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Changing densities of generalist species underlie apparent homogenization of UK bird communities

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Generalist species are becoming increasingly dominant in European bird communities. This has been taken as evidence of biotic homogenization, whereby generalist 'winners' systematically replace specialist 'losers'. We test this pattern by relating changes in the average specialization of UK bird communities to changes in the density of species with different degrees of habitat specialization. Although we find the expected decline in community specialization, this was driven by a combination of a strong increase in the density of the most generalist quartile of species and declines in the density of moderately generalist species. Contrary to expectation, specialist species increased slightly over the 18-year study period but had little effect on the overall trend in community specialization. Our results indicate that the apparent homogenization of UK bird communities is not driven by the replacement of specialists by generalists, but instead by the changing fortunes of generalist species.

Keywords: biotic homogenization, Breeding Bird Survey, community specialization index, monitoring.

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

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

We followed changes in UK bird communities over 18 years, with a mean of 2598 (±597 sd) 1-km^2 survey squares monitored each year. Our aims were to quantify changes in community specialization and to assess the extent to which these changes reflect changes in the populations of specialist and generalist species.

METHODS

Bird density data

Data from the UK Breeding Bird Survey (BBS), a national-scale survey designed to monitor changes in bird populations across the UK, were used to

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track changes in community structure. The survey started in 1994, and we used data from this point up to 2012. Survey squares of 1 km^2 in area were selected for the BBS using a stratified random sampling design, with more squares in areas with a higher human population density to maximize the use of available volunteers. In each BBS square, a volunteer walks two 1-km line-transects across the square on two visits during the breeding season (April–June), with the visits separated by at least 4 weeks. Each transect is divided into 200-m-long transect sections, and the birds seen in each transect section are recorded in three distance bands (<25 m, 25–100 m and > 100 m), or as flying. Volunteers also record the habitat in each transect section according to a hierarchical coding system (Crick 1992). Data from 2001 were excluded from analyses as access to the countryside was restricted in that year due to foot-and-mouth disease. In the other years, 1570–3718 squares were surveyed each year, with a total of 5155 squares surveyed during the study period.

We used records in the first two bounded distance bands, and excluded records of flying birds, with the exception of Common Swifts *Apus apus*, hirundines and raptors, as these species are either aerial feeders or hunt from the air, so flying birds of these species are likely to be using resources within the BBS square. Feral forms of Rock Dove *Columba livia*, Mallard *Anas platyrhynchos* and Greylag Goose *Anser anser* were recorded separately from wild forms by volunteers and are treated separately here. We removed birds that were likely to be transient migrants or lingering winter visitors, with the aim of ensuring the bird community recorded consisted of the species likely to be using the square for breeding. To do this, we removed unusually high counts of waders, indicating flocks away from breeding areas, records of European Golden Plovers *Pluvialis apricaria* from unsuitable lowland habitat, species that are regular passage migrants or winter visitors to the UK, but that have fewer than 10 breeding pairs, and species with fewer than 10 records in the entire BBS dataset. Following application of these filters, our dataset consisted of approximately 1.2 million records of 195 bird species (see Supporting Information Table S1 for a list of species).

To turn raw abundances into estimates of density, we estimated detection probabilities for each species in each BBS square. For each species, the distance band in which each observation was recorded was modelled as a function of visit date (i.e. early or late) and the primary habitat class (the 12 habitat classes are defined in Table S2) in the transect section in which the bird was recorded using a half-normal distance model in the R package MRDS (Laake *et al.* 2015). If there were fewer than 20 observations in a habitat class, the habitat class was combined with similar habitats to form a broader habitat class to be used as a covariate (for example, if there were fewer than 20 observations in flowing water, that habitat would be grouped with wetlands and standing water to form a broader wetland habitat class; see Table S2 for other broader habitat classes). These covariates allow variation in detectability over the breeding season and between habitats to be modelled. These models were used to predict the probability of individuals of a species being detected in each transect section, and these were averaged per species to obtain the predicted detection probability for that visit to a BBS square. The density of each species in a BBS square was then calculated by dividing the raw count by the detection probability. Detection functions could not be calculated for 10 species, so for these species we estimated detection probabilities using models fitted to observations of similar surrogate species (Table S3). Raw counts were used for Swifts, hirundines and raptors, as the majority of records of these species related to flying individuals for which distance data were not available. We obtained similar results to those reported in the main paper when we repeated the analysis using raw counts for all species (Figs S1 and S2).

