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Using habitat-specific population trends to evaluate the consistency of the effect of species traits on bird population change

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ABSTRACT

Many species are undergoing rapid population declines, while other species have increased. Previous work has related population change to species traits to elucidate the drivers of population change. However, this assumes that these drivers operate consistently across habitats. We use national-scale monitoring data on UK bird abundance from 1994–2012 to calculate habitat-specific population trends, allowing us to evaluate whether the effect of species traits was consistent between habitats. Although we found significant interactions with habitat for traits relating to migratory behaviour, diet, nest site and habitat specialisation, the direction of these trait effects was generally consistent between habitats. This suggests that large-scale processes operating across habitats are responsible for many changes in bird populations, although processes operating within habitats can modulate the effect of these drivers. Despite this, differences in population trends between habitats remain when variation in population trends due to species identity is accounted for, indicating that some habitat effects do occur. By identifying the scale at which drivers of population change operate, it is possible to target conservation actions more directly. Population declines were most evident in woodland and urban habitats, and we suggest that these habitats should be the focus of increased research and conservation effort if declines evident in many bird species are to be reversed.

1. Introduction

Large-scale biodiversity monitoring programmes, often utilising the participation of citizen scientists, have revealed rapid population changes in multiple taxa (Jiguet et al., 2012; Powney and Isaac, 2015). These include declines in common moth species (Conrad et al., 2006) and climate induced changes in bird and butterfly populations (Devictor et al., 2012). Population declines are especially evident in certain habitats. In Europe, for example, widespread declines in farmland birds and more localised declines in woodland birds have been well documented (Donald et al., 2001; Hewson and Noble, 2009). These declines could result from a general reduction in habitat quality (i.e. be a property of a habitat), but could also be driven by the responses of certain species typical of a habitat to broad-scale environmental drivers (i.e. be a property of species), or some interaction between these habitat and species effects.

Understanding the extent to which habitat versus species effects drive population trends is important for directing conservation strategies. If population declines are primarily driven by habitat effects, then this supports the use of conservation interventions targeted in particular habitats to address specific changes in quality, while if population declines are primarily driven by species effects then species-specific conservation responses or landscape-scale measures that operate across habitats may be more appropriate to halt declines.

Investigations to date have tended to focus on either habitat effects or species effects, so understanding of their relative importance and interactions is limited. While some studies have identified contrasting population trends between habitats, others have examined how bird population trends vary with species' characteristics, described by a range of ecological traits. Studies of European birds have revealed consistent associations with habitat specialism, with generalists having more positive population trends than specialists (Julliard et al., 2004; Le Viol et al., 2012; Salido et al., 2012; Shultz et al., 2005; Van Turnhout et al., 2010), and highlighted declines in populations of Afro-Palearctic migrants (Ockendon et al., 2012; Salido et al., 2012; Sanderson et al., 2006; Van Turnhout et al., 2010), particularly of species wintering in the humid bioclimatic zone (Thaxter et al., 2010). However, these studies look at national population trends, so do not allow the consistency of these trait effects to be evaluated between habitats. For example, the importance of traits such as migratory strategy for driving population trends varies spatially (Morrison et al., 2013), part of which may be associated with spatial variation in habitat cover. Given strong contrasts in population trends between habitats, it is therefore important to assess the extent to which the ecological traits associated with population trend may also vary between habitats to inform conservation action. If

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the importance of different traits varied strongly between habitats, this would indicate that the drivers of population trend are likely to differ between them.

Analysing habitat-specific population trends of species potentially allows the importance of habitat-level and species-level drivers of population change to be evaluated. We extend the methods developed by Newson et al. (2009) to calculate habitat-specific population trends for 89 bird species in the UK. Analysis of this dataset has shown that the broad pattern of these habitat-specific trends is consistent with the widespread operation of the buffer effect, where declining species retreat to high quality habitats while increasing species spread into lower quality habitats (Sullivan et al., 2015). However, the high degree of variation around this broad pattern suggests that other processes are also important in driving variation in population trends between habitats. In this study, we analyse these habitat-specific population trends with the aim of (1) identifying habitats where bird population trends are especially negative, (2) evaluating the relative importance of habitat- and species-effects in driving trends, and (3) assessing the consistency of trait effects between habitats.

2. Materials and methods

2.1. Habitat specific population trends

We calculated species' population trends using data from the Breeding Bird Survey (BBS), which since its inception in 1994 has been the principal monitoring scheme for populations of widespread breeding birds in the UK. The BBS uses a stratified random sampling design, ensuring representative coverage of habitats throughout the UK (Baillie et al., 2014). BBS squares are also stratified by region to ensure maximum utilisation of available volunteers; BBS squares are weighted in later analyses to correct for biases in sampling effort introduced by this. Each BBS square is visited twice during the breeding season (mid-March to late-June), with the visits separated by at least four weeks. In each square, volunteers walk two 1 km transects (as close to parallel as possible), and record all bird species seen or heard within 200 m transect sections. We used the maximum count of the two visits, and excluded flying birds except for aerial feeders, displaying skylarks *Alauda arvensis* and hovering common kestrels *Falco tinnunculus*.

Volunteers record up to two habitat classes for each 200 m transect section following a hierarchical coding system described by Crick (1992). Following Newson et al. (2009), we reclassified habitats into 12 habitat classes given in Table A1 (see Table A2 for number of BBS squares and transect sections surveyed in each year). These were deciduous woodland (abbreviated to DECID), mixed woodland (MIXW), coniferous woodland (CONIF), upland semi-natural open habitats (UPSN), lowland semi-natural open habitats (LOSN), arable farmland (ARAB), pasture (PAST), mixed farming (MIXF), rural settlements (RURA), urban settlements (URBA), wetlands (WETL) and flowing water (FLOW). Separate population trends were calculated for each habitat. To do this, data were subset by habitat types so that only transect sections of a particular habitat contributed to the calculation of that habitat's trends. Log-linear generalised linear models with Poisson error terms were constructed using the GENMOD procedure in SAS 9.2 (SAS Institute, 2008), with bird count modelled as a function of site (i.e. BBS square) and categorical year to give population indices in each year, with a dispersion parameter (deviance divided by the degrees of freedom) to account for overdispersion. Subsetting data in this way by habitat meant that the number of transect sections per site varied. To control for this we included the log of the number of transect sections containing the given habitat type as an offset variable (Newson et al., 2009).

