

1 **TRAIT CORRELATES OF CLIMATIC NICHE TRACKING IN BRITISH BIRDS**

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24 **ABSTRACT**

25 Growing evidence indicates that species respond idiosyncratically when exposed to the  
26 same changes in climate. As a result, understanding the potential influence of biological  
27 traits on species' distributional responses is a research priority. Yet, empirical support  
28 for hypothesised influences of traits on climate change responses remains equivocal.

29 In this paper, we developed a novel approach to determine whether biological  
30 traits predict the degree of climatic niche tracking of British breeding birds in response  
31 to recent climate change. First, we quantified how well predicted positive and negative  
32 changes in probability of presence from climate-based species distribution models  
33 agreed with observed local gains and losses in species' occupancy – our measure of  
34 climatic niche tracking. Second, we examined whether the degree of climatic niche  
35 tracking could be predicted by species' ecological and life-history traits, as well as  
36 phylogenetic relationships.

37 Overall, British breeding birds displayed a low degree of climatic niche tracking  
38 over the period of our study, though this varied substantially among species. Models  
39 incorporating traits and phylogeny explained a low proportion of the variation in climatic  
40 niche tracking. Nevertheless, we did find statistical evidence that species with lower  
41 lifespans tracked their climatic niches more closely, whilst species with a mixed diet  
42 displayed a lower degree of climatic niche tracking.

43 We present here a tractable approach for quantifying the degree to which  
44 observed local range gains and losses can be related to climate redistribution and apply  
45 it to British breeding birds. Although we do not find strong evidence that traits predict the  
46 degree of climatic niche tracking, we discuss why this is likely to be a consequence of

47 the features of our study system rather than the approach itself. We believe this  
48 approach may prove to be useful as datasets of temporal changes in species  
49 distributions become increasingly available.

50

51 **Keywords:** climatic niche tracking, species distribution models, traits, climate change,  
52 range shifts, birds, temporal validation

53

## 54 INTRODUCTION

55 Global climatic conditions are changing rapidly and further dramatic changes are  
56 projected for this century (IPCC, 2013). Spatial and temporal variability in rates of  
57 change lead to the continuous redistribution of climatic conditions across the globe  
58 (Loarie *et al.*, 2009). If species have evolved physiological adaptations to local climatic  
59 conditions (Phillimore *et al.*, 2010), they may respond to climate change by either  
60 migrating to track their existing climatic associations, persisting *in situ* within altered  
61 climatic conditions through plasticity or adaptation, or becoming locally extinct (La Sorte  
62 & Jetz, 2012). Understanding how species respond to climate redistribution is critical for  
63 improving our forecasts of species' future responses and the conservation value of our  
64 mitigation actions.

65 It is now clear that animal species are responding idiosyncratically to changes in  
66 climate (Chen *et al.*, 2011; Rapacciuolo *et al.*, 2014a), as they did in the Pleistocene  
67 (Stewart, 2008; Hofreiter & Stewart, 2009). As a result, a growing body of theory  
68 focuses on the potential influence of biological traits on the distributional responses of  
69 species to climate change (Williams *et al.*, 2008; Foden *et al.*, 2013). While substantial