Quantifying species specialization

For each species, we calculated a species specialization index (SSI) as the coefficient of variation of the density of a species across the 12 habitat classes across all BBS squares, with values close to zero indicating little variation in density between habitats (i.e. generalist species), and high values indicating considerable variation between habitats (i.e. specialist species). We grouped species into four habitat specialization groups based on the quartiles of SSI values; species with SSI values in the first quartile (Q1, SSI <0.81) were considered to be very generalist, species in the second quartile (Q2, SSI ≥0.81 and <1.29) moderately generalist, species in the third quartile (Q3, SSI ≥1.29 and <1.82) moderately specialist, and species in the fourth quartile (Q4, SSI ≥1.82) very specialist. Changes in the total density of species in each quartile give an indication of differences in general population trends of specialist and generalist species. The total density of birds across all species in a given quartile was calculated by sub-setting the dataset such that it only contained species in a given habitat specialization quartile, and then summing the density of those birds in each BBS square–year combination. Densities were natural log-transformed prior to analysis, with a constant of one added prior to transformation as some densities were equal to zero. For each quartile, we modelled the total density across all species in that quartile as a function of year (treated as a continuous variable), with BBS square identity as a random effect, using linear mixed effects models implemented in the R package lme4 (Bates *et al.* 2014). We also calculated the number of increasing and declining species in each quartile, using national BBS trends from Risely *et al.* (2013) to identify which species were increasing and declining, to give an indication of how variable population trends were within SSI quartiles. SSI was calculated using data from all years (i.e. 1994–2012); however, habitat specialization may have changed during the study period. To ensure this did not affect our results, we also calculated SSI only using data from the start of the study period (1994–1997). Both measures of SSI were strongly positively correlated ($r_{193} = 0.847$, $P < 0.001$), and changes in the density of birds in each quartile showed similar patterns using both measures of SSI (Figs S1 and S2). Only SSI values calculated across all years are presented in the main paper.

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

Quantifying the contribution of species and groups of species to CSI

Following Davey *et al.* (2013), a jackknife approach was used to quantify the contribution of species to temporal trends in CSI. To estimate the overall trend in CSI over the study period, we used a linear mixed effects model of CSI (natural log-transformed prior to analysis) as a function of year (treated as a continuous variable), with BBS square identity fitted as a random effect. The coefficient of the year term indicates the rate of change in CSI. We restricted models to linear effects because our primary intent was to quantify the rate of change in CSI over time, and to investigate the impact of removing species on this rate of change. To quantify the contribution of species/groups of species, individual species or groups of species were removed from the dataset as appropriate, CSI was recalculated and the model was re-fitted. The percentage change in the year coefficient (Δ_β) was calculated as $\Delta_\beta = (\beta_2 - \beta_1)/|\beta_1| \times 100$, where β_1 is the year coefficient when all species were included in the calculation of CSI, and β_2 is the year coefficient when CSI was calculated with a species or group of species removed. Positive values indicate that the slope of the relationship was less negative when the species was omitted and therefore that the trend of the species was contributing to homogenization. Negative values show that the slope of the relationship was more negative when the species was omitted, indicating that the species was reducing the slope of the relationship, so countering homogenization. To understand the drivers of any change in community specialization, these percentage change values were calculated when each individual species and each SSI quartile species group was removed from the dataset, as well as when non-native species were removed.

We used a linear model to model individual species' influence on the trend in CSI (Δ_β) as a function of their SSI and national BBS trend, and the interaction between SSI and BBS trend. We square root-transformed the response variable (percentage change in CSI trend) to meet model assumptions, and also square root-transformed the explanatory variables, which were strongly positively skewed, to improve our sampling of parameter space. Both percentage change in CSI trend and national BBS trend could be negative, so we square root-transformed the absolute values before applying the original sign. This analysis could only be conducted using species for which national BBS trends were available ($n = 127$). Removing species without BBS trends could mean that we missed the influence of rare species on CSI trend. However, this is unlikely as we found that individual species' influence on the trend in CSI did not vary significantly between species with and without a national BBS trend (Wilcoxon test, $W = 3937$, $P = 0.310$). All analyses were carried out using R (R Core Team 2014). The R code used for statistical analysis is provided in Appendix S1. Marginal and conditional R^2 values for mixed-effects models were calculated following Nakagawa and Schielzeth (2013), implemented in the MuMIn package (Barton 2014) in R.

