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Article:

1   **Using habitat-specific population trends to evaluate the consistency of the effect of species traits**

2   **on bird population change**

3   Martin J. P. Sullivan[1,2], Stuart E. Newson[1] * and James W. Pearce-Higgins[1]

4   [1] British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK.

5   [2] School of Geography, University of Leeds, Leeds, LS2 9JT, UK.

6   *Author for correspondence: stuart.newson@bto.org.

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20   Many species are undergoing rapid population declines, while other species have increased.

21   Previous work has related population change to species traits to elucidate the drivers of population

22   change. However, this assumes that these drivers operate consistently across habitats. We use

23   national-scale monitoring data on UK bird abundance from 1994-2012 to calculate habitat-specific

24   population trends, allowing us to evaluate whether the effect of species traits was consistent

25   between habitats. Although we found significant interactions with habitat for traits relating to

26   migratory behaviour, diet, nest site, body mass and habitat specialisation, the direction of these trait

27   effects were generally consistent between habitats. This suggests that large-scale processes

28   operating across habitats are responsible for many changes in bird populations, although processes

29   operating within habitats can modulate the effect of these drivers. Despite this, differences in

30   population trends between habitats remain when variation in population trends due to species

31   identity is accounted for, indicating that some habitat effects do occur. By identifying the scale at

32   which drivers of population change operate, it is possible to target conservation actions more

33   directly. Population declines were most evident in woodland and urban habitats, and we suggest

34   these habitats should be the focus of increased research and conservation effort if declines evident

35   in many bird species are to be reversed.

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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. Whilst 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 migrants (Ockendon et al. 2012; Salido et al. 2012; Sanderson et al. 2006;

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68   Van Turnhout et al. 2010), particularly of species wintering in the humid bioclimatic zone (Thaxter et

69   al. 2010). However, these studies look at national population trends, so do not allow the consistency

70   of these trait effects to be evaluated between habitats. For example, the importance of traits such as

71   migratory strategy for driving population trends varies spatially (Morrison et al. 2013), part of which

72   may be associated with spatial variation in habitat cover. Given strong contrasts in population trends

73   between habitats, it is therefore important to assess the extent to which the ecological traits

74   associated with population trend may also vary between habitats to inform conservation action. If

75   the importance of different traits varied strongly between habitats, this would indicate that the

76   drivers of population trend are likely to differ between them.

77   Analysing habitat-specific population trends of species potentially allows the importance of habitat-

78   level and species-level drivers of population change to be evaluated. We extend the methods

79   developed by Newson et al. (2009) to calculate habitat-specific population trends for 89 bird species

80   in the UK. Analysis of this dataset has shown that the broad pattern of these habitat-specific trends

81   is consistent with the widespread operation of the buffer effect, where declining species retreat to

82   high quality habitats while increasing species spread into lower quality habitats (Sullivan et al. 2015).

83   However, the high degree of variation around this broad pattern suggests that other processes are

84   also important in driving variation in population trends between habitats. In this study, we analyse

85   these habitat-specific population trends with the aim of (1) identifying habitats where bird

86   population trends are especially negative, (2) evaluating the relative importance of habitat- and

87   species-effects in driving trends, and (3) assessing the consistency of trait effects between habitats.

88   **2. Materials and methods**

89   2.1 Habitat specific population trends

90   We calculated species' population trends using data from the Breeding Bird Survey (BBS), which

91   since its inception in 1994 has been the principal monitoring scheme for populations of widespread

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92   breeding birds in the UK. The BBS uses a stratified random sampling design, ensuring representative

93   coverage of habitats throughout the UK (Baillie et al. 2014). BBS squares are also stratified by region

94   to ensure maximum utilisation of available volunteers; BBS squares are weighted in later analyses to

95   correct for biases in sampling effort introduced by this. Each BBS square is visited twice during the

96   breeding season (mid-March to late-June), with the visits separated by at least four weeks. In each

97   square, volunteers walk two 1 km transects (as close to parallel as possible), and record all bird

98   species seen or heard within 200m transect sections. We used the maximum count of the two visits,

99   and excluded flying birds except for aerial feeders, displaying skylarks *Alauda arvensis* and hovering

100   common kestrels *Falco tinnunculus*.

101   Volunteers record up to two habitat classes for each 200m transect section following a hierarchical

102   coding system described by Crick (1992). Following Newson *et al.*(2009), we reclassified habitats into

103   12 habitat classes given in Table A1 (see Table A2 for number of BBS squares and transect sections

104   surveyed in each year). These were deciduous woodland (abbreviated to DECID), mixed woodland

105   (MIXW), coniferous woodland (CONIF), upland semi-natural open habitats (UPSN), lowland semi-

106   natural open habitats (LOSN), arable farmland (ARAB), pasture (PAST), mixed farming (MIXF), rural

107   settlements (RURA), urban settlements (URBA), wetlands (WETL) and flowing water (FLOW).