70 progress in this area has been achieved for ectothermic vertebrates (Buckley, 2010;  
71 Huey *et al.*, 2012), empirical support toward trait-based hypotheses of climate change  
72 responses in endotherms remains contrasting (Angert *et al.*, 2011; Cahill *et al.*, 2013;  
73 McCain & King, 2014). One reason for this may be that the majority of studies to date  
74 have focused on related but slightly different questions. Some have focused on trait  
75 correlates of overall distributional response or vulnerability, without specific attention to  
76 climate responses (Angert *et al.*, 2011; Pocock, 2011; Bradshaw *et al.*, 2014). These  
77 studies are of limited use for understanding trait effects on climate responses since  
78 these responses are confounded with responses to additional synergistic drivers of  
79 change. Other studies, while focusing on climatic associations, typically focus on  
80 changes in species' geographic ranges as a whole (Kharouba *et al.* 2009, Dobrowski *et*  
81 *al.* 2011, Smith *et al.* 2013; but see McCain and King 2014). However, migration,  
82 persistence, and extinction are not mutually exclusive responses to climate change  
83 across the range of a single species (Tingley *et al.*, 2012; Rapacchiolo *et al.*, 2014a;  
84 Rowe *et al.*, 2014). Instead, overall species' trends result from the net demographic  
85 impacts of these three possible responses (Angert *et al.*, 2011). Identifying local  
86 responses independent of overall trends is a crucial step towards a comprehensive  
87 spatially-explicit assessment of species' vulnerability to climate change. This is  
88 especially important given that synergistic drivers of change (e.g. land use change and  
89 extreme disturbance events) also impact biodiversity heterogeneously across space  
90 and may exacerbate local vulnerability (Turner, 2010).

91 In this paper, we overcome some of the limitations of existing studies by using a  
92 recently-published method (Rapacchiolo *et al.*, 2014b) to spatially quantify the

93 agreement between observed range changes and predictions based on climate  
94 redistribution – a spatially-explicit measure of climate niche tracking. Our objectives  
95 were to examine whether British breeding birds are tracking their climatic niches over  
96 time and whether biological traits are related to the degree of climatic niche tracking.  
97 First, we built climate-based species distribution models and generated predictions of  
98 change in the probability of presence of bird species based on the redistribution of each  
99 species' historical climatic niche across Great Britain. Second, we quantified how the  
100 agreement between these predictions and observed species' gains and losses over the  
101 same time interval varied spatially throughout species' geographic ranges. British  
102 breeding birds are one of only a handful of systems enabling such analyses at a large  
103 spatial scale, since their distributions have been sampled comprehensively at repeated  
104 time intervals across all of Great Britain's 10-km Ordnance Survey National Grid  
105 squares (Sharrock, 1976; Gibbons *et al.*, 1993). Given this unusually-constant sampling  
106 effort over time and space, we were able to derive estimates of local range gains and  
107 losses over an approximately 30-year period and relate them to climate redistribution  
108 over the same spatial and temporal scale.

109 Finally, because the degree to which species track their climatic conditions is  
110 likely to depend on their particular ecological and life-history traits (Williams *et al.*, 2008;  
111 Huey *et al.*, 2012; Foden *et al.*, 2013), we tested four hypotheses of the effect of traits  
112 on climatic niche tracking. We hypothesised that: (i) more mobile species which can  
113 disperse greater distances would be better able to track their climatic niches across  
114 newly-suitable areas (Schloss *et al.*, 2012); (ii) species with faster life histories would be  
115 better able to track their climatic niches due to their higher intrinsic rate of population

116 growth and resulting ability to recover quickly from low numbers (Angert *et al.*, 2011;  
117 Auer & King, 2014); (iii) habitat specialists would be less able to track their climatic  
118 niches given their greater difficulty in establishing populations in new habitats and/or  
119 keeping high numbers under altered conditions (Angert *et al.*, 2011). (iv) higher-trophic-  
120 level species would display less climatic niche tracking given the higher number of  
121 trophic links separating them from the direct effects of climate on primary producers  
122 (Huntley *et al.*, 2004). Furthermore, we tested for phylogenetic signal in climatic niche  
123 tracking in order to assess whether additional attributes of species not captured by our  
124 traits could be associated with variation in climatic niche tracking.

