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Supplementary material

Appendix S1. Breeding bird survey design, production of population trends and statistical analysis.

Appendix S2. Sensitivity of results to different thresholds for including species.

Appendix S3. As Fig. 1b, but showing species codes. See Appendix S5 for species names.

Appendix S4. Responses of specialists and generalists.

Appendix S5. Population trends and habitat preferences of study species.

Appendix S1. Breeding bird survey design and production of population trends.

Survey design

The UK breeding bird survey (BBS) is the principal national monitoring scheme designed to monitor changes in bird populations in the UK, and has been running since 1994. Birds are counted along line transects crossing 1km squares. These 1km BBS squares (the sampling units of the survey) are randomly selected according to a stratified random sampling approach. In this, the UK is divided into 83 sampling regions, and BBS squares are selected randomly within these, with the number of BBS squares selected reflecting the density of volunteers in each sampling region. This approach ensures consistent national coverage while maximising the utilisation of available volunteers. Differences in regional sampling design are taken into account in analyses (see Producing population trends section below for details), ensuring that results are not biased by this sampling approach. A mean of 2660 ± 644 SD squares were surveyed each year during the study period (1994 – 2012).

In each 1km BBS square, volunteers walk two 1km line transects across the square. Each 1km transect is divided into five 200m transect sections (i.e. 10 transect sections per BBS square), and birds and details of habitat are recorded in each transect section. Birds are recorded in three distance bands (<100m, 100-200m and >200m), or as in flight. Volunteers are instructed not to record juveniles, and to avoid duplicate counts of the same bird. Each BBS square is visited twice during the breeding season (mid-March to late-June), with visits spaced at least four weeks apart to ensure that the survey targets both resident species that are more vocal early in the breeding season and late arriving migrants.

Producing population trends

National BBS trends are produced using standard analytical procedures described previously (e.g. [16]). The maximum count of each bird species in each BBS square across the two visits was used for analysis. We did this (rather than take the sum or average count across the two visits) because the

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two visits were designed to target different seasonal peaks in the abundance (due to late arriving migrants) and detectability (due to seasonal variation in territorial behaviour) of different bird species. Records of flying birds were excluded from analyses, because these were not necessarily using the BBS square, with the exception of hunting raptors, aerial feeding swifts and hirundines and displaying skylarks, as these were likely to be using the BBS square. Large counts of six wader species (oystercatcher, golden plover, lapwing, snipe, curlew and redshank) are excluded to remove counts from non-breeding flocks, while counts of golden plover in unsuitable lowland BBS squares are also excluded. The purpose of these filters is to remove observations of birds that likely to not be using the BBS square for breeding. Data from 2001 are also excluded from analysis, as in that year access restrictions due to foot and mouth disease prevented many volunteers from accessing BBS squares.

The count of each bird species in each BBS square was modelled as a function of year (as a categorical term) and BBS square identity, using generalised linear models with a Poisson error term and log link function, with a dispersion parameter (deviance divided by the degrees of freedom) to account for overdispersion. These models were implemented using PROC GENMOD in SAS software Version 9.3. Each observation is weighted by the number of 1km squares in the sampling region divided by the number of BBS squares counted in that sampling region, to account for differences in sampling density between regions.

The annual indices of abundance generated by these models are sensitive to annual fluctuations in abundance, so a post-hoc smooth was used to produce smoothed population trends. A thin-plate spline was used to do this (PROC TSPLINE), with the degrees of freedom of the spline set as 0.3 times the number of years in the time series [17]. Smooth trends are constructed using the entire time series (in this case 1994 to 2012), with trends expressed as the change in the smoothed population change between the second year of the time series (i.e. 1995) and the second last year of the time series (i.e. 2011). The first and last years are excluded as they have a large influence on the direction of trends.

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Bootstrapping was used to generate estimates of the standard error for each trend. BBS squares where the species had been recorded in at least one year were sampled with replacement 199 times, and in each sample the procedure of fitting a Poisson generalized linear model and then a post-hoc smooth to the annual indices was calculated, generating a distribution of population trend values from which the standard error was obtained.

Previous work has found that the effect of accounting for observer effects and detectability had very minor effects on population trends, and did not recommend incorporating them in the analytical procedure for generating BBS trends [18, 19], so we did not account for these when generating trends in this study.

Producing habitat-specific population trends

The procedure for producing habitat-specific trends was similar to that used to produce national population trends, with the key difference being that only transect sections crossing a particular habitat contribute to the habitat-specific trend for that habitat. Volunteers recorded up to two habitat types in each transect using a hierarchical coding system described in [20]. These were aggregated following [10] into 12 broad habitat types (defined in Table S1).