We did not analyse change in annual population indices directly, as they are sensitive to yearly fluctuations. Instead, we fitted a post-hoc smoothed trend through the annual indices using non-parametric thin-plate splines, constraining the degrees of freedom to be the nearest integer to 0.3 × length of time-series (Baillie et al., 2014). We calculated the population trend for each species between 1995 and 2011 as (smoothed population index$_{2011}$ − smoothed population index$_{1995}$) / smoothed population index$_{1995}$. The first and last years of our dataset (1994 and 2012) were excluded from this calculation as they have a large influence of the direction of trends so may bias population changes (Baillie et al., 2014). For each species we repeated this procedure of calculating annual indices and then fitting post-hoc smooths on 199 bootstraps (Baillie et al., 2014), sampling with replacement each time. We calculated standard errors and confidence intervals around population trends from these bootstraps. Species were classed as increasing or declining if the 95% confidence limits of the population trend did not overlap zero. Habitat-specific population trends for all species are presented in Appendix B.

2.2. Ecological variables

We collated trait data on breeding season diet, nest site, mass, habitat specialisation, winter bioclimatic zone and thermal niche in order to test for trait–habitat interactions. Data on diet, mass and nest site were obtained from Snow and Perrins (2004), with the former two traits previously collated by Robinson (2005). Breeding season diet was categorised into the following mutually exclusive categories: herbivorous, granivorous, carnivorous–vertebrates (hereafter referred to as carnivorous), carnivorous–invertivorous (hereafter insectivorous) and omnivorous. Nest site was classified as into the following mutually exclusive categories: requiring low vegetation to nest (i.e. species nesting in shrubs <2 m above the ground, species nesting in low vegetation, and ground nesting species that nest in long grass or under other low vegetation [e.g. whinchat *Saxicola rubetra*]), other ground nesting species (hereafter ground nesting), nesting in tree cavities, and nesting in trees. Species that did not fit into these categories, for example species nesting in buildings or on water, were classed as other. Mass was taken as the mean mass of males and females. We obtained an index of species habitat specialisation (SSI) from Davey et al. (2012). This was calculated as the coefficient of variation of species densities across the 12 habitat classes (Table A1), with higher values indicating increasing habitat specialisation. Data on the wintering bioclimatic zone of species were obtained from Ockendon et al. (2012); Thaxter et al. (2010) and Morrison et al. (2013). Species were classified as resident, partial or short-distance (i.e. wintering north of the Sahara) migrant, or for trans-Saharan migrants wintering in either the arid, humid or southern bioclimatic zones. Only two species wintered in the southern bioclimatic zone, so these were combined with species wintering in the arid zone in subsequent analyses (humid zone species were treated separately as previous work has found they have contrasting population trends to other sub-Saharan migrants (Thaxter et al., 2010). An index of species thermal niche (STI), representing the mean breeding season temperature in a species' European distribution, was obtained from Devictor et al. (2008).

2.3. Statistical analysis

Analysis of population trends was performed in R (R Core Team, 2014). We conducted analyses to (1) partition variation in habitat-specific population trends between species and habitats, (2) test for differences in population trends between habitats and (3) examine how consistent the effects of species traits were among habitats (details below). We used the natural log of population trend + 1 in order to homogenize variances and ensure normality of residuals. Previous studies of population trends have restricted analyses to species that are on average recorded in more than 30 BBS squares each year as there may be insufficient power to detect declines in less well recorded species (Joys et al., 2003). This may lead to rare and declining species being excluded (Renwick et al., 2012). Instead, we used a more lenient threshold and included species-habitat combinations where a species was recorded on an average of 10 or more BBS squares per habitat type each year, but then down-weighted the importance of trends with high degrees of uncertainty in subsequent modelling by specifying case weights as the reciprocal of population trend standard error, which was also logged to reflect our treatment of the population trend data. This approach allows infrequently recorded species with clear population trends to contribute to models, so maximises the number of species that can be included in the study, while reducing the influence of species with highly uncertain population trends. Despite the use of a more lenient threshold, a number of rare species were recorded too infrequently to be included in this study. In addition, we excluded common gull *Larus canus*, lesser black-backed gull *Larus fuscus*, herring gull *Larus argentatus*, black-headed gull *Chroicocephalus ridibundus* and grey heron *Ardea cinerea* from analyses, as the BBS survey design is not appropriate for assessing population trends of these colonial species (Baillie et al., 2014). In total there were 746 habitat-specific population trends of 89 species used in analysis.

We followed the method of Reino (2005), adapted from Legendre and Legendre (2012), to partition the proportion of variation in population trends attributable to species and habitat. We fitted a linear model with population trend as a function of habitat and species (M1), as well as models with just habitat (M2) or species (M3) as explanatory variables. Explained variation in the full additive model consists of variation attributable to habitat, variation attributable to species, and shared variation due to correlations between species and habitat, while explained variation in the two constituent models consists of variation attributable to the target variable (species or habitat) and shared variation. This shared variation can be isolated by subtracting explained variation in the full model from the sum of explained variation in the two constituent models (i.e. shared variation = M2 + M3 − M1). This shared variation can then be subtracted from the constituent models (M2 and M3) to give the proportion of variation attributable to species and habitat. Unexplained variation in the full additive model (M1) is attributable to species–habitat interactions, as adding a species–habitat interaction term leads to a saturated model with no unexplained variation.