RESULTS

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

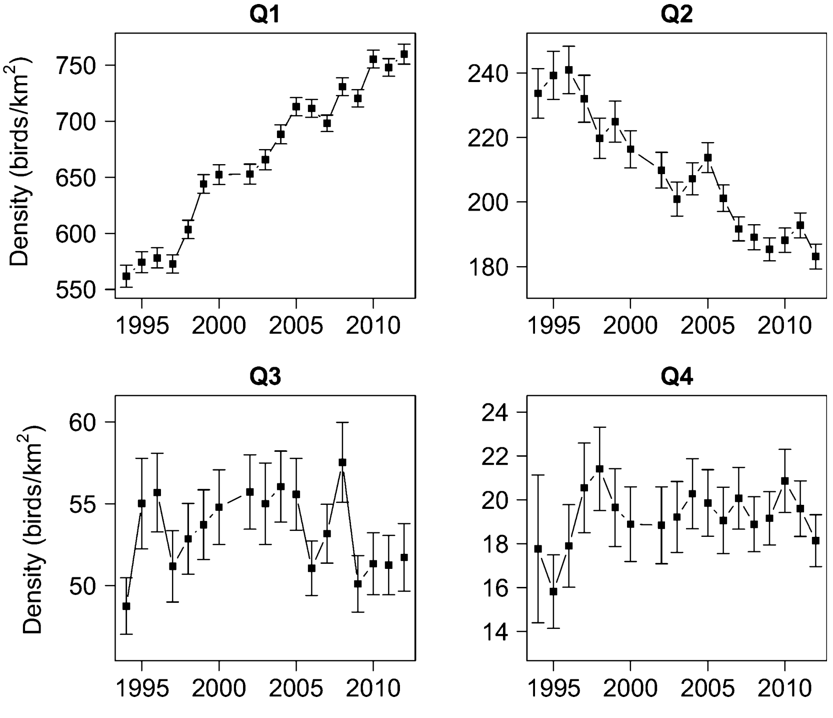

Figure 1. Change in density of birds in each quartile of habitat specialization (SSI). Species in the first quartile (Q1) had SSI values <0.81, species in the second quartile (Q2) had SSI values ≥0.81 and <1.29, species in the third quartile (Q3) had SSI values ≥129 and <1.82, and species in the fourth quartile had SSI values ≥1.82. Points show the mean density of all birds in a given quartile in BBS squares, with error bars showing standard errors.

more than half of species in the other quartiles were increasing (Fig. S3).

CSI declined over the study period ($\beta = -0.004 \pm < 0.001$, $\chi^2_1 = 1255.2$, $P < 0.0001$, marginal $R^2 = 0.004$, conditional $R^2 = 0.885$; Fig. 2). A similar, although slightly less steep, trend in CSI was observed when based on an unweighted mean of SSI values across the species present, and therefore indicative of changes in occupancy rather than abundance ($\beta = -0.001 \pm <0.001$, $\chi^2_1 = 290.6$, $P < 0.0001$, marginal $R^2 = 0.001$, conditional $R^2 = 0.867$; Fig. 2). The decrease in CSI has thus been driven by both changes in species abundance and changes in species composition. Changes in the densities of Q1 species were largely responsible for driving these trends; when Q1 species were removed, the overall trend in CSI was weakly positive (Fig. 3b). The trend in CSI remained negative when all other quartiles were removed (Fig. 3), although it was significantly less negative when Q2 species were removed (as indicated by non-overlapping trend confidence intervals, Fig. 3b). This indicates that species in Q1, and to a lesser extent Q2, are responsible for driving the negative trend in CSI. The effect of each quartile on the trend of CSI was similar when CSI was calculated as an unweighted mean of SSI (Fig. S2). Changes in the density of non-native species had little effect on CSI (–4.3% change in year coefficient when removed), despite an overall increase in the density of non-native species over the study period ($\beta = 0.032 \pm 0.001$, $\chi^2_1 = 1260.4$, $P < 0.0001$, marginal $R^2 = 0.013$, conditional $R^2 = 0.641$, Supporting Information Fig. S4).