Counts of each species in each visit to a BBS were obtained by summing counts in that visit in transect sections containing a given habitat. As in the production of national trends, the maximum count in a BBS square across visits was used in analysis. A consequence of this approach is that the number of transect sections containing a particular habitat, and thus contributing towards the trend, varies between BBS squares. We assume that ln(count) is proportional to ln(transect length), so modify the Poisson generalised linear models of count as a function of year and BBS square identity to include the natural log of the number of transect sections containing a particular habitat as an offset term.

Calculating habitat preference

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The buffer effect is formulated in terms of high and low quality habitat, however, robust data on habitat quality are not available for many of our study species. We therefore used habitat preference as a proxy for habitat quality. This was quantified using Jacobs index of habitat preference (J), calculated as $J_{h,s} = (u_{h,s} - a_{h,s})/(u_{h,s} + a_{h,s} - 2u_{h,s}a_{h,s})$, 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. We used raw counts rather than detectability adjusted densities in this analysis to calculate $u_{h,s}$. This was because there were insufficient observations of many species in all habitats to calculate robust habitat-specific estimates of detectability. To assess whether variation in detectability between habitats could have influenced our habitat preference index we calculated Jacobs index using detectability adjusted densities for the 16 species with trends in all habitats (these species were selected as there were sufficient observations in all habitats to generate robust habitat-specific estimates of detection probability), and assessed the correlation between these Jacobs index accounting for detectability and Jacobs index using raw counts. To calculate detection probabilities for each transect section, distance analysis models for each species were constructed using the R package mrds [21], using a half-normal function to model the decline in detection probability with distance, incorporating transect section habitat as a covariate. Counts of a species in each transect section were converted to densities by dividing by this detection probability. We found that values of J calculated using raw counts and values of J calculated using densities were strongly positively correlated ($r = 0.938$, $P < 0.001$), indicating that the influence of variation in detectability between habitats on the habitat preference index values would be minor

Species selection

Habitat-specific trends were produced for species-habitat combinations for which the species was recorded in the habitat on average in at least ten BBS squares each year. In this analysis we only use species for which trends were produced in at least two habitats. 94 species met these criteria. Of

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these, nine species were removed as they were either subject to habitat-specific control

programmes (feral pigeon *Columba livia* in urban areas) and/or management for hunting which

could have altered habitat preferences and habitat-specific trends (these were grey partridge *Perdix*

perdix, red-legged partridge *Alectoris rufa*, pheasant *Phasianus colchicus* and red grouse *Lagopus*

lagopus), or were known to be poorly monitored by the breeding bird survey (black-headed gull

Chroicocephalus ridibundus, common gull *Larus canus*, herring gull *Larus argentatus* and lesser black-

backed gull *Larus fuscus*) [16], leaving 85 species which were used for analysis. Including all 94

species did not qualitatively change results (Appendix S2). Habitat-specific trends could be produced

in 7.9 ± 3.7 (standard deviation) habitats for the 85 species used for analysis (Fig. S1). The 85 species

included in this study account for 93.9% of the individual birds recorded by the BBS.

Statistical analyses

We conducted three analyses to test for hypothesised signatures of the buffer effect (Table 1). The

first analysis (Analysis 1 in Table 1) was based in the expectation that if the buffer effect was

operating populations should increase and decrease more strongly in poorer quality habitats. From

this, we expect a positive relationship between population trend and habitat preference for

nationally declining species to reverse direction to become negative for nationally increasing species,

so a significant interaction with this form between national BBS trend and habitat preference index

would be consistent with the predictions of the buffer effect. We modelled this using the following

formula:

$log\ (HAB_{h,s}) = \alpha + \beta_1 BBS_s + \beta_2 J_{h,s} + \beta_3 BBS_s : J_{h,s} + Species_s + \varepsilon$ (Eqn 1)

Where $HAB_{h,s}$ is the habitat-specific trend of species *s* in habitat *h*, BBS_s is the national BBS trend of

species *s*, $J_{h,s}$ is the habitat preference index (Jacobs index *J*) of species *s* in habitat *h*, $BBS_s : J_{h,s}$ is an

interaction term between habitat-specific trend and habitat preference index, $Species_s$ is a random

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effect allowing the intercept of the model to vary between species, ε is the error term , and α and β_{1-3} are estimated coefficients of the model.