To test whether population trends differed between habitats, we used a mixed effects model with species as a random effect to model population trend as a function of habitat. Mixed effects models were constructed in lme4 (Bates et al., 2014). The purpose of the species random effect was to account for the expected correlation of population trends of the same species. We repeated this analysis on a subset of species that occurred in all habitats, to test whether differences in population trends between habitats were a consequence of differences in species composition, or due to differing trends between habitats for the same species. Differences in population trends across all species between habitats could be driven by increasing species increasing more or less than the national average or declining species decreasing more or less than the national average. We explored this by repeating the modelling procedure described above separately for a subset of increasing species and a subset of declining species assessed from national population trends between 1995 and 2011 (Risely et al., 2013). We tested whether population trends in each habitat were significantly different from the overall mean population trend across all habitats and species (using the Satterthwaite approximation of degrees of freedom), and also used simultaneous tests of generalised linear hypotheses implemented in multcomp (Hothorn et al., 2008) to test for significant differences between habitat types. This analysis was repeated using a broader categorisation of five functional habitat classes (woodland — BROAD, CONIF and MIXW, semi-natural open — UPSN and LOSN, farmland — ARAB, PAST and MIXF, human — RURA and URBA and wetland — WETL and FLOW). To investigate whether population trends of specialist species varied between habitats, we first assessed whether species selected a habitat more frequently than expected given its availability by calculating Jacobs index, $J_{h,s} = (u_{h,s} - a_{h,s}) / (u_{h,s} + a_{h,s} - 2\, u_{h,s}\, a_{h,s})$, where $u_{h,s}$ is the proportion of observations of species s in habitat h and $a_{h,s}$ is the proportion of transect sections in BBS squares where species s was recorded that contained habitat h. Jacobs index ranges from -1 to 1, with values >0 indicating more frequent selection of a habitat than expected given availability. We then used mixed effects models to model population trend as a function of habitat, restricting this analysis to species with Jacobs index values greater than 0. We repeated this with species where $J > 0.25$, focusing the analysis further onto habitat specialists.

We tested for inter-habitat differences in the effect of species traits on population change by constructing a general linear mixed effects model (LMM) with habitat, traits and interactions between traits and habitat for traits where we hypothesised a priori that the effect of the trait would vary among habitats (see Table 1 for hypotheses) as explanatory variables. We included SSI, STI, the natural logarithm of body mass, migratory strategy (resident, short distance or partial migrant,

Table 1
Hypothesised trait–habitat interactions. Predictions that were found to be supported are shown in bold.

Trait	Mechanism leading to interaction	Predicted interactions
Migratory strategy	(1) Consequences of phenological mismatch less severe in habitats with more stable resource environments (Both et al., 2010) or in cooler habitats were spring arrives later.	**(1.1) Declines of long-distance migrants stronger in deciduous woodland than coniferous woodland.** **(1.2) Declines of long-distance migrants weaker in uplands.**
	(2) Interaction between processes in the breeding and non-breeding grounds lead to stronger declines in long-distance migrants in habitats with the greatest human influence (Vickery et al., 2014).	**(2) Declines of long-distance migrants stronger in farmland.**
Nest site	(3) Ground nesting species sensitive to agricultural activity in breeding season (Van Turnhout et al., 2010).	(3) Population trends of ground nesting birds more negative in farmland.
	(4) Eutrophication and subsequent scrub encroachment into grasslands and changes in woodland ground cover favours species nesting in low vegetation over ground nesting species (Corney et al., 2008; Van Turnhout et al., 2010).	(4) Population trends of ground nesting birds more negative in semi-natural grassland and woodland.
	(5) Loss of understory vegetation in woodland due to deer browsing (Holt et al., 2010).	(5) Population trends of species nesting in low vegetation more negative in woodland.
	(6) Availability of tree cavities limiting populations of cavity nesting species (Newton, 1998).	(6) More negative population trends of cavity nesting species in woodland.
Diet	(7) Shortage of seeds in farmland reduces winter survival of granivorous species (Siriwardena et al., 2008).	(7) More negative population trends of granivorous species in arable farmland.
	(8) Agricultural intensification, including pesticide use, reduces the abundance of invertebrates in agricultural areas, reducing food availability of insectivorous species (Hallmann et al., 2014).	(8) More negative population trends of insectivorous species in farmland.
SSI	(9) Adaptable generalist species better able to exploit resources in human-modified habitats (Davey et al., 2012; Shultz et al., 2005).	(9) Relationship between habitat specialisation and population trend more negative in farmland and human settlements.
STI	(10) Greater impact of climate change relative to other environmental change in semi-natural habitats (Eglington and Pearce-Higgins, 2012; Kampichler et al., 2012).	(10) Positive effect of STI on population trend less evident in farmland and human settlements.

long-distance migrant wintering in the humid bioclimatic zone, long-distance migrant wintering elsewhere in sub-Saharan Africa), diet (insectivorous, granivorous, herbivorous, carnivorous or omnivorous) and nest site (ground, low vegetation, trees, tree cavities or other) as main effects. Given our hypotheses, interactions with habitat were included for STI, SSI, the humid and arid/southern levels of migratory strategy, the insectivorous and granivorous levels of diet, and the ground, low vegetation and tree cavity levels of nest site. There were at least three species for each trait–habitat interaction combination (mean = 15 ± 10 SD species, see Table A3 for number of species in each trait–habitat combination). Species was included as a random effect. This model was simplified by sequential removal of non-significant terms, followed by aggregation of factor levels until a minimum adequate model was obtained (Crawley, 2007). We calculated variance inflation factors (VIF) to assess multicolinearity in predictor variables; these were <3 for all variables expect for diet, where VIF = 4.98. Diet was correlated with body mass, with granivorous and insectivorous species tending to be lighter than other species. Both body mass and diet were retained in our analysis, however repeating the analysis excluding body mass reduced multicoliniarity (VIF < 2) but resulted in the same minimum adequate model. We assessed model fit by plotting residuals against fitted values, as well as plotting residuals against each explanatory variable. In all cases no patterns were observed (Fig. A1).

We reduced the number of comparisons made during model selection by first assessing the significance of interactions with habitat as a whole, and only assessing the significance of interactions with individual habitat classes if the interaction with habitat was significant. Had we looked at all interactions with habitat classes in the full model then there would have been 124, giving a high probability of significant results occurring by chance. The Bonferroni adjustment for this number of tests is $\alpha = 0.0004$. However, such corrections have been criticized for being overly conservative as highly significant results may be rejected (Crawley, 2007). We therefore take a pragmatic approach to dealing with multiple testing, interpreting results where $P < 0.0004$ as strongly supported, but still considering strongly significant results with larger P values (i.e. $P \leq 0.01$ but ≥ 0.0004) as worthy of discussion. Results where $0.05 > P > 0.01$ are presented and retained in the minimum adequate model, but interpreted with caution. The significance of main effects that were also retained in the minimum adequate model as interactions was assessed by likelihood ratio tests of the model without the main effect and interaction term against the more complicated model just lacking the interaction term.