108   Separate population trends were calculated for each habitat. To do this, data were subset by habitat

109   types so that only transect sections of a particular habitat contributed to the calculation of that

110   habitat's trends. Log-linear generalised linear models with Poisson error terms were constructed

111   using the GENMOD procedure in SAS 9.2 (SAS Institute 2008), with bird count modelled as a function

112   of site (i.e. BBS square) and categorical year to give population indices in each year, with a dispersion

113   parameter (deviance divided by the degrees of freedom) to account for overdispersion. Subsetting

114   data in this way by habitat meant that the number of transect sections per site varied. To control for

115   this we included the log of the number of transect sections containing the given habitat type as an

116   offset variable (Newson et al. 2009).

117   We did not analyse change in annual population indices directly, as they are sensitive to yearly

118   fluctuations. Instead, we fitted a post-hoc smoothed trend through the annual indices using non-

119   parametric thin-plate splines, constraining the degrees of freedom to be the nearest integer to 0.3 x

120   length of time-series (Baillie et al. 2014). We calculated the population trend for each species

121   between 1995 and 2011 as (smoothed population index$_{2011}$ – smoothed population index$_{1995}$) /

122   smoothed population index$_{1995}$. The first and last years of our dataset (1994 and 2012) were

123   excluded from this calculation as they have a large influence of the direction of trends so may bias

124   population changes (Baillie et al. 2014). For each species we repeated this procedure of calculating

125   annual indices and then fitting post-hoc smooths on 199 bootstraps (Baillie et al. 2014), sampling

126   with replacement each time. We calculated standard errors and confidence intervals around

127   population trends from these bootstraps. Species were classed as increasing or declining if the 95%

128   confidence limits of the population trend did not overlap zero. Habitat-specific population trends for

129   all species are presented in Appendix B.

130   <u>2.2 Ecological variables</u>

131   We collated trait data on breeding season diet, nest site, mass, habitat specialisation, winter

132   bioclimatic zone and thermal niche in order to test for trait – habitat interactions. Data on diet, mass

133   and nest site were obtained from Snow and Perrins (2004), with the former two traits previously

134   collated by Robinson (2005). Breeding season diet was categorised into the following mutually

135   exclusive categories: herbivorous, granivorous, carnivorous – vertebrates (hereafter referred to as

136   carnivorous), carnivorous – invertivorous (hereafter insectivorous) and omnivorous. Nest site was

137   classified as into the following mutually exclusive categories: requiring low vegetation to nest (i.e.

138   species nesting in shrubs < 2m above the ground, species nesting in low vegetation, and ground

139   nesting species that nest in long grass or under other low vegetation (e.g. winchat *Saxicola rubetra*)),

140   other ground nesting species (hereafter ground nesting), nesting in tree cavities, and nesting in

141   trees. Species that did not fit into these categories, for example species nesting in buildings or on

142   water, were classed as other. Mass was taken as the mean mass of males and females. We obtained

143   an index of species habitat specialisation (SSI) from Davey et al. (2012). This was calculated as the

144   coefficient of variation of species densities across the 12 habitat classes (Table A1), with higher

145   values indicating increasing habitat specialisation. Data on the wintering bioclimatic zone of species

146   were obtained from Ockendon et al. (2012), Thaxter et al. (2010) and Morrison et al. (2013). Species

147   were classified as resident, partial or short-distance (i.e. wintering north of the Sahara) migrant, or

148   for trans-Saharan migrants wintering in either the arid, humid or southern bioclimatic zones. Only

149   two species wintered in the southern bioclimatic zone, so these were combined with species

150   wintering in the arid zone in subsequent analyses (humid zone species were treated separately as

151   previous work has found they have contrasting population trends to other sub-Saharan migrants

152   (Thaxter et al. 2010). An index of species thermal niche (STI), representing the mean breeding

153   season temperature in a species' European distribution, was obtained from Devictor et al. (2008).

154   2.3 Statistical analysis

155   Analysis of population trends was performed in R (R Core Team 2014). We conducted analyses to (1)

156   partition variation in habitat-specific population trends between species and habitats, (2) test for

157   differences in population trends between habitats and (3) examine how consistent the effects of

158   species traits were among habitats (details below). We used the natural log of population trend + 1

159   in order to homogenize variances and ensure normality of residuals. Previous studies of population

160   trends have restricted analyses to species that are on average recorded in more than 30 BBS squares

161   each year as there may be insufficient power to detect declines in less well recorded species (Joys et

162   al. 2003). This may lead to rare and declining species being excluded (Renwick et al. 2012). Instead,

163   we used a more lenient threshold and included species-habitat combinations where a species was

164   recorded on an average of 10 or more BBS squares per habitat type each year, but then down-

165   weighted the importance of trends with high degrees of uncertainty in subsequent modelling by

166   specifying case weights as the reciprocal of population trend standard error, which was also logged

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167 to reflect our treatment of the population trend data. This approach allows infrequently recorded

168 species with clear population trends to contribute to models, so maximises the number of species

169 that can be included in the study, while reducing the influence of species with highly uncertain

170 population trends. Despite the use of a more lenient threshold, a number of rare species were

171 recorded too infrequently to be included in this study. In addition, we excluded common gull *Larus*

172 *canus*, lesser black-backed gull *Larus fuscus*, herring gull *Larus argentatus*, black-headed gull

173 *Chroicocephalus ridibundus* and grey heron *Ardea cinerea* from analyses, as the BBS survey design is

174 not appropriate for assessing population trends of these colonial species (Baillie et al. 2014). In total

175 there were 746 habitat-specific population trends of 89 species used in analysis.