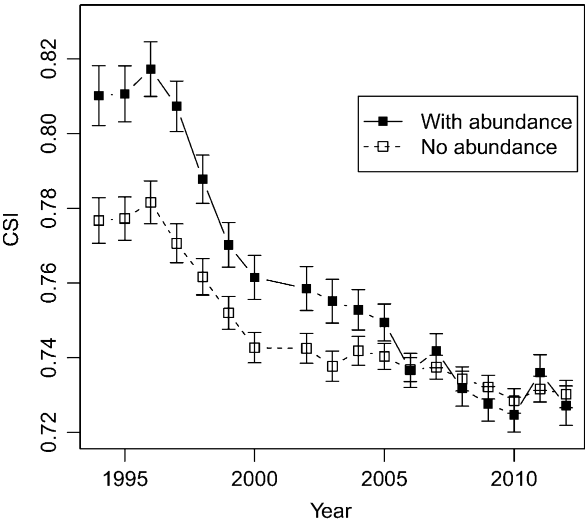

Figure 2. Change in the community specialization index (CSI) of UK bird communities. CSI has been calculated as the community-weighted mean of species specialization index (SSI), incorporating the effect of species abundance (filled squares, solid line), and the unweighted mean of SSI, thus only including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

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

DISCUSSION

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

Recent analyses of European bird population trends have shown a similar pattern, with common species showing a tendency to decline in abundance and the rarest species tending to increase (Inger *et al.* 2015). This was partly attributed to long-term population declines in relatively widespread farmland birds (Donald *et al.* 2001), and the potential benefits of conservation management for rare species (e.g. Donald *et al.* 2007, Hoffmann *et al.* 2010). The pattern we have observed has

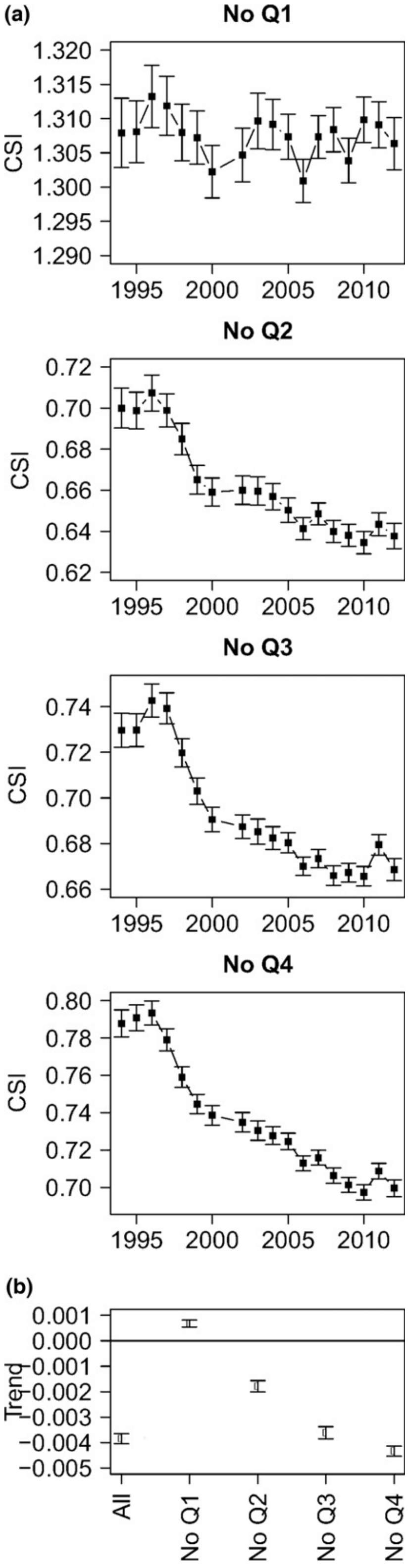

Figure 3. Effect of removing quartiles of species with different degrees of habitat specialization on the overall trend in CSI. (a) Points show the mean CSI across BBS squares in a given year, with error bars showing standard errors. (b) Mean and 95% confidence intervals of trend in CSI over time are shown. Removing Q1 species (most generalist) and Q2 species reduced rates of homogenization (118.0 and 35.9% change in CSI trend when removed, respectively), whereas removing Q3 and Q4 (most specialist) species had little effect (–6.5 and –12.9% change in CSI trend when removed, respectively).