125

## 126 **METHODS**

### 127 **Species distribution data**

128 We used occupancy records for 226 British breeding birds at a 10-km grid square  
129 resolution in two time periods of intensive recording effort ( $t_1$ : 1968–1972;  $t_2$ : 1988–  
130 1991), each leading to the publication of a national breeding bird atlas (Sharrock, 1976;  
131 Gibbons *et al.*, 1993). To avoid problems related to building models with extremely  
132 small sample sizes (Wisz *et al.*, 2008), we excluded 43 species occupying fewer than  
133 20 grid squares in either time period. We excluded a further 71 predominantly-aquatic  
134 species (i.e. marine birds, waterfowl, and shorebirds), given the substantial difficulties in  
135 defining local range gains/losses for these species. Although species' absence from  
136 each 10–km grid square was not recorded during sampling, 98 – 100% grid squares in  
137 Great Britain were sampled meticulously during both time periods, with high levels of  
138 replicate recording and under-recorded areas targeted by extra recording schemes

139 (Sharrock, 1976; Gibbons *et al.*, 1993). Thus, we assumed that each surveyed grid  
140 square in which a species was not recorded represented an absence. However,  
141 preliminary analysis indicated that model fit was particularly low in coastal grid squares  
142 with very little land cover. Based on these results, we excluded grid squares with less  
143 than 10% land cover. We therefore proceeded to analyse presence-absence data for  
144 112 bird species across 2603 of Great Britain's 10-km grid squares at two time periods.

145

### 146 **Observed range changes**

147 We compared species' occupancy ( $y$ ) between  $t_1$  and  $t_2$  across grid squares to identify  
148 observed changes in occupancy ( $\Delta y$ ) – including instances of gain (where  $y_{t1} = 0$  and  $y_{t2}$   
149 = 1), persistence (where  $y_{t1} = 1$  and  $y_{t2} = 1$ ) and loss (where  $y_{t1} = 1$  and  $y_{t2} = 0$ ) – as well  
150 as areas that remained unoccupied (where  $y_{t1} = 0$  and  $y_{t2} = 0$ ).

151

### 152 **Climate predictors**

153 We obtained data on four climate variables – mean temperature of the coldest month  
154 (°C), mean temperature of the warmest month (°C), ratio of actual to potential  
155 evapotranspiration (standard moisture index), and total annual precipitation (mm) – from  
156 the Climate Research Unit ts2.1 (Mitchell & Jones, 2005) and the Climate Research  
157 Unit 61-90 (New *et al.*, 1999). We chose these variables to reflect known climatic  
158 constraints on bird distributions (Lennon *et al.*, 2000; Illán *et al.*, 2014). In each grid  
159 square, we calculated the mean value of each predictor over the periods 1966 – 1972  
160 and 1986 – 1991, corresponding to  $t_1$  and  $t_2$ , respectively, with two years tagged onto  
161 the start. We included these additional years since the presence-absence of birds in a

162 particular breeding season is likely to depend on the climate of previous years (Araújo  
163 *et al.*, 2005; Bradshaw *et al.*, 2014).

164

### 165 **Climatic niches and climate redistribution**

166 We estimated the realised climatic niches of bird species by correlating presence-  
167 absence data with climate variables in period  $t_1$  using generalised boosted models  
168 (GBMs; Ridgeway 1999). We chose GBMs as they were the most temporally-  
169 transferable single method in a previous study of climatic associations in British birds  
170 (Rapacciuolo *et al.*, 2012) and perform consistently-well in additional studies of temporal  
171 transferability (Dobrowski *et al.*, 2011; Smith *et al.*, 2013). We fitted these models using  
172 the *gbm* package (Ridgeway, 2013) in R version 3.1.3 (R Core Team, 2014). We used  
173 custom code provided by Elith *et al.*, (2008) to identify the optimal number of trees to be  
174 fitted in each model and avoid over-fitting calibration data. This code performs a 10-fold  
175 cross-validation procedure for each 50-tree increment, checking for improvements in  
176 calculated deviance on held-out data. Final models were fitted using the optimal number  
177 of trees identified through cross-validation (with a minimum of 1000 trees), 5 nodes, a  
178 learning rate of 0.001, and a bag fraction of 0.5. We assessed model fit in  $t_1$  using the  
179 area under curve (AUC) of the receiver operating characteristic function (Hanley &  
180 McNeil, 1982) – a measure of discrimination – and the point biserial correlation (COR)  
181 (Elith *et al.*, 2006) – the Pearson correlation between observations and predictions. We  
182 calculated these measures of fit by averaging their values over each of the 10 folds held  
183 out during model calibration.