176 We followed the method of Reino et al. (2005), adapted from Legendre and Legendre (2012), to

177 partition the proportion of variation in population trends attributable to species and habitat. We

178 fitted a linear model with population trend as a function of habitat and species (M1), as well as

179 models with just habitat (M2) or species (M3) as explanatory variables. Explained variation in the full

180 additive model consists of variation attributable to habitat, variation attributable to species, and

181 shared variation due to correlations between species and habitat, while explained variation in the

182 two constituent models consists of variation attributable to the target variable (species or habitat)

183 and shared variation. This shared variation can be isolated by subtracting explained variation in the

184 full model from the sum of explained variation in the two constituent models (i.e. shared variation =

185 M2 + M3 − M1). This shared variation can then be subtracted from the constituent models (M2 and

186 M3) to give the proportion of variation attributable to species and habitat. Unexplained variation in

187 the full additive model (M1) is attributable to species-habitat interactions, as adding a species-

188 habitat interaction term leads to a saturated model with no unexplained variation.

189 To test whether population trends differed between habitats, we used a mixed effects model with

190 species as a random effect to model population trend as a function of habitat. Mixed effects models

191 were constructed in lme4 (Bates et al. 2014). The purpose of the species random effect was to

192 account for the expected correlation of population trends of the same species. We repeated this

193 analysis on a subset of species that occurred in all habitats, to test whether differences in population

194 trends between habitats were a consequence of differences in species composition, or due to

195 differing trends between habitats for the same species. Differences in population trends across all

196 species between habitats could be driven by increasing species increasing more or less than the

197 national average or declining species decreasing more or less than the national average. We

198 explored this by repeating the modelling procedure described above separately for a subset of

199 increasing species and a subset of declining species assessed from national population trends

200 between 1995 and 2011 (Risely et al. 2013). We tested whether population trends in each habitat

201 were significantly different from the overall mean population trend across all habitats and species

202 (using the Satterthwaite approximation of degrees of freedom), and also used simultaneous tests of

203 generalised linear hypotheses implemented in multcomp (Hothorn et al. 2008) to test for significant

204 differences between habitat types. This analysis was repeated using a broader categorisation of five

205 functional habitat classes (woodland –BROAD, CONIF and MIXW, semi-natural open – UPSN and

206 LOSN, farmland – ARAB, PAST and MIXF, human – RURA and URBA and wetland – WETL and FLOW).

207 To investigate whether population trends of specialist species varied between habitats, we first

208 assessed whether species selected a habitat more frequently than expected given its availability by

209 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

210 observations of species s in habitat h and $a_{h,s,}$ is the proportion of transect sections in BBS squares

211 where species s was recorded that contained habitat h. Jacobs index ranges from -1 to 1, with values

212 >0 indicating more frequent selection of a habitat than expected given availability. We then used

213 mixed effects models to model population trend as a function of habitat, restricting this analysis to

214 species with Jacobs index values greater than 0. We repeated this with species where J > 0.25,

215 focusing the analysis further onto habitat specialists.

216 We tested for inter-habitat differences in the effect of species traits on population change by

217 constructing a general linear mixed effects model (LMM) with habitat, traits and interactions

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218   between traits and habitat for traits where we hypothesised *a priori* that the effect of the trait

219   would vary among habitats (see Table 1 for hypotheses) as explanatory variables. We included SSI,

220   STI, the natural logarithm of body mass, migratory strategy (resident, short distance or partial

221   migrant, long-distance migrant wintering in the humid bioclimatic zone, long-distance migrant

222   wintering elsewhere in sub-Saharan Africa), diet (insectivorous, granivorous, herbivorous,

223   carnivorous or omnivorous) and nest site (ground, low vegetation, trees, tree cavities or other) as

224   main effects. Given our hypotheses, interactions with habitat were included for STI, SSI, the humid

225   and arid/ southern levels of migratory strategy, the insectivorous and granivorous levels of diet, and

226   the ground, low vegetation and tree cavity levels of nest site. There were at least three species for

227   each trait-habitat interaction combination (mean = 15 ± 10 SD species, see Table A3 for number of

228   species in each trait-habitat combination). Species was included as a random effect. This model was

229   simplified by sequential removal of non-significant terms, followed by aggregation of factor levels

230   until a minimum adequate model was obtained (Crawley 2007). We calculated variance inflation

231   factors (VIF) to assess multicolinearity in predictor variables; these were < 3 for all variables expect

232   for diet, where VIF = 4.98. Diet was correlated with body mass, with granivorous and insectivorous

233   species tending to be lighter than other species. Both body mass and diet were retained in our

234   analysis, however repeating the analysis excluding body mass reduced multicoliniarity (VIF < 2) but

235   resulted in the same minimum adequate model. We assessed model fit by plotting residuals against

236   fitted values, as well as plotting residuals against each explanatory variable. In all cases no patterns

237   were observed (Fig. A1).