We repeated this test for inter-habitat differences in trait effects using phylogenetic generalised least squares (PGLS) to account for correlations between species trends that result from shared evolutionary history (Felsenstein, 1985). We used a phylogenetic tree of British birds obtained from Thomas (2008). We implemented the model using Pagel's correlation structure (Paradis et al., 2004) in the gls procedure in nlme (Pinheiro and Bates, 2007). The λ parameter in Pagel's correlation structure determines how similar the covariances are to those in a Brownian motion model of trait evolution, with values of 1 indicating Brownian motion and 0 indicating random trait evolution. Following Revell (2010) we parameterised λ simultaneously with coefficient estimation when fitting the PGLS.

3. Results

3.1. Differences in overall population trends between habitats

There were significant differences in population trends between habitat classes ($\chi^2 = 66.1$, $P < 0.0001$). Trends were significantly more negative in all woodland habitat classes and in urban/suburban habitats compared to the overall mean population trend across habitats (Fig. 1a). Population trends were most positive in wetlands and standing water, followed by both upland and lowland semi-natural grassland/heath, but were not significantly different from the overall mean across habitats (Fig. 1a). Largely similar patterns were evident when the analysis was restricted to species selecting a habitat more frequently than expected given availability (Fig. A2), although population trends were less negative in deciduous woodland, stable instead of negative in mixed woodland, positive instead of negative in coniferous woodland, and more negative in arable and mixed farmland (Fig. A2). Trends differed significantly between broad functional habitat classes ($\chi^2 = 43.8$, $P < 0.001$, Fig. 1b), driven by contrasting patterns for rural settlements and urban/suburban settlements in the human class and wetlands/standing water and flowing water in the wetland class (Fig. 1a).

When separating species showing positive national population trends from declining species, population trends of increasing species were significantly less positive in deciduous and mixed woodland than in other habitats (Fig. 1c), while species that were declining nationally were declining more strongly in deciduous woodlands and in urban/suburban areas than other habitats (Fig. 1d).These differences in the magnitude of population trends were reflected in significant differences in the distribution of population trends between habitats ($\chi^2 = 147.0$, $P < 0.0001$, Table A4). The highest proportion of declining species were found in urban/suburban areas (32.7% of species declining), deciduous woodland (33.8%) and mixed woodland (38.3%). Large numbers of declining species were also found in rural settlements (29.6%) and in farmland habitat classes (23.9%–28.2%), but were offset by a high proportion (46.3%–54.4%) of species with increasing population trends in those habitats. In most habitats more species were estimated to be increasing in abundance than declining, with this pattern only reversed in mixed and deciduous woodland.

3.2. Partitioning variation in trend between species and habitats

Variation in habitat-specific population trends was largely explained by a strong independent effect of species (71.5% of variation in saturated model explained). Habitat alone explained 2.6% of variation, with the combined effect of habitat and species explaining a further 0.4%. As this is a saturated model the remaining 25.5% of variation can be attributed to the interaction between species and habitats. This can be seen in considerable variation in species trends between habitats, with 23 species out of the 89 for which trends were calculated showing significant increases in one habitat and significant declines in another.

The importance of species does not mean that the differences in population trend between habitats (Fig. 1a) are unrelated to habitat. Observed contrasts in habitat-specific trends remained when this analysis was repeated only including generalist species that occur in all habitats (Fig. A3, $\chi^2 = 26.9$, $P = 0.005$).

3.3. Variation in population trends in relation to species traits

Migratory strategy, nest site and diet were retained in the minimum adequate mixed effects model (Table A5). Species wintering in the humid zone had more negative population trends than other species ($\beta = -0.613 \pm 0.152$, $\chi^2 = 15.8$, $P < 0.0001$). Population trends of ground nesting species were more negative than species nesting in other places ($\beta = -0.420 \pm 0.144$, $\chi^2 = 8.6$, $P = 0.003$). Although both granivore and insectivore factor levels of diet were retained in the minimum adequate model, neither was statistically significant as a main effect ($\chi^2 \leq 0.3$, $P \geq 0.608$).

The above traits were all retained in the minimum adequate phylogenetic model as well. However, in that analysis ground nesting was not significant as a main effect, while insectivorous species had more positive population trends than non-insectivorous species ($\beta = 0.445 \pm 0.171$, F = 7.0, $P = 0.008$). Several traits had significant effects in the phylogenetic analysis but not in the mixed effect model analysis (coefficients of both models in Table A5). Species requiring low vegetation to nest had more positive population trends ($\beta = 0.500 \pm 0.138$, F = 13.5, $P = 0.0002$), while population trend was negatively related to