The second analysis (Analysis 2 in Table 1) was also based on the expectation the populations should increase or decrease more strongly in poorer quality habitats. For declining species, we therefore expect habitat-specific population trends to be more negative in avoided habitats than preferred habitats, and thus expect the sign of the relationship between habitat-specific trend and habitat preference index to be positive. Conversely, for increasing species, we expect habitat-specific population trends to be more positive in avoided habitats than preferred habitats, so thus expect the sign the relationship between habitat-specific trend and habitat preference index to be negative. To test this, we firstly calculated the coefficient of the relationship between habitat-specific trend and habitat preference index for each species:

$$ln(HAB_{h,s}+1) = \alpha_s + \beta_s J_{h,s} + \varepsilon \qquad \text{(Eqn 2)}$$

Where $HAB_{h,s}$ is the habitat-specific trend of species s in habitat h, $J_{h,s}$ is the habitat preference index (Jacobs index J) of species s in habitat h, ε is the error term and β_s is the coefficient of the relationship between habitat-specific trend and habitat preference index for species s. These coefficients were standardised by dividing them by their standard error. This pulled coefficients with more uncertainty to be closer to zero. The second step of this analysis was to assess the correlation between these standardised coefficients and the national BBS trend for each species. A negative correlation, indicating that coefficients were more negative for nationally increasing specie and more positive for nationally declining species, would be consistent with the predictions of the buffer effect.

The third analysis (Analysis 3 in Table 1) tested whether increasing populations became more equally distributed between habitats, as individuals increasingly move to lower quality habitats due to high quality habitats becoming saturated. If this was happening, we expected that the difference in

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preference between the most preferred and least preferred habitat would decrease over time for increasing species, and increase over time for declining species. For each species, we calculated the range in habitat preference index values at the start (1994-1997) and end (2009-2012) of the study period, and from this calculated the change in the range of habitat preference index values over the study period (Δ J range) for each species. We then used a linear model to model Δ J range as a function of national BBS trend. A negative relationship would indicate that the difference in habitat preference index values was decreasing for increasing species and increasing for declining species, so would be consistent with the predictions of the buffer effect. We repeated this analysis using the change in the inter-quartile range of habitat preference index values instead of the change in range. This relationship between Δ J inter-quartile range and national BBS trend was similar to the relationship between Δ J range and national BBS trend reported in the main text, but was not statistically significant (β = -0.027 ± 0.028 SE, t = -0.942, P = 0.349).

Table S1. Definition of broad habitat classes.

Broad habitat class	Constituent habitat classes
Broadleaved woodland	Broadleaved
	Broadleaved water-logged
	Regenerating natural or semi-natural wood[2]
	Young coppice[1]
	New plantation [1]
	Clear-felled woodland[1]
Coniferous woodland	Coniferous
	Coniferous water-logged
	Regenerating natural or semi-natural wood[2]
	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[2]
	Young coppice[1]
	New plantation [1]
	Clear-felled woodland[1]
Semi-natural grass, heath and bog	Chalk downland
	Downland chalk scrub
Upland if mean altitude of BBS square ≥300m	Grass moor (unenclosed)
	Grass moor mixed with heather (unenclosed)
Lowland if <300m	Other dry grassland
	Dry heath
	Wet heath
	Mixed heath
	Bog
	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 (50–450 m^2)
	Lake/unlined reservoir
	Lined reservoir
	Gravel pit, sand pit, etc

	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 (2–5 m wide)
	Large canal (more than 5 m wide)