184 We used the realised climatic niches identified in  $t_1$  to generate (i) modelled  
185 estimates of probability of presence in  $t_1$  ( $m_{t1}$ ) based on climate predictor values for that  
186 period, and (ii) modelled estimates of probability of presence in  $t_2$  ( $m_{t2}$ ) after updating  
187 climate predictor values to reflect the redistribution of climatic conditions in  $t_2$ . We then  
188 estimated change in modelled probability of presence given the redistribution of climatic  
189 conditions ( $\Delta m$ ) by subtracting  $m_{t1}$  from  $m_{t2}$ . It is important to note that the predicted  
190 probability that a species will shift its range is not only conditional on its modelled  
191 change in probability of presence but also on its baseline probability of presence  
192 (Rapacciuolo *et al.*, 2014b). As a result, we weighted  $\Delta m$  values relative to  $m_{t1}$  ( $\Delta m_w$ ;  
193 calculated by dividing negative  $\Delta m$  values by  $m_{t1}$  and positive  $\Delta m$  values by  $1 - m_{t1}$ ).  
194  $\Delta m_w$  values range from -1 – a 100% loss in predicted probability of presence to 1 – a  
195 100% gain in probability of presence.

196

## 197 **Climatic niche tracking**

### 198 *Temporal validation plots*

199 We estimated the relationship between observed changes in occupancy ( $\Delta y$ ) and  
200 predicted changes given climate redistribution ( $\Delta m_w$ ) throughout the study area using  
201 temporal validation (TV) plots (Rapacciuolo *et al.*, 2014b). The approach of TV plots is  
202 illustrated in Figure 1. For a given species, TV plots quantify the agreement between the  
203 probability of observing instances of loss, persistence, or gain (collectively,  $\Delta y$  values)  
204 and changes in modelled probability of presence given the redistribution of climate  
205 variables (negative and positive  $\Delta m_w$  values) throughout study sites. They do so by  
206 fitting two non-parametric functions with a logit link. The *loss* function (red line; Fig. 1c)

207 models the probability that a grid square is lost from the species' distribution (1; red tick  
208 marks in bottom rug plot of Fig. 1c) or not (0; all non-loss observations, expect stable  
209 absences, which cannot experience additional loss) as a function of  $\Delta m_w$  values. In  
210 parallel, the *gain* function (blue line; Fig. 1c) models the probability that a grid square  
211 has been gained (1; blue tick marks in top rug plot of Fig. 1c) or not (0; all non-gain  
212 observations, expect persistence observations, which cannot experience additional  
213 gain) as a function of  $\Delta m_w$  values. By subtracting the loss from the gain function to  
214 calculate a single curve (continuous black line; Fig. 1c), TV plots estimate the relative  
215 probability that sites are observed to be gained, remain stable (neither gained nor lost),  
216 or be lost for any given value of  $\Delta m_w$  across the modelled range of  $\Delta m_w$  values (see  
217 Rapacciuolo et al., 2014b for additional details).

218

### 219 *Measuring climatic niche tracking*

220 Assuming that changes in climate fully drive observed range changes and the  
221 processes of local gain and loss are unlimited and instantaneous (i.e. there are no time  
222 lags) every site with a predicted  $\Delta m_w$  value of -1 should be observed to be lost whilst  
223 every site with a predicted  $\Delta m_w$  value of 1 should be observed to be gained. Although  
224 there is an infinite number of monotonically-increasing curves connecting these two  
225 points, an ideal expectation for perfect niche tracking can be defined as a 1:1 line  
226 between observed and predicted changes passing from the origin (dashed black line;  
227 Fig. 1c). This line represents an ideal expectation for perfect niche tracking since it  
228 reflects the condition where every modelled  $\Delta m_w$  value exactly equals the probability of  
229 observing a given change.