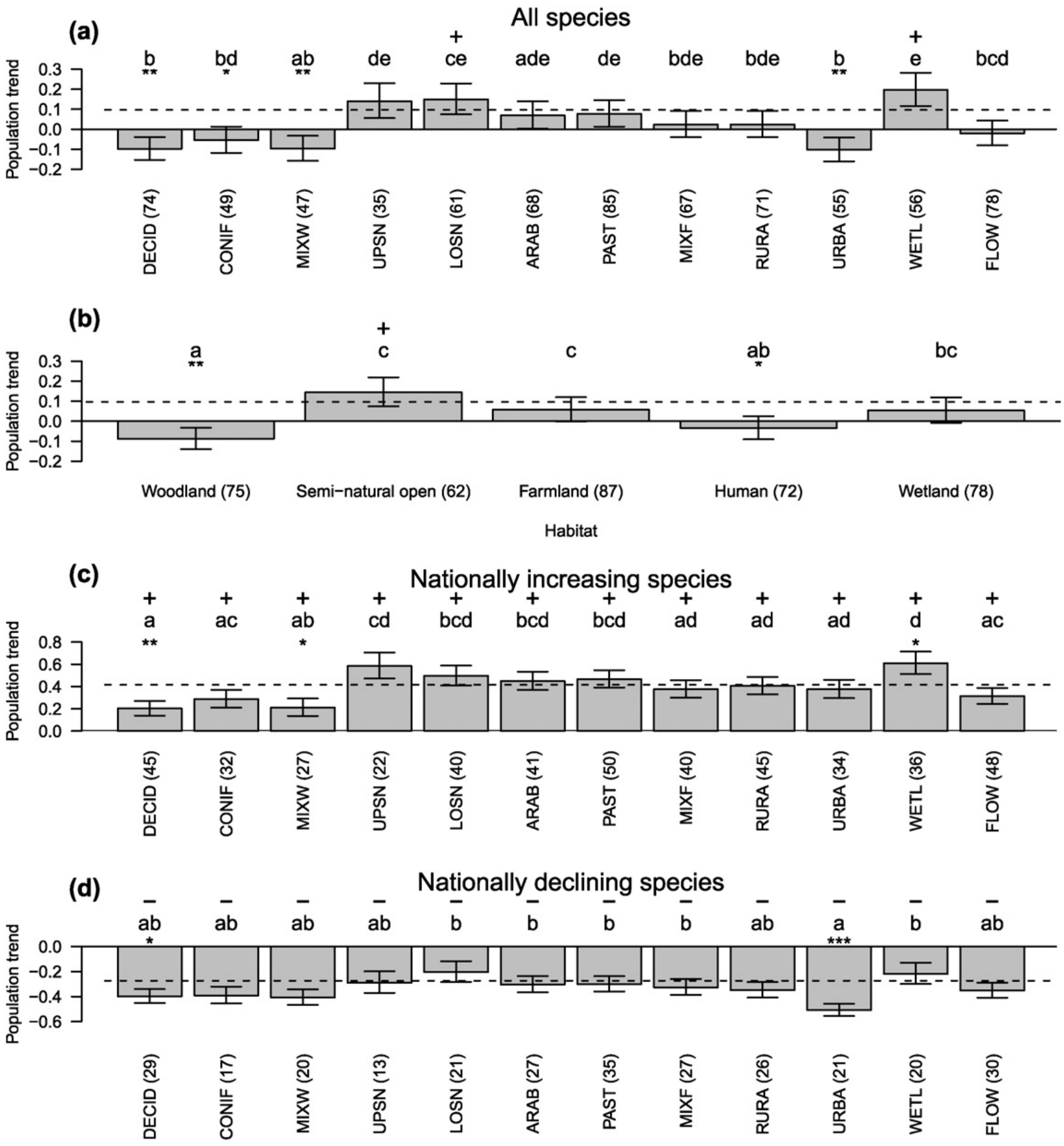

Fig. 1. Variation in population trend between habitats. (a) Mean population trends in each habitat estimated from a LMM modelling log (population trend + 1) as a function of habitat, with species as a random effect. Error bars show standard errors. (b) Modelled mean population trends in aggregated functional habitat classes. See Table 1 for definition of habitat abbreviations. (c) As (a), but only including species with nationally increasing population trends. (d) As (a), but only including species with nationally declining population trends The dashed line shows the grand mean of population trends across all habitats; asterisks show significant and near-significant differences from this (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Population trends that are significantly different from zero ($P < 0.05$) are marked with + if they are greater than zero and − if they are less than zero. Lower-case letters written above bars show results of pairwise tests for differences between habitats — habitats with different letters had significantly different population trends. Sample sizes (number of species) are given in parentheses after each habitat name. Differences in population trends after controlling for significant trait main effects are similar and are shown in Fig. A4.

STI ($\beta = -0.056 \pm 0.024$, $F = 5.5$, $P = 0.0195$). SSI and the arid/southern bioclimatic zone factor level of migratory strategy were included in the minimum adequate phylogenetic model, but were not significant as main effects ($F \leq 1.2$, $P \geq 0.188$).

3.4. Consistency of trait effects between habitats

The effects of ecological traits were often consistent among habitats, with interactions mainly strengthening or weakening the effect of traits in certain habitats (Table 2). However, the direction of several trait effects was reversed; in the mixed effects model analysis granivorous and insectivorous species had more positive population trends than other species in upland semi-natural habitats but more negative population trends in other habitats, while in the phylogenetic analysis the direction of STI, SSI and ground nesting trait effects varied between habitats (Table 2).

Of the hypothesised trait–habitat interactions (Table 1), only interactions between migratory strategy and habitat were supported (Table 2, see Table A5 for coefficients). As hypothesised, population trends of Afro-Palearctic migrants wintering in the humid bioclimatic zone were less negative in coniferous woodlands (LMM: $\chi^2 = 13.0$, $P = 0.0003$, PGLS: $F = 10.5$, $P = 0.001$) and upland semi-natural habitats (the latter only in the LMM analysis, $\chi^2 = 9.8$, $P = 0.0017$) and more negative in arable and mixed farmland (LMM: $\chi^2 = 22.6$, $P < 0.0001$, PGLS: $F = 26.0$, $P < 0.0001$). To check this was not a result of a single-species outlier, this effect remained when the rapidly declining turtle dove *Streptopelia turtur*, which uses these habitats, was excluded ($\chi^2 = 20.2$, $P < 0.0001$). Migrants wintering in the arid/southern bioclimatic zone had positive population trends in upland semi-natural habitats compared to negative trends elsewhere (PGLS analysis only, $F = 7.2$, $P = 0.002$).

Table 2
Consistency of trait effects among habitats.

Model	Habitat	Migratory strategy		Diet		Nest	STI	SSI
		Humid	Arid/southern	Granivore	Insectivore	Ground		
LMM	DECID	↓	NS	(↓)	(↓)	↓	NS	NS
	CONIF	↘***	NS	(↓)	(↓)	↓	NS	NS
	MIXW	↓	NS	(↓)	(↓)	↓	NS	NS
	UPGR	↘**	NS	↑**	↑**	↓	NS	NS
	LOGR	↘**	NS	(↓)	(↓)	↓	NS	NS
	ARAB	↓↓***	NS	(↓)	(↓)	↓	NS	NS
	PAST	↓	NS	(↓)	(↓)	↓	NS	NS
	MIXF	↓↓***	NS	(↓)	(↓)	↓	NS	NS
	RURA	↓↓***	NS	(↓)	(↓)	↓	NS	NS
	URBA	↓	NS	↓↓***	↓↓**	↓↓***	NS	NS
	WETL	↓	NS	↓↓***	(↓)	↓	NS	NS
	FLOW	↘*	NS	↓↓***	(↓)	↓	NS	NS
PGLS	DECID	↓	(↓)	↑	↑	(↓)	↓	(↓)
	CONIF	↘**	(↓)	↑	↑	(↓)	↓	(↓)
	MIXW	↓	(↓)	↗***	↑	(↓)	↓	(↓)
	UPGR	↓	↑**	↑	↑	↑***	↓	(↓)
	LOGR	↘**	(↓)	↑	↑	(↓)	↓	↑**
	ARAB	↓↓***	(↓)	↑	↑	(↓)	↑***	(↓)
	PAST	↓	(↓)	↑	↑	(↓)	↓	(↓)
	MIXF	↓↓***	(↓)	↑	↑	(↓)	↑***	(↓)
	RURA	↓↓***	(↓)	↑	↑	(↓)	↑***	(↓)
	URBA	↓↓***	↓↓**	↗***	↑	↓↓***	↑***	(↓)
	WETL	↓	(↓)	↗***	↑	(↓)	↓	(↓)
	FLOW	↓	(↓)	↗***	↑	(↓)	↓	(↓)