238   We reduced the number of comparisons made during model selection by first assessing the

239   significance of interactions with habitat as a whole, and only assessing the significance of

240   interactions with individual habitat classes if the interaction with habitat was significant. Had we

241   looked at all interactions with habitat classes in the full model then there would have been 124,

242   giving a high probability of significant results occurring by chance. The Bonferonni adjustment for

243   this number of tests is α = 0.0004. However, such corrections have been criticized for being overly

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244 conservative as highly significant results may be rejected (Crawley 2007). We therefore take a

245 pragmatic approach to dealing with multiple testing, interpreting results where $P <0.0004$ as strongly

246 supported, but still considering strongly significant results with larger P values (i.e. $P \leq 0.01$ but $\geq$

247 0.0004) as worthy of discussion. Results where $0.05 > P > 0.01$ are presented and retained in the

248 minimum adequate model, but interpreted with caution. The significance of main effects that were

249 also retained in the minimum adequate model as interactions was assessed by likelihood ratio tests

250 of the model without the main effect and interaction term against the more complicated model just

251 lacking the interaction term.

252 We repeated this test for inter-habitat differences in trait effects using phylogenetic generalised

253 least squares (PGLS) to account for correlations between species trends that result from shared

254 evolutionary history (Felsenstein 1985). We used a phylogenetic tree of British birds obtained from

255 Thomas (2008). We implemented the model using Pagel's correlation structure (Paradis et al. 2004)

256 in the gls procedure in nlme (Pinheiro and Bates 2007). The λ parameter in Pagel's correlation

257 structure determines how similar the covariances are to those in a Brownian motion model of trait

258 evolution, with values of 1 indicating Brownian motion and 0 indicating random trait evolution.

259 Following Revell (2010) we parameterised λ simultaneously with coefficient estimation when fitting

260 the PGLS.

261 **3. Results**

262 <u>3.1 Differences in overall population trends between habitats</u>

263 There were significant differences in population trends between habitat classes ($\chi^2 = 66.1$, $P <$

264 0.0001). Trends were significantly more negative in all woodland habitat classes and in urban/

265 suburban habitats compared to the overall mean population trend across habitats (Fig. 1a).

266 Population trends were most positive in wetlands and standing water, followed by both upland and

267 lowland semi-natural grassland/ heath, but were not significantly different from the overall mean

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268   across habitats (Fig. 1a). Largely similar patterns were evident when the analysis was restricted to

269   species selecting a habitat more frequently than expected given availability (Fig. A2), although

270   population trends were less negative in deciduous woodland, stable instead of negative in mixed

271   woodland, positive instead of negative in coniferous woodland, and more negative in arable and

272   mixed farmland (Fig. A2). Trends differed significantly between broad functional habitat classes (χ^2 =

273   43.8, $P < 0.001$, Fig. 1b), driven by contrasting patterns for rural settlements and urban/ suburban

274   settlements in the human class and wetlands/ standing water and flowing water in the wetland class

275   (Fig. 1a).

276   When separating species showing positive national population trends from declining species,

277   population trends of increasing species were significantly less positive in deciduous and mixed

278   woodland than in other habitats (Figure 1c), while species that were declining nationally were

279   declining more strongly in deciduous woodlands and in urban/ suburban areas than other habitats

280   (Figure 1d).These differences in the magnitude of population trends were reflected in significant

281   differences in the distribution of population trends between habitats (χ^2 = 147.0, $P < 0.0001$, Table

282   A4). The highest proportion of declining species were found in urban/ suburban areas (32.7% of

283   species declining), deciduous woodland (33.8%) and mixed woodland (38.3%). Large numbers of

284   declining species were also found in rural settlements (29.6%) and in farmland habitat classes (23.9%

285   - 28.2%), but were offset by a high proportion (46.3% - 54.4%) of species with increasing population

286   trends in those habitats. In most habitats more species were estimated to be increasing in

287   abundance than declining, with this pattern only reversed in mixed and deciduous woodland.

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289   3.2 Partitioning variation in trend between species and habitats

290   Variation in habitat-specific population trends was largely explained by a strong independent effect

291   of species (71.5% of variation in saturated model explained). Habitat alone explained 2.6% of

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292   variation, with the combined effect of habitat and species explaining a further 0.4%. As this is a

293   saturated model the remaining 25.5% of variation can be attributed to the interaction between

294   species and habitats. This can be seen in considerable variation in species trends between habitats,

295   with 23 species out of the 89 for which trends were calculated showing significant increases in one

296   habitat and significant declines in another.

297   The importance of species does not mean that the differences in population trend between habitats

298   (Fig. 1a) are unrelated to habitat. Observed contrasts in habitat-specific trends remained when this

299   analysis was repeated only including generalist species that occur in all habitats (Fig. A3, χ^2 = 26.9, P

300   = 0.005).

301   <u>3.3 Variation in population trends in relation to species traits</u>

302   Migratory strategy, nest site and diet were retained in the minimum adequate mixed effects model

303   (Table A5). Species wintering in the humid zone had more negative population trends than other

304   species (β = -0.613 ± 0.152, χ^2 = 15.8, P < 0.0001). Population trends of ground nesting species were

305   more negative than species nesting in other places (β = -0.420 ± 0.144, χ^2 = 8.6, P = 0.003). Although

306   both granivore and insectivore factor levels of diet were retained in the minimum adequate model,

307   neither was statistically significant as a main effect (χ^2 ≤ 0.3, P ≥ 0.608).

