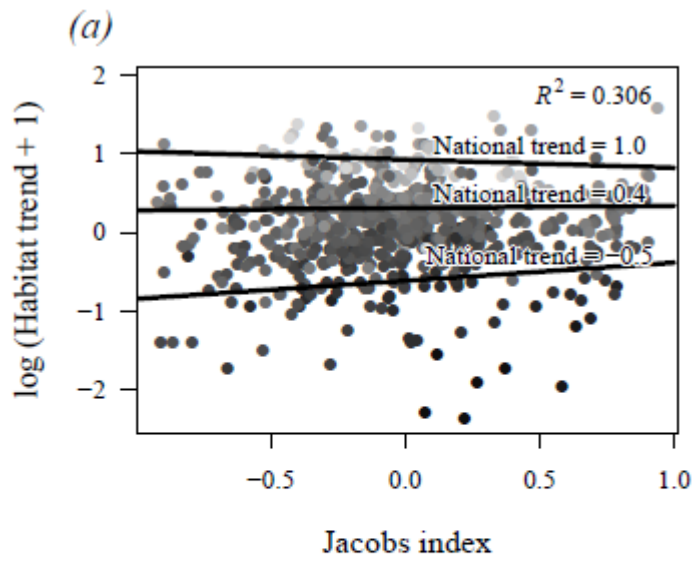
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214 **Figure 1.** (a) Relationship between population trend and Jacobs index of habitat preference ( $J$ ),  
215 modelled by a LMM with  $J$ , national trend and their interaction as covariates. The relationship  
216 between population trend and Jacobs index has been plotted with the BBS trend set to -0.5 (i.e.  
217 population halving), 0.4 and 1.0 (population doubling) in order to visualise the interaction between  
218 Jacobs index and BBS trend. Points show habitat-specific trends of all species, with paler shading  
219 indicating more positive national trends. The  $R^2$  value shown is the variation explained by the fixed  
220 effects component of the model. (b) Relationship between national BBS trend for each species and  
221 coefficient of relationship between habitat-specific population trend and  $J$ . Only species with at least  
222 five habitat-specific population trends were included. A version of the graph indicating species  
223 identity is given in Appendix S3 (c) Relationship between change in the range of  $J$  values for each  
224 species between 1994-1997 and 2009-2012, and national BBS trend.

225