Arrows show the direction of trait effects, with arrows in parentheses denoting non-significant effects. Asterisks show the significance of trait habitat interactions; $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$. Double arrows show a strengthening of a trait effect in a habitat, while angled arrows denote a weakening of trait effects. Traits that were not significant and thus removed from the minimum model are marked NS. Traits that were not significant in either modelling approach are not shown. Model coefficients are given in Table A5.

Although other hypothesised trait–habitat interactions were not supported, some trait–habitat interactions that we did not predict a priori were statistically significant. Population trends of humid zone migrants were less negative in lowland semi-natural habitats (LMM: $\chi^2 = 9.8$, $P = 0.0017$, PGLS: $F = 10.5$, $P = 0.001$) and flowing water (the latter only in the LMM, $\chi^2 = 5.5$, $P = 0.019$), while population trends of both humid and arid/southern migrants were more negative in urban settlements (PGLS only, $F = 26.0$, $P < 0.0001$ and $F = 9.7$, $P = 0.002$ respectively). Granivorous species had more negative population trends in urban settlements (LMM: $\chi^2 = 17.8$, $P < 0.0001$, PGLS: $F = 26.1$, $P < 0.0001$) and in both wetland habitats than in other habitats ($\chi^2 = 13.4$, $P = 0.0002$, PGLS: $F = 26.1$, $P < 0.0001$). In the mixed model analysis both granivorous and insectivorous species had more positive population trends in upland semi-natural habitats ($\chi^2 = 7.0$, $P = 0.008$ and $\chi^2 = 9.5$, $P = 0.002$ respectively) and insectivorous species had more negative population trends in urban settlements ($\chi^2 = 9.9$, $P = 0.002$), while in the phylogenetic analysis granivorous species had more negative population trends in mixed woodland (Table A5). Ground-nesting species had more negative population trends in urban settlements than in other habitats (LMM: $\chi^2 = 15.4$, $P < 0.0001$, PGLS: $F = 24.5$, $P < 0.0001$). In the phylogenetic analysis, STI had a contrasting effect between habitats, with a positive effect in arable and mixed farmland and rural and urban settlements compared to a negative effect in other habitats ($F = 22.5$, $P < 0.0001$). SSI had a non-significant negative effect in all habitats except for lowland semi-natural habitats, where it had a positive effect on population trend ($F = 7.5$, $P = 0.006$).

4. Discussion

Population trends of UK breeding birds varied among habitats, with generally negative population trends in woodland and urban habitats. Despite these differences, the strongest component of variation was between species, indicating that many of the drivers of UK bird population trends are likely to be acting across habitats. However, species-scale effects are not the only driver of population change, as we found that variation in the strength of trait effects between habitats accounted for about a quarter of the variation in population trends. Our results are consistent in this respect with a previous study in the Netherlands investigating variation in the response of bird communities to temperature and land-use change (Kampichler et al., 2012), and suggest that habitat-level drivers can ameliorate or enhance the effect of broad scale drivers.

4.1. Effect of species traits on population trends

Many of the effects of species traits reported here are consistent with those found in previous studies looking at European bird population trends. Thus, as demonstrated previously, long distance humid zone migrants (Ockendon et al., 2012; Thaxter et al., 2010) and ground nesting species (Van Turnhout et al., 2010) were the most likely to decline in abundance. Declines of ground nesting species in the Netherlands have been attributed to increased nitrogen deposition and related increases in nitrophillous vegetation (Van Turnhout et al., 2010). Our results are consistent with this, with species requiring low vegetation to nest having more positive population trends in the phylogenetic analysis, but may also reflect the impact of increasing populations of generalist, particularly mammalian, predators upon ground-nesting species such as waders (MacDonald and Bolton, 2008).

In contrast to previous studies, which have found that bird communities in Europe are becoming increasingly dominated by warm associated species (Devictor et al., 2008, 2012; Kampichler et al., 2012), we find (in the phylogenetic analysis only) population declines in species associated with warmer regions. There are two potential explanations for this. Firstly, the UK experienced three successive winters with severe cold spells towards the end of the time series, including one month (December 2010) where temperatures were 5 °C below the 1971–2000 mean (Met Office, 2015), which were likely to have impacted populations of cold sensitive species (Pearce-Higgins et al., 2015). Excluding data from these three years weakens the overall relationship between population trend and STI ($\beta = -0.019 \pm 0.027$). Secondly, in our analyses population trends of each species are weighted equally, so may give a different inference to that from analyses of change using weighted average community temperature associations in which the contribution of species is weighted by their abundance (e.g. Devictor et al., 2012;

Kampichler et al., 2012). Using our data to estimate changes in the Community Temperature Index (CTI) in a comparable way to these previous studies replicates the previously observed positive trend ($\beta = 0.004 \pm 0.001$). Thus while we do not find that warm associated species are more likely to have increased, our data do not contradict previous studies that have documented increases in community averaged temperature associations, with differences in results instead due to methodological differences.

We did not find a significant relationship between population trend and body mass. Habitat specialisation was retained in the phylogenetic minimum adequate model due to a significant interaction with habitat, but was not significant as a main effect. Both traits have been found in be correlated with population trend in previous studies, with larger species and habitat generalists having more positive population trends (Salido et al., 2012; Shultz et al., 2005). Despite these traits not being significant, the direction of these trait effects in this study (positive relationship with mass, negative relationship with habitat specialisation) were consistent with previous studies.