308   The above traits were all retained in the minimum adequate phylogenetic model as well. However,

309   in that analysis ground nesting was not significant as a main effect, while insectivorous species had

310   more positive population trends than non-insectivorous species (β = 0.445 ± 0.171, F = 7.0, P =

311   0.008). Several traits had significant effects in the phylogenetic analysis but not in the mixed effect

312   model analysis (coefficients of both models in Table A5). Species requiring low vegetation to nest

313   had more positive population trends (β = 0.500 ± 0.138, F = 13.5, P = 0.0002), while population trend

314   was negatively related to STI (β = -0.056 ± 0.024, F = 5.5, P = 0.0195). SSI and the Arid/ Southern

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315   bioclimatic zone factor level of migratory strategy were included in the minimum adequate

316   phylogenetic model, but were not significant as main effects ($F \leq 1.2$, $P \geq 0.188$).

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318   <u>3.4 Consistency of trait effects between habitats</u>

319   The effects of ecological traits were often consistent among habitats, with interactions mainly

320   strengthening or weakening the effect of traits in certain habitats (Table 2). However, the direction

321   of several trait effects was reversed; in the mixed effects model analysis granivorous and

322   insectivorous species had more positive population trends than other species in upland semi-natural

323   habitats but more negative population trends in other habitats, while in the phylogenetic analysis

324   the direction of STI, SSI and ground nesting trait effects varied between habitats (Table 2).

325   Of the hypothesised trait-habitat interactions (Table 1), only interactions between migratory

326   strategy and habitat were supported (Table 2, see Table A5 for coefficients). As hypothesised,

327   population trends of Afro-Palearctic migrants wintering in the humid bioclimatic zone were less

328   negative in coniferous woodlands (LMM: χ^2 = 13.0, P = 0.0003, PGLS: F = 10.5, P = 0.001) and upland

329   semi-natural habitats (the latter only in the LMM analysis, χ^2 = 9.8, P = 0.0017) and more negative in

330   arable and mixed farmland (LMM: χ^2 = 22.6, P <0.0001, PGLS: F = 26.0, P <0.0001). To check this was

331   not a result of a single-species outlier, this effect remained when the rapidly declining turtle dove

332   *Streptopelia turtur*, which uses these habitats, was excluded (χ^2 =20.2, P < 0.0001). Migrants

333   wintering in the arid/ southern bioclimatic zone had positive population trends in upland semi-

334   natural habitats compared to negative trends elsewhere (PGLS analysis only, F = 7.2, P = 0.002).

335   Although other hypothesised trait-habitat interactions were not supported, some trait-habitat

336   interactions that we did not predict *a priori* were statistically significant. Population trends of humid

337   zone migrants were less negative in lowland semi-natural habitats (LMM: χ^2 = 9.8, P = 0.0017, PGLS:

338   F = 10.5, P = 0.001) and flowing water (the latter only in the LMM, χ^2 = 5.5, P = 0.019), while

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339 population trends of both humid and arid/ southern migrants were more negative in urban

340 settlements (PGLS only, F = 26.0, P <0.0001 and F = 9.7, P = 0.002 respectively). Granivorous species

341 had more negative population trends in urban settlements (LMM: χ^2 = 17.8, P < 0.0001, PGLS: F =

342 26.1, P < 0.0001) and in both wetland habitats than in other habitats (χ^2 = 13.4, P = 0.0002, PGLS: F =

343 26.1, P < 0.0001). In the mixed model analysis both granivorous and insectivorous species had more

344 positive population trends in upland semi-natural habitats (χ^2 = 7.0, P = 0.008 and χ^2 = 9.5, P = 0.002

345 respectively) and insectivorous species had more negative population trends in urban settlements

346 (χ^2 = 9.9, P = 0.002), while in the phylogenetic analysis granivorous species had more negative

347 population trends in mixed woodland (Table A5). Ground-nesting species had more negative

348 population trends in urban settlements than in other habitats (LMM: χ^2 = 15.4, P < 0.0001, PGLS: F =

349 24.5, P < 0.0001). In the phylogenetic analysis, STI had a contrasting effect between habitats, with a

350 positive effect in arable and mixed farmland and rural and urban settlements compared to a

351 negative effect in other habitats (F = 22.5, P < 0.0001). SSI had a non-significant negative effect in all

352 habitats except for lowland semi-natural habitats, where it had a positive effect on population trend

353 (F = 7.5, P = 0.006).

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355 **4. Discussion**

356 Population trends of UK breeding birds varied among habitats, with generally negative population

357 trends in woodland and urban habitats. Despite these differences, the strongest component of

358 variation was between species, indicating that many of the drivers of UK bird population trends are

359 likely to be acting across habitats. However, species-scale effects are not the only driver of

360 population change, as we found that variation in the strength of trait effects between habitats

361 accounted for about a quarter of the variation in population trends. Our results are consistent in this

362 respect with a previous study in The Netherlands investigating variation in the response of bird

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363 communities to temperature and land-use change (Kampichler et al. 2012), and suggest that habitat-

364 level drivers can ameliorate or enhance the effect of broad scale drivers.