[1] Of the appropriate woodland type (deciduous, coniferous or mixed).
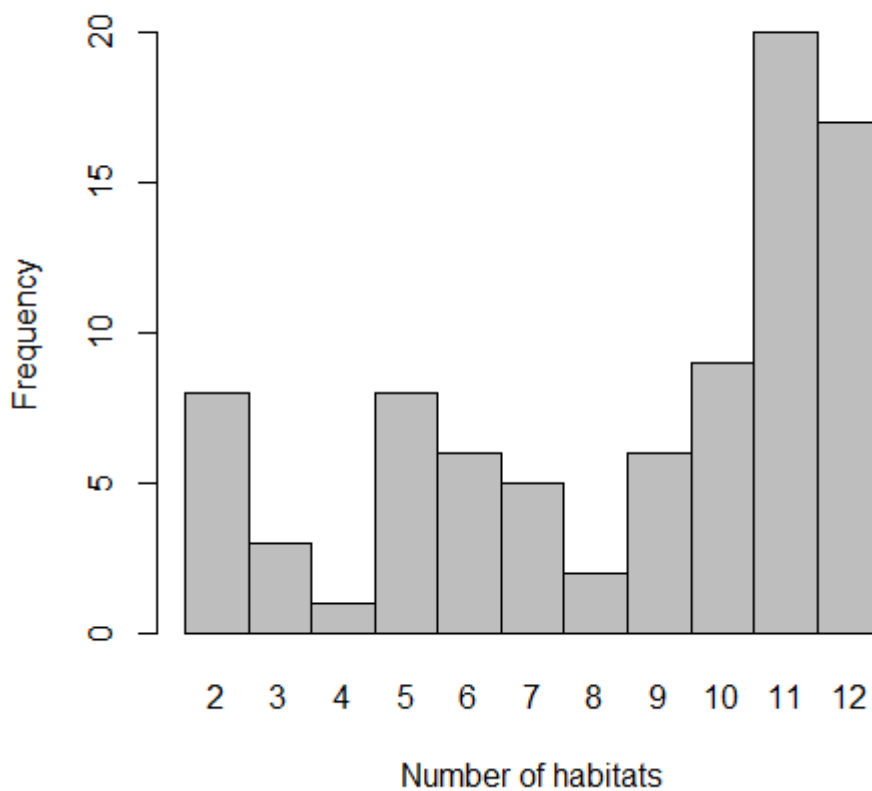
Fig S1. Frequency distribution of number of habitats for which habitat specific trends could be

produced for study species.

Appendix S2. Sensitivity of results to different thresholds for including species.

Table S1. Results of main analyses when all species were included.

| Analysis	Number of species	Test statistic	P
Analysis 1: Interaction between BBS trend and Jacobs index of habitat preference	94	χ^2 = 5.24	0.022
Analysis 2: Correlation between national BBS trend and relationship between habitat-specific population trend and Jacobs index of habitat preference	78	r =-0.317	0.005
Analysis 3: Relationship between change in range of habitat preferences and national BBS trend	94	t = -3.729	0.0003

Table S2. Significance of interaction between national BBS trend and Jacobs index of habitat preference in model explaining habitat specific population trends with different thresholds for including population trends.

Threshold minimum number of BBS squares	Number of species	χ^2	P
10	85	5.74	0.0166
30	71	11.09	0.0009
50	59	18.12	<0.0001

Table S3. Sensitivity of correlation between national BBS trend and relationship between habitat-specific population trend and Jacobs index of habitat preference to threshold for including a species.

Threshold minimum number of habitats	Number of species	r	P
3	78	-0.321	0.0045
5	73	-0.333	0.0039
7	59	-0.364	0.0046
9	53	-0.405	0.0029