4.2. Consistency of drivers between habitats

Previously reported declines in humid zone migrants (Ockendon et al., 2012; Thaxter et al., 2010; Vickery et al., 2014) were particularly severe relative to other species in rural settlements, arable and mixed farmland. Such spatial variation is suggestive of a role of breeding season drivers of population decline (see also Morrison et al., 2013; Ockendon et al., 2012). As detrimental impacts during the breeding season have been reported in single species studies for the majority of European long-distance migrants breeding in farmland (Vickery et al., 2014), stronger declines in agricultural and rural settlement habitats could result from the interacting or additive effects of reduced resources in the breeding season due to agricultural intensification combined with habitat degradation and climatic stresses in the wintering grounds (Vickery et al., 2014). However, variation in habitat-specific trends could also result from density dependent processes. As species decline in response to a species-scale driver these declines are predicted to be stronger in less preferred habitats as species retreat to their preferred habitats (Sullivan et al., 2015).

One potential mechanism causing variation in habitat-specific trends of humid zone migrants could be that the arrival times of humid zone migrants may be constrained by their reliance on resource pulses following early spring rains prior to migration, potentially leading to phenological mismatch in their breeding grounds (Ockendon et al., 2012). The effect of this upon breeding success and population trends is likely to be less severe in habitats, such as coniferous woodland, where resources are less seasonal in abundance than in other habitats, such as deciduous woodland (Both et al., 2010). We found that declines in humid zone migrants were less severe in coniferous woodland, and to a lesser extent semi-natural grassland and heath, than in other habitats, providing some support for humid zone migrant declines being less negative in habitats with stable resources or relatively late phenologies. However, the less negative population trend of humid zone migrants in coniferous woodland was also at least partly due to such habitats being distributed further north (Fig. A5; see also Morrison et al., 2013; Ockendon et al., 2012), potentially because they have later phenologies or greater prey abundance than in the south (Conrad et al., 2006; Smith et al., 2011). This may also explain the steeper declines of humid zone migrants in rural areas and arable and mixed farmland, as these have a southerly distribution in the UK, so experience earlier springs and hence greater potential for phenological mismatch (Morrison et al., 2013). We note that the effect of phenological mismatch on habitat-specific population trends is further complicated by variation in migratory species' ability to change their arrival time (Møller et al., 2008) and by the potential for increased post-fledging survival to offset negative effects of phenological mismatch on productivity (Reed et al., 2013).

The weak negative relationship between habitat specialisation and population trend in most habitats in the phylogenetic analysis is consistent with the increasing domination of bird communities by generalist species reported previously in the UK (Davey et al., 2012), Sweden (Davey et al., 2013) and across Europe (Le Viol et al., 2012). The significant contrast between semi-natural open habitats, where this relationship was more positive than in other habits, was only apparent in the phylogenetic analysis and was not significant at the Bonferroni adjusted alpha level, but is consistent with a previous assessment of rates of change in community specialisation in UK birds (Davey et al., 2012) and on Dutch heath compared to farmland (Kampichler et al., 2012).

The effect of species thermal niche on population trends varied between habitats in the phylogenetic analysis, with a positive effect in more anthropogenic habitats (arable and mixed farmland, rural and urban settlements) and a negative effect in other habitats. A similar division in the direction of the effect of species thermal niche between more anthropogenic and more natural habitats has been reported by Kampichler et al. (2012), however in that study warm associated species increased in more natural habitats and became less dominant in farmland. The reasons for variation between habitats in the effect of temperature on bird communities in both studies are unclear, and warrant further investigation, but could reflect differences in the importance of climate and non-climate drivers of bird populations in different habitats (Eglington and Pearce-Higgins, 2012), or variation in the thermal association of species between habitats (e.g. Clavero et al., 2011; Kampichler et al., 2012).

We did not find support for the hypothesised interactions between diet and habitat (Table 1), although several others were identified. The hypothesis that granivorous species were declining more strongly in farmland was not supported, however, the more negative population trends of granivorous species in urban settlements and the two wetland habitats was highly statistically significant in both modelling approaches. The more negative trends of granivorous species in wetlands was not driven by a single species, as it remained significant when the wetland associated reed bunting *Emberiza schoeniclus* was removed ($\chi^2 = 14.9$, $P = 0.0001$), so the mechanisms behind this pattern need further exploration. The more negative population trends of granivorous and ground nesting birds in urban areas are discussed below.

4.3. Reasons for declines in woodlands and urban areas

Although our results suggest that species effects are more important than habitat effects, we do find support for consistent variation in trends between habitats. Declines were particularly evident in woodland habitats and urban/suburban settlements, the latter contrasting with more positive trends in rural settlements. These differences were not due to differences in species composition between habitats, as these patterns remained when the analysis was repeated only including species found in all habitats (Fig. A3).

While declines in woodland bird populations have been noted previously (Hewson and Noble, 2009), the strong negative population trends of birds in urban/suburban areas contrasts with trends in rural settlements, and is the first time that such a difference has been documented in UK bird populations, but reflects wider evidence that urbanisation is associated with negative impacts on biodiversity (Aronson et al., 2014). Interestingly, despite negative overall population trends, large numbers of species were increasing in urban/suburban areas, suggesting that environmental change there is creating both winners and losers. Indeed, population trends of nationally increasing species were comparable to the average across all habitats, with the overall negative trend instead driven by nationally declining species having more negative population trends in urban settlements than in other habitats (Fig. 1d). Population declines were most evident in strong urban specialists (Jacobs index >0.25) and species not positively associated with urban settlements (Jacobs index ≤0), while declines were not evident in species moderately associated with urban settlements (Jacobs index >0 and ≤0.25).

Population trends of granivorous and ground nesting birds were more negative in urban areas in both mixed and phylogenetic models. A number of granivorous and/or ground-nesting species typical of open farmland, such as linnet *Carduelis cannabina*, skylark *A. arvensis*, meadow pipit *Anthus pratensis* and yellowhammer *Emberiza citrinella*, were declining especially strongly in urban areas (Appendix B). These changes could be due to loss of urban wastelands for brownfield development, decline in the quality of open habitats in and bordering urban/suburban areas, or a density dependent shift in habitat preferences towards higher quality habitats outside urban areas as national populations decline (Sullivan et al., 2015). Although we did not specifically examine population trends of species nesting in cavities in buildings, house sparrows *Passer domesticus* and common swifts *Apus apus*, which both nest in or on buildings, were both declining more strongly in urban and suburban areas compared to other habitats. Both these species may be affected by renovations to buildings reducing the availability of cavities (Shaw et al., 2008).