365 <u>4.1 Effect of species traits on population trends</u>

366 Many of the effects of species traits reported here are consistent with those found in previous

367 studies looking at European bird population trends. Thus, as demonstrated previously, long distance

368 humid zone migrants (Ockendon et al. 2012; Thaxter et al. 2010) and ground nesting species (Van

369 Turnhout et al. 2010) were the most likely to decline in abundance. Declines of ground nesting

370 species in the Netherlands have been attributed to increased nitrogen deposition and related

371 increases in nitrophillous vegetation (Van Turnhout et al. 2010). Our results are consistent with this,

372 with species requiring low vegetation to nest having more positive population trends in the

373 phylogenetic analysis, but may also reflect the impact of increasing populations of generalist,

374 particularly mammalian, predators upon ground-nesting species such as waders (MacDonald and

375 Bolton 2008).

376 In contrast to previous studies, which have found that bird communities in Europe are becoming

377 increasingly dominated by warm associated species (Devictor et al. 2008; Devictor et al. 2012;

378 Kampichler et al. 2012), we find (in the phylogenetic analysis only) population declines in species

379 associated with warmer regions. There are two potential explanations for this. Firstly, the UK

380 experienced three successive winters with severe cold spells towards the end of the time series,

381 including one month (December 2010) where temperatures were 5°C below the 1971-2000 mean

382 (Met Office 2015), which were likely to have impacted populations of cold sensitive species (Pearce-

383 Higgins et al. 2015). Excluding data from these three years weakens the overall relationship between

384 population trend and STI (β = -0.019 ± 0.027). Secondly, in our analyses population trends of each

385 species are weighted equally, so may give a different inference to that from analyses of change using

386 weighted average community temperature associations in which the contribution of species is

387 weighted by their abundance (e.g. Devictor et al. 2012; Kampichler et al. 2012). Using our data to

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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).

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413 One potential mechanism causing variation in habitat-specific trends of humid zone migrants could

414 be that the arrival times of humid zone migrants may be constrained by their reliance on resource

415 pulses following early spring rains prior to migration, potentially leading to phenological mismatch in

416 their breeding grounds (Ockendon et al. 2012). The effect of this upon breeding success and

417 population trends is likely to be less severe in habitats, such as coniferous woodland, where

418 resources are less seasonal in abundance than in other habitats, such as deciduous woodland (Both

419 et al. 2010). We found that declines in humid zone migrants were less severe in coniferous

420 woodland, and to a lesser extent semi-natural grassland and heath, than in other habitats, providing

421 some support for humid zone migrant declines being less negative in habitats with stable resources

422 or relatively late phenologies. However, the less negative population trend of humid zone migrants

423 in coniferous woodland was also at least partly due to such habitats being distributed further north

424 (Fig. A5; see also Morrison et al. 2013; Ockendon et al. 2012), potentially because they have later

425 phenologies or greater prey abundance than in the south (Conrad et al. 2006; Smith et al. 2011). This

426 may also explain the steeper declines of humid zone migrants in rural areas and arable and mixed

427 farmland, as these have a southerly distribution in the UK, so experience earlier springs and hence

428 greater potential for phenological mismatch (Morrison et al. 2013). We note that the effect of

429 phenological mismatch on habitat-specific population trends is further complicated by variation in

430 migratory species' ability to change their arrival time (Møller et al. 2008) and by the potential for

431 increased post-fledging survival to offset negative effects of phenological mismatch on productivity

432 (Reed et al. 2013).

433 The weak negative relationship between habitat specialisation and population trend in most habitats

434 in the phylogenetic analysis is consistent with the increasing domination of bird communities by

435 generalist species reported previously in the UK (Davey et al. 2012), Sweden (Davey et al. 2013) and

436 across Europe (Le Viol et al. 2012). The significant contrast between semi-natural open habitats,

437 where this relationship was more positive than in other habits, was only apparent in the

438 phylogenetic analysis and was not significant at the Bonferoni adjusted alpha level, but is consistent

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439   with a previous assessment of rates of change in community specialisation in UK birds (Davey et al.

440   2012) and on Dutch heath compared to farmland (Kampichler et al. 2012).

441   The effect of species thermal niche on population trends varied between habitats in the

442   phylogenetic analysis, with a positive effect in more anthropogenic habitats (arable and mixed

443   farmland, rural and urban settlements) and a negative effect in other habitats. A similar division in

444   the direction of the effect of species thermal niche between more anthropogenic and more natural

445   habitats has been reported by Kampichler et al. (2012), however in that study warm associated

446   species increased in more natural habitats and became less dominant in farmland. The reasons for

447   variation between habitats in the effect of temperature on bird communities in both studies are

448   unclear, and warrant further investigation, but could reflect differences in the importance of climate

449   and non-climate drivers of bird populations in different habitats (Eglington and Pearce-Higgins

450   2012), or variation in the thermal association of species between habitats (e.g. Clavero et al. 2011;

451   Kampichler et al. 2012).

452   We did not find support for the hypothesised interactions between diet and habitat (Table 1),

453   although several others were identified. The hypothesis that granivorous species were declining

454   more strongly in farmland was not supported, however, the more negative population trends of

455   granivorous species in urban settlements and the two wetland habitats was highly statistically

456   significant in both modelling approaches. The more negative trends of granivorous species in

457   wetlands was not driven by a single species, as it remained significant when the wetland associated

458   reed bunting *Emberiza schoeniclus* was removed (χ^2 = 14.9, *P* = 0.0001), so the mechanisms behind

459   this pattern need further exploration. The more negative population trends of granivorous and

460   ground nesting birds in urban areas are discussed below.