some similarities to this, but suggests that in the UK, the most widespread species (e.g. Woodpigeon, Great Tit *Parus major* and Goldfinch *Carduelis carduelis*) have actually increased in abundance. These are species that occupy the greatest range of habitats, and therefore are potentially most resilient to anthropogenic pressures. The most rapidly declining species were the moderate generalists, which includes many of the farmland birds (e.g. Yellowhammer *Emberiza citrinella*, Grey Partridge *Perdix perdix* and Northern Lapwing *Vanellus vanellus*) that occupy a number of habitat types but have declined widely in the UK in response to agricultural intensification (Chamberlain *et al.* 2000, Eglington & Pearce-Higgins 2012). Declines in CSI have been greatest in UK farmland habitats (Davey *et al.* 2012), supporting this explanation. There also appear to be divergent impacts of warming upon habitat generalists and specialists, which may have contributed to this pattern (Davey *et al.* 2012, Pearce-Higgins *et al.* 2015), although it is unclear how the sensitivity of species to climate change varies between the different SSI quartiles, or how the impacts of warming may interact with land-use change to drive these patterns.

Our analyses followed Davey *et al.* (2012), and defined habitat specialization based on associations with 12 habitat categories. The inferences we obtained are sensitive to this definition. SSI values obtained by defining habitat specialization using four habitat categories (woodland, wetland, urban and open) are uncorrelated with those using 12 habitat categories ($r = 0.14$), and if these SSI values are used, declines are evident in habitat specialists (Q4) and strong generalists (Q1), while the density of moderate generalists (Q2) and moderate specialists (Q3) increases (Fig. S1). A consequence of using broader habitat categories is that species primarily associated with

Table 1. Ten species contributing most to driving the decline in CSI over the study period.

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

% change, percentage change in the trend in CSI when a species is removed; SSI, species specialization index for a species; BBS trend, national population trend for a species over the study period.

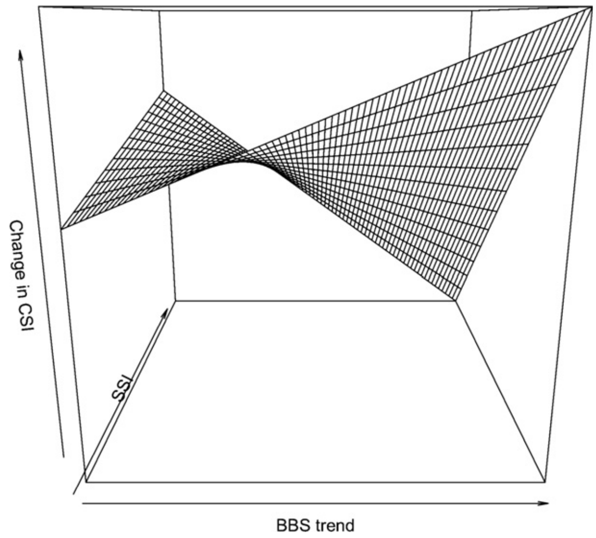

Figure 4. Modelled surface showing the interaction between SSI and BBS trend in influencing the change in CSI trend when species were removed in a jackknife procedure. The modelled surface shows predicted change in CSI trend when a species is removed from the dataset, with predictions from a linear model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

one habitat type within a broad habitat will be considered more generalist, whereas species associated with all habitat types within a broad habitat will be considered more specialist. For example, Siskins *Carduelis spinus* are strongly associated with coniferous woodland, but not with other woodland habitats (12 habitat SSI = 2.11, Q4), so appear less strongly associated with any habitat type when all woodland types are combined into one category (four habitat SSI = 1.23, Q1). Yellowhammers, on the other hand, are associated with a wide range of open habitats (12 habitat SSI = 1.04, Q2), so appear strongly associated with the open broad habitat category (four habitat SSI = 1.99, Q4), despite not being strongly associated with any of the 12 habitat categories. Because of this, we consider that using 12 habitat categories to calculate SSI gives a more meaningful representation of habitat specialization than using four categories, although it is clear that the precision of measurement of habitat specialization has a strong impact on community specialization metrics.