General drivers that could be operating in urban and suburban areas include increased infilling of green space with houses (Evans et al., 2009), predation by cats (Beckerman et al., 2007), disease transmission at garden bird feeders (Robinson et al., 2010) and increased noise and light pollution (Francis et al., 2009). Similar drivers are likely to be operating in urban areas across Europe, so declines in urban bird populations may be evident in other countries. Further work will be important to evaluate the role of these habitat-level drivers in urban and suburban areas.

Apart from the main patterns apparent across all habitats, population trends in woodland did not vary strongly with species traits. For example, species associated with both the shrub layer (e.g. common whitethroat *Sylvia communis*, European robin *Erithacus rubecula*) and with mature trees (e.g. nuthatch *Sitta europaea*, great spotted woodpecker *Dendrocopos major*) had less positive population trends in deciduous woodlands than other habitats. Populations of both nationally increasing and nationally declining species tended to be more negative in woodlands than in other habitats, supporting the importance of general drivers of declines in woodland. However, declines were more severe in species that did not positively select woodland (Jacobs index ≤0), meaning that declines in woodland were stronger for generalist species and specialist species associated with other habitats than for woodland specialists. This may indicate that declining non-woodland specialists are retracting to their preferred habitats (Sullivan et al., 2015). However, population trends of deciduous woodland specialists were still negative, and may be more severe than indicated by this study as populations of woodland specialists underwent large declines prior to the start of the BBS (Defra, 2013). Candidate drivers include increased deer browsing (Newson et al., 2012), eutrophication, canopy shading, and reduction in the shrub layer, with associated taxonomic homogenisation of woodland floor plant communities (Keith et al., 2009) and increases in grass species at the expense of herbs (Corney et al., 2008). These changes may be responsible for declines in species using the understory and shrub layer of woodlands (Hewson and Noble, 2009), with changes in canopy shading hinting at changes in woodland structure that may have influenced arboreal species. Population trends of woodland birds, as revealed by the woodland birds indicator, are similar in many parts of Europe (Gregory et al., 2007), so the declines noted here may be evident in other European countries. However, trends of woodland birds in central and eastern Europe are stable in contrast to a declining indicator elsewhere (Gregory et al., 2007). Two differences between these areas and the UK are lower densities of deer in continental Europe (Burbaitė and Csányi, 2010) and a higher nitrogen inputs in farming (and thus potentially greater eutrophication of woodland) in western Europe compared to eastern Europe (Liu et al., 2010).

Population trends in farmland were more positive than those in some other habitats. However, the trends produced here are relative to a baseline of the beginning of the BBS in 1994, when farmland bird populations were already low following steep declines between the mid-1970s and mid 1980s (Defra, 2013). Ongoing declines in some species are evident, however, with 1/4th of species declining in farmland. Indeed, the generally positive population trends of species in farmland is likely to be driven by generalist species, as restricting the analysis to species with a strong preference for farmland (i.e. Jacobs index >0.25) resulted in a negative overall population trend in mixed farmland and a stable overall population trend in arable farmland.

4.4. Comparison with indicators

Different patterns were revealed by analysing habitat-specific population trends compared to species-based indicators. Although there has been a long term decline, the woodland bird indicator has largely been stable since the beginning of the BBS in 1994 (Defra, 2013), although this national assessment masks declines in woodland specialists, particularly in southern Britain, which are largely offset by increases further north (Massimino et al., 2015). However, habitat-specific trends of woodland birds have declined in this period. In contrast, both the farmland and wetland bird indicator trends have decreased over the BBS period (Defra, 2013), while habitat-specific trends have been positive over this period. A key difference between indicators and habitat-specific trends is that the former contains habitat specialists (Renwick et al., 2012), while the latter also includes populations of generalists using that habitat. While many farmland specialists are declining, many generalist species associated with farmland are increasing (Massimino et al., 2015). Therefore, while around 1/4th of species for which farmland-specific population trends were calculated were declining, these were offset by increases in other species. Restricting our analysis to habitat specialists resulted in habitat-specific trends of woodland species being less negative or even positive, while trends in farmland became less positive or even negative (Fig. A2), supporting this explanation for differences between our results and wild bird indicators. For many applications indicators will be more relevant, as they focus on population trends of habitat specialists that are likely to be greater conservation priorities than generalists. However, analysis of habitat-specific trends sheds light onto the differing fortunes of a wider suite of species in different habitats and may therefore indicate previously undescribed patterns of environmental change. They are also likely to be particularly useful to monitor habitats with few specialists.

4.5. Conclusions and conservation implications

Producing habitat-specific trends for birds in the UK has revealed considerable differences in population trends between habitats, with notable declines in birds in woodland and in urban/suburban areas. Population trends were largely driven by species-scale effects, particularly related to migratory strategy, with consistent declines in species that winter in the humid zone of Africa. However, variation in the strength of trait effects between habitats suggests that processes operating in certain habitats can enhance or reduce the effects of larger-scale drivers operating across habitats. For example, reduced declines in humid-zone migrants in northern and less seasonal habitats were consistent with potential impacts of phenological mismatch. Importantly, the general consistency in the direction of trait effects indicates that while declines of certain groups of species were less severe in certain habitats, populations were still declining in these habitats, so they are unlikely to provide a refuge for these species.

It is important to assess whether large-scale drivers of population decline are also dominant in other taxa, as our results are from highly mobile species living in fragmented landscapes, where large-scale drivers may be more important. Indeed, our results contrast with two previous studies that suggest habitat-level effects are more important than species-level effects in explaining population declines in mammals (Cowlishaw et al., 2009; Fisher et al., 2003). However, our results may be used to infer that, for UK birds at least, habitat-specific conservation solutions to large-scale population declines may have only limited success. Certainly devising conservation strategies to address large-scale drivers of population change acting across habitats, such as the impacts of climate change or declines in long-distance migrants, will be challenging, but research in this area is of upmost importance. However, given strong declines in woodland and urban birds, there is an urgent need for further work to understand their causes. While our findings for woodland birds are not novel (Hewson and Noble, 2009), we believe that the negative trends we have identified for urban populations of species are, and should be urgently examined and addressed as an emerging signal of environmental degradation, particularly as it is in such environments that the greatest proportion of people encounter biodiversity.

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Appendix A. Supplementary data

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