461   <u>4.3 Reasons for declines in woodlands and urban areas</u>

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462   Although our results suggest that species effects are more important than habitat effects, we do find

463   support for consistent variation in trends between habitats. Declines were particularly evident in

464   woodland habitats and urban/ suburban settlements, the latter contrasting with more positive

465   trends in rural settlements. These differences were not due to differences in species composition

466   between habitats, as these patterns remained when the analysis was repeated only including species

467   found in all habitats (Fig. A3).

468   While declines in woodland bird populations have been noted previously (Hewson and Noble 2009),

469   the strong negative population trends of birds in urban/ suburban areas contrasts with trends in

470   rural settlements, and is the first time that such a difference has been documented in UK bird

471   populations, but reflects wider evidence that urbanisation is associated with negative impacts on

472   biodiversity (Aronson et al. 2014). Interestingly, despite negative overall population trends, large

473   numbers of species were increasing in urban/ suburban areas, suggesting that environmental change

474   there is creating both winners and losers. Indeed, population trends of nationally increasing species

475   were comparable to the average across all habitats, with the overall negative trend instead driven by

476   nationally declining species having more negative population trends in urban settlements than in

477   other habitats (Fig 1d). Population declines were most evident in strong urban specialists (Jacobs

478   index > 0.25) and species not positively associated with urban settlements (Jacobs index ≤ 0), while

479   declines were not evident in species moderately associated with urban settlements (Jacobs index >0

480   and ≤ 0.25).

481   Population trends of granivorous and ground nesting birds were more negative in urban areas in

482   both mixed and phylogenetic models. A number of granivorous and/ or ground-nesting species

483   typical of open farmland, such as linnet *Carduelis cannabina*, skylark *Alauda arvensis*, meadow pipit

484   *Anthus pratensis* and yellowhammer *Emberiza citrinella*, were declining especially strongly in urban

485   areas (Appendix B). These changes could be due to loss of urban wastelands for brownfield

486   development, decline in the quality of open habitats in and bordering urban/ suburban areas, or a

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487 density dependent shift in habitat preferences towards higher quality habitats outside urban areas

488 as national populations decline (Sullivan et al. 2015). Although we did not specifically examine

489 population trends of species nesting in cavities in buildings, house sparrows *Passer domesticus* and

490 common swifts *Apus apus*, which both nest in or on buildings, were both declining more strongly in

491 urban and suburban areas compared to other habitats. Both these species may be affected by

492 renovations to buildings reducing the availability of cavities (Shaw et al. 2008).

493 General drivers that could be operating in urban and suburban areas include increased infilling of

494 green space with houses (Evans et al. 2009), predation by cats (Beckerman et al. 2007), disease

495 transmission at garden bird feeders (Robinson et al. 2010) and increased noise and light pollution

496 (Francis et al. 2009). Similar drivers are likely to be operating in urban areas across Europe, so

497 declines in urban bird populations may be evident in other countries. Further work will be important

498 to evaluate the role of these habitat-level drivers in urban and suburban areas.

499 Apart from the main patterns apparent across all habitats, population trends in woodland did not

500 vary strongly with species traits. For example, species associated with both the shrub layer (e.g.

501 common whitethroat *Sylvia communis*, European robin *Erithacus rubecula*) and with mature trees

502 (e.g. nuthatch *Sitta europaea*, great spotted woodpecker *Dendrocopos major*) had less positive

503 population trends in deciduous woodlands than other habitats. Populations of both nationally

504 increasing and nationally declining species tended to be more negative in woodlands than in other

505 habitats, supporting the importance of general drivers of declines in woodland. However, declines

506 were more severe in species that did not positively select woodland (Jacobs index ≤ 0), meaning that

507 declines in woodland were stronger for generalist species and specialist species associated with

508 other habitats than for woodland specialists. This may indicate that declining non-woodland

509 specialists are retracting to their preferred habitats (Sullivan et al. 2015). However, population

510 trends of deciduous woodland specialists were still negative, and may be more severe than indicated

511 by this study as populations of woodland specialists underwent large declines prior to the start of

512   the BBS (Defra 2013). Candidate drivers include increased deer browsing (Newson et al. 2012),

513   eutrophication, canopy shading, and reduction in the shrub layer, with associated taxonomic

514   homogenisation of woodland floor plant communities (Keith et al. 2009) and increases in grass

515   species at the expense of herbs (Corney et al. 2008). These changes may be responsible for declines

516   in species using the understory and shrub layer of woodlands (Hewson and Noble 2009), with

517   changes in canopy shading hinting at changes in woodland structure that may have influenced

518   arboreal species. Population trends of woodland birds, as revealed by the woodland birds indicator,

519   are similar in many parts of Europe (Gregory et al. 2007), so the declines noted here may be evident

520   in other European countries. However, trends of woodland birds in central and eastern Europe are

521   stable in contrast to a declining indicator elsewhere (Gregory et al. 2007). Two differences between

522   these areas and the UK are lower densities of deer in continental Europe (Burbaitė and Csányi 2010)

523   and a higher nitrogen inputs in farming (and thus potentially greater eutrophication of woodland) in

524   western Europe compared to eastern Europe (Liu et al. 2010).