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

We calculated SSI using data on habitat associations pooled across the study period, so treated it as a fixed attribute of a species. This means that our results reflect changes in species abundance and community composition. However, SSI can change through time (Barnagaud *et al.* 2011), with species that exhibit density-dependent habitat selection spreading out into less favourable habitats as their populations increase and retreating to favourable habitats as populations decline (Sullivan *et al.* 2015a). This can potentially increase rates of community homogenization (Barnagaud *et al.* 2011), as increasing species become more generalist and declining species become more specialist. In this analysis, our interest was in analysing changes in bird communities rather than changes in the attributes of individual species, so we did not investigate this here, except for showing that similar changes in the density of specialist and generalist species are observed when quartiles are defined based on habitat specialization in the initial years of the study period as over the whole study period (Fig. S1).

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

Community-weighted means, such as CSI, are often used as indicators of change in communities in time and space (Devictor *et al.* 2008, Davey *et al.* 2012, Le Viol *et al.* 2012, Vimal & Devictor 2015). However, such metrics have been criticized as they only indicate the balance of (in the case of CSI) specialists and generalists, and do not indicate whether these changes are due to increases in generalists or declines in specialists (Gosselin 2012). We showed that changes in CSI in UK birds were primarily driven by increases in very generalist species and declines in moderately generalist species, and are little affected by changes in the density of specialist species, supporting this criticism. On average, specialist species were found at lower densities than generalist species (Fig. S5) and so are likely to have less influence on community-weighted metrics. Our approach of accompanying analysis of CSI with more detailed analysis of changes in the density of specialists and generalists gave greater insight into the mechanisms acting on a bird community than would analysis of change in CSI alone, and could be applied to other analyses using community-weighted means.

Environmental change can act as an environmental filter, with only a subset of the original species pool able to persist in altered conditions (Helmus *et al.* 2010, Mouillot *et al.* 2013). Generalist species are expected to be more likely to be able to pass through a given environmental filter due to their greater niche breadth (Clavel *et al.* 2010). Under this model of biotic homogenization, environmental change is expected to lead to declines in specialist species, with generalist species increasing to exploit new opportunities. Our results, together with those of Inger *et al.* (2015), contrast with this expectation by showing that the overall abundance of rare and specialized species has not declined, with declines evident instead in abundant, moderately generalist species. How can these results be reconciled with this model of biotic homogenization? Natural habitats in the UK have been heavily fragmented and modified by humans for over 2000 years (Rackham 1986), and this long history of human impact is likely to have considerably reduced populations of habitat specialists so that there was a low baseline in terms of population size at the start of the study. Thus, the modest increase in the overall density of the most specialized quartile of species reported in this study is not inconsistent with the expectation that environmental change negatively affects habitat specialists, and instead is likely to reflect remaining populations of habitat specialists benefiting from conservation actions. Drivers of population change that act across habitats appear to be more important in explaining change in UK bird populations than processes operating within particular habitats (Sullivan *et al.* 2015b), and these landscape-scale drivers are likely to affect particularly widespread generalist species (Gaston & Fuller 2007). Patterns of population change among these widespread generalists are consistent with the prediction that generalist species are more resistant to environmental change, with increases in the overall density of the most generalist quartile of species and declines in the density of moderate generalists (Fig. 1).

To conclude, despite the continued decline in the habitat specialization of UK bird communities, the overall density of specialist species has not declined. This apparent homogenization therefore does not appear to have been at the expense of specialist species of the greatest conservation concern. Instead, the decline in CSI was driven by increases in the density of the most generalist quartile of species, and by declines in the density of moderate generalists. These results reflect previous work comparing changes in the populations of abundant and rare species (Inger *et al.* 2015), and collectively indicate that recent changes in bird communities across Europe have been characterized by declines in relatively abundant, moderately generalist species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. R code used in statistical analysis.

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

Table S2. Definition of habitat classes.

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

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

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

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

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

Figure S5. Relationship between population density and habitat specialization.