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

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

Introduction

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

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

Materials and methods

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

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

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

We conducted three analyses to test for hypothesised signatures of the buffer effect (Table 1), using data for 85 species recorded in a minimum of two separate habitats at a threshold of at least ten times per year (see Appendix S1 for more detail, and Appendix 2 for results for different thresholds for species inclusion). Firstly, habitat-specific trends of species were modelled as a function of national trend, habitat preference index (*J*) and their interaction, using a linear mixed effects model with species identity as a random effect (Analysis 1 in Table 1)). In this model, observations were weighted by 1/habitat-specific trend SE to account for uncertainty in trend estimation. Secondly, we used linear regression to model the relationship between habitat-specific trend and *J* for all species recorded in at least five habitats (73 species, see Appendix S2 for results with different threshold number of habitats), and then looked at the correlation between the estimated coefficient of this relationship (divided by the standard error of the parameter estimate) with national trend (Analysis 2 in Table 1). Finally, we calculated the range of *J* for each species at the start and end of the survey period, and used linear regression to model changes in this range as a function of national trend (Analysis 3 in Table 1). These analyses assume normally distributed errors, so we used ln (habitat-specific trend +1) to ensure normality of residuals and avoid heteroscedacity of variances. Analyses were performed in R, using lme4 for mixed-effects models [12].

Results

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

Values of *J* at the start of the study period were strongly correlated with those at the end ($r = 0.948$, $P < 0.0001$), indicating only weak shifts in habitat preference occurred. However, small changes in *J* were evident. These changes ($\Delta J_{h,s}$) were correlated with changes in proportional habitat use ($\Delta u_{h,s}$; r = 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 values (i.e. difference in J between a species most preferred and most avoided habitat) tended to decrease over the study period for nationally increasing species, but increase over the study period for nationally declining species (Fig. 1c, linear regression between Δ J range and national trend: β = -0.104 ± 0.030 SE, t = -3.427, P = 0.0009).

Discussion

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

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

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

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

Processes other than density-dependent habitat selection can buffer populations in high quality habitats. For example, high quality habitats may have more non-breeding individuals (floaters) that take the place of breeding individuals as populations decline [14]. This could lead to more stable breeding populations in high quality habitats, but total populations (breeders + floaters) could still fluctuate. Our results reflect changes in total populations (as surveyors recorded all adult birds observed), so they are unlikely to be explained by buffering by floaters, although this remains possible if floaters have lower detectability. Site-dependent population regulation is an alternative that differs slightly from the buffer effect in that individuals shift to better quality sites as they become available rather than in response to territoriality [15]. Further work is needed to explore how widespread different buffering mechanisms are, for example through analysis of demographic data and settlement decisions. Understanding the relative importance of density-dependent processes like the buffer effect in regulating populations, and investigating potential their interactions with drivers of environmental change, is likely to allow the responses of species to environmental change to be predicted with greater accuracy.

Data accessibility

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

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Competing interests

We have no competing interests.

Author contributions

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

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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

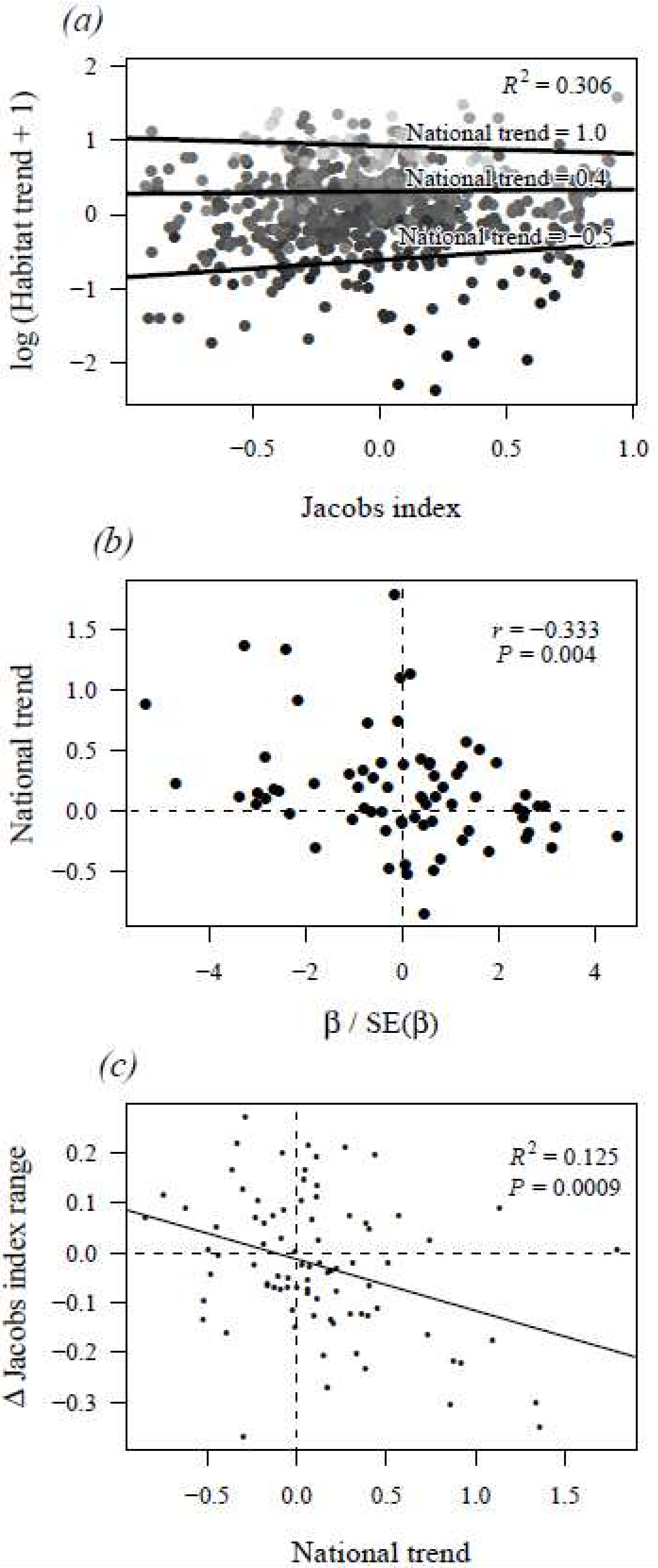
(a)
$R^2 = 0.306$
National trend = 1.0
National trend = 0.4
National trend = −0.5
log (Habitat trend + 1)
2
1
0
−1
−2
−0.5
0.0
0.5
1.0
Jacobs index
(b)
$r = -0.333$
$P = 0.004$
National trend
1.5
1.0
0.5
0.0
−0.5
−4
−2
0
2
4
β / SE(β)
(c)
$R^2 = 0.125$
$P = 0.0009$
Δ Jacobs index range
0.2
0.1
0.0
−0.1
−0.2
−0.3
−0.5
0.0
0.5
1.0
1.5
National trend

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