525   Population trends in farmland were more positive than those in some other habitats. However, the

526   trends produced here are relative to a baseline of the beginning of the BBS in 1994, when farmland

527   bird populations were already low following steep declines between the mid-1970s and mid 1980s

528   (Defra 2013). Ongoing declines in some species are evident, however, with $1/4^{th}$ of species declining

529   in farmland. Indeed, the generally positive population trends of species in farmland is likely to be

530   driven by generalist species, as restricting the analysis to species with a strong preference for

531   farmland (i.e. Jacobs index > 0.25) resulted in a negative overall population trend in mixed farmland

532   and a stable overall population trend in arable farmland.

533   4.4 Comparison with indicators

534   Different patterns were revealed by analysing habitat-specific population trends compared to

535   species-based indicators. Although there has been a long term decline, the woodland bird indicator

536   has largely been stable since the beginning of the BBS in 1994 (Defra 2013), although this national

537   assessment masks declines in woodland specialists, particularly in southern Britain, which are largely

538   offset by increases further north (Massimino et al. 2015). However, habitat-specific trends of

539   woodland birds have declined in this period. In contrast, both the farmland and wetland bird

540   indicator trends have decreased over the BBS period (Defra 2013), while habitat-specific trends have

541   been positive over this period. A key difference between indicators and habitat-specific trends is

542   that the former contains habitat specialists (Renwick et al. 2012), while the latter also includes

543   populations of generalists using that habitat. While many farmland specialists are declining, many

544   generalist species associated with farmland are increasing (Massimino et al. 2015). Therefore, while

545   around 1/4th of species for which farmland-specific population trends were calculated were

546   declining, these were offset by increases in other species. Restricting our analysis to habitat

547   specialists resulted in habitat-specific trends of woodland species being less negative or even

548   positive, while trends in farmland became less positive or even negative (Fig. A2), supporting this

549   explanation for differences between our results and wild bird indicators. For many applications

550   indicators will be more relevant, as they focus on population trends of habitat specialists that are

551   likely to be greater conservation priorities than generalists. However, analysis of habitat-specific

552   trends sheds light onto the differing fortunes of a wider suite of species in different habitats and

553   may therefore indicate previously undescribed patterns of environmental change. They are also

554   likely to be particularly useful to monitor habitats with few specialists.

555   4.5 Conclusions and conservation implications

556   Producing habitat-specific trends for birds in the UK has revealed considerable differences in

557   population trends between habitats, with notable declines in birds in woodland and in urban/

558   suburban areas. Population trends were largely driven by species-scale effects, particularly related

559   to migratory strategy, with consistent declines in species that winter in the humid zone of Africa.

560   However, variation in the strength of trait effects between habitats suggests that processes

561   operating in certain habitats can enhance or reduce the effects of larger-scale drivers operating

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562   across habitats. For example, reduced declines in humid-zone migrants in northern and less seasonal

563   habitats was consistent with potential impacts of phenological mismatch. Importantly, the general

564   consistency in the direction of trait effects indicates that while declines of certain groups of species

565   were less severe in certain habitats, populations were still declining in these habitats, so they are

566   unlikely to provide a refuge for these species.

567   It is important to assess whether large-scale drivers of population decline are also dominant in other

568   taxa, as our results are from highly mobile species living in fragmented landscapes, where large-scale

569   drivers may be more important. Indeed, our results contrast with two previous studies that suggest

570   habitat-level effects are more important than species-level effects in explaining population declines

571   in mammals (Cowlishaw et al. 2009; Fisher et al. 2003). However, our results may be used to infer

572   that, for UK birds at least, habitat-specific conservation solutions to large-scale population declines

573   may have only limited success. Certainly devising conservation strategies to address large-scale

574   drivers of population change acting across habitats, such as the impacts of climate change or

575   declines in long-distance migrants, will be challenging, but research in this area is of upmost

576   importance. However, given strong declines in woodland and urban birds, there is an urgent need

577   for further work to understand their causes. Whilst our findings for woodland birds are not novel

578   (Hewson and Noble 2009), we believe that the negative trends we have identified for urban

579   populations of species are, and should be urgently examined and addressed as an emerging signal of

580   environmental degradation, particularly as it is in such environments that the greatest proportion of

581   people encounter biodiversity.

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765 **Tables**

766 **Table 1.** Hypothesised trait-habitat interactions. Predictions that were found to be supported are
767 shown in bold.

Trait	Mechanism leading to interaction	Predicted interactions
Migratory	(1) Consequences of phenological mismatch less	**(1.1) Declines of long-distance**

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strategy	severe in habitats with more stable resource environments (Both et al. 2010) or in cooler habitats were spring arrives later.	**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.

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781 **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

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	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.

Figures

Figure 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.