1   **Appendix S3.** As Fig. 1b, but showing species codes, and with all 94 species. See Appendix S5 for species names.
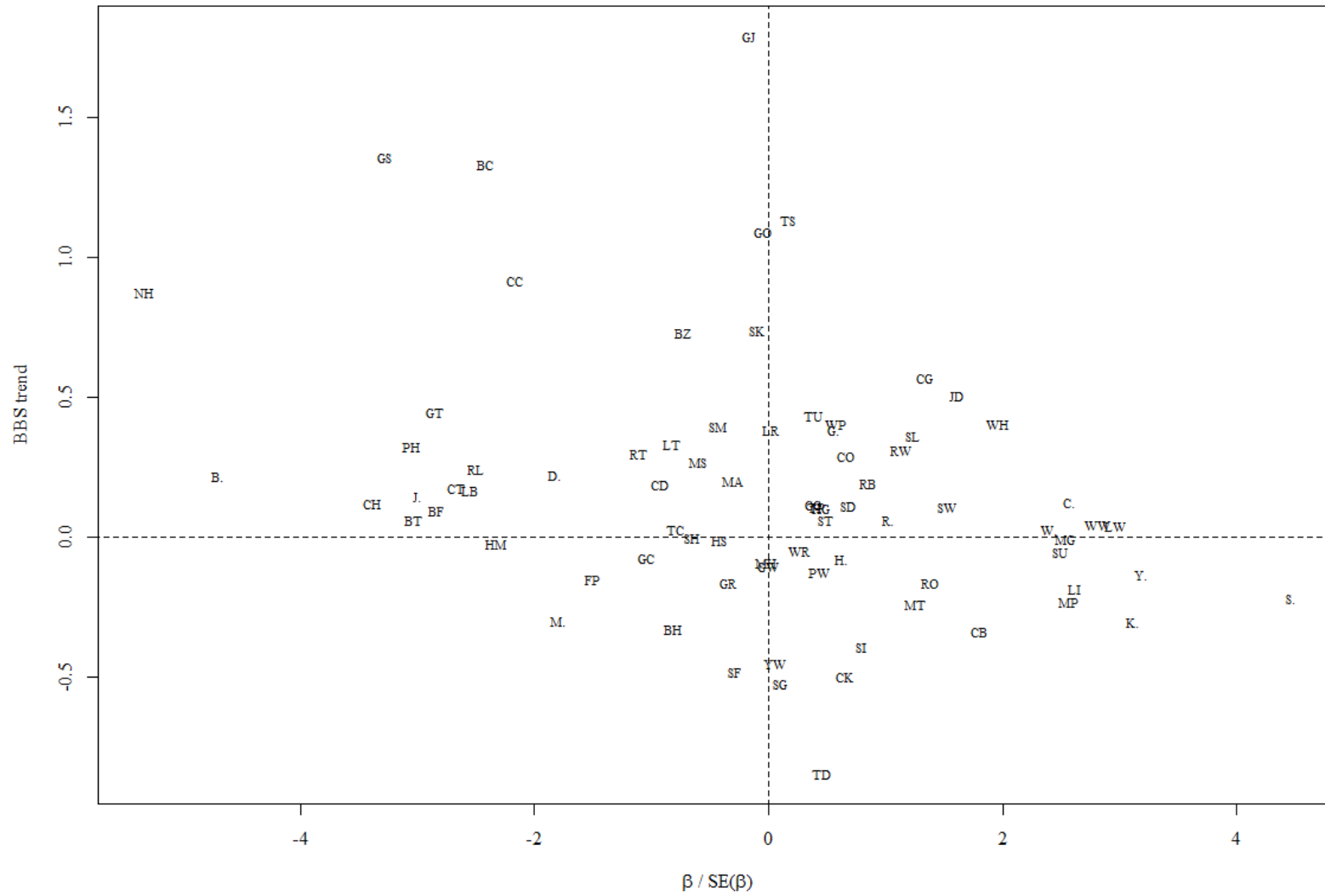
2

3   **Appendix S4.** Responses of specialists and generalists

4   Differences in quality between habitats is required for the buffer effect to operate, as it is necessary

5   to generate differences in per-capita survival and fecundity rates, as well as differences in habitat

6   selection. Variation in habitat quality may be lower for generalist species compared to specialist

7   species, so the buffer effect may be weaker or absent in generalists. If this were the case, we would

8   expect a three way interaction between habitat preference, national population trend and a species

9   degree of habitat specialism in influencing species habitat-specific population trends. For specialist

10   species, we would expect a positive relationship between habitat preference and habitat-specific

11   trend, reversing to become negative for nationally increasing species (i.e. analysis 1 in Table 1, with

12   the two-way interaction between habitat preference and national population trend being one of the

13   hypothesised signatures of the buffer effect), while for generalist species we would expect this

14   reversal in the direction of the habitat-trend habitat-preference relationship to weaken or be absent

15   altogether.

16   Testing this requires a measure of the degree to which species are specialist or generalist. We used

17   species-specialisation index (SSI), obtained from Johnston *et al.* [22]. SSI for each species is

18   estimated as the coefficient of variation (standard deviation/mean) of the abundance of that species

19   across habitats, with high values indicating more specialised species. We incorporated this term into

20   the model used in analysis 1 (Eqn. 1), allowing a three-way interaction with habitat preference index

21   and national population trend:

22     $ln (HAB_{h,s} +1) = \alpha + \beta_1 BBS_s + \beta_2 J_{h,s} + \beta_2 SSI_s + \beta_4 BBS_s{:}J_{h,s} + \beta_5 BBS_s{:}SSI_S + \beta_6 SSI_s{:}J_{h,s} + \beta_7 BBS_s{:}J_{h,s}{:}SSI_s +$

23     $Species_s + \varepsilon,$

24   where SSI_s is the species specialization index for species S, and other terms are as in Eqn. 1.

25   We found the three way interaction term not to be significant ($\chi^2 = 0.07$, $P = 0.8$). This indicates that

26   the form of the interaction between habitat preference index and national population trend did not vary

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between specialists and generalists, so does not support the buffer effect acting more strongly on

specialists than generalists. One explanation for this is that even the most generalist species in our

dataset (carrion crow *Corvus corone*, SSI = 0.47) showed some variation in habitat preference, so

that even for generalists there was sufficient variation in habitat quality for the buffer effect to operate.

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