230 Based on this assumption, we quantified climatic niche tracking using  
231 Rapacciuolo *et al.* (2014b)'s accuracy of temporal validation ( $Acc_{TV}$ ), which accounts for  
232 the deviation between the ideal expectation and the modelled relationship between  
233 observed and predicted changes (the TV curve).  $Acc_{TV}$  is given by the mean absolute  
234 deviation between the ideal and the TV curve across all grid squares (Fig. 2), subtracted  
235 from 1 (Rapacciuolo *et al.*, 2014b).  $Acc_{TV}$  values of 1 indicate perfect climatic niche  
236 tracking, whilst values  $< 1$  indicate progressively lower tracking.

237 We tested whether  $Acc_{TV}$  values derived from temporal validation plots reliably  
238 measured climatic niche tracking using simulation (Appendix S1). We simulated range  
239 changes in a virtual species over a 2600-site artificial landscape based on change in  
240 two uniformly-distributed random climate covariates. We simulated varying scenarios of  
241 climatic niche tracking by modifying the degree to which range changes in the virtual  
242 species were determined by the specified functional response to climate. As expected,  
243 when the specified climate functional response fully determined the virtual species'  
244 range changes (i.e. perfect climate niche tracking),  $Acc_{TV}$  values had a mean ( $\pm$   
245 standard deviation) of  $0.94 \pm 0.01$  (based on 999 simulation runs; Appendix S1, Fig. 1).  
246  $Acc_{TV}$  values decreased progressively with climatic niche tracking; values of  $0.41 \pm 0.03$   
247 were associated with scenarios where 100% of the virtual species' range changes were  
248 random with respect to climate change.

249 Since temporal validation plots use changes in modelled probability of presence  
250 weighted by baseline probability of presence ( $m_{t1}$ ), they may be sensitive to errors in  
251 model calibration in  $t_1$ . For instance, say we have a site where  $m_{t1} = 0.8$  but the species  
252 is absent in  $t_1$  ( $y_{t1} = 0$ ): even a small increase in probability of presence in  $t_2$  ( $\Delta m = 0.1$ )

253 will lead to a large weighted modelled change ( $\Delta m_w = 0.1/(1 - 0.8) = 0.5$ ) and, thus, a  
254 large deviation from observed change if the species remains absent ( $y_{t_2} = 0$ ). As a  
255 result, we also used our simulation to examine the effect of calibration errors on  $\text{Acc}_{\text{TV}}$   
256 values (Appendix S1). Keeping the degree of niche tracking constant, we found that  
257  $\text{Acc}_{\text{TV}}$  values were indeed sensitive to calibration errors and decreased with calibration  
258 accuracy (Appendix S1, Fig. S2). However, relatively large errors in model calibration  
259 ( $\text{AUC} = 0.70 \pm 0.01$ ;  $\text{COR} = 0.36 \pm 0.02$ ) were necessary to substantially affect  $\text{Acc}_{\text{TV}}$   
260 values ( $\leq 0.85$ ) when tracking was perfect. Thus, to remove the confounding effect of  
261 calibration error on  $\text{Acc}_{\text{TV}}$  values, we selected conservative thresholds for  $t_1$  AUC and  
262 COR representing acceptable calibration errors based on our simulations ( $\text{AUC} = 0.8$ ;  
263  $\text{COR} = 0.4$ ). We then excluded all species with calibration AUC and COR values below  
264 these thresholds (18 out of 112 species).

265

## 266 **Effect of phylogeny and traits on climatic niche tracking**

### 267 *Phylogenetic signal*

268 We used a recently-published molecular phylogeny (Thomas, 2008; Cassey *et al.*,  
269 2012) to identify evolutionary relationships among 109 species from the full set of 112.  
270 We tested whether closely-related species tended to have more similar  $\text{Acc}_{\text{TV}}$  values  
271 than species drawn at random from the phylogeny by estimating the maximum  
272 likelihood value of Pagel's  $\lambda$  (Pagel, 1999).  $\lambda$  measures the agreement between  
273 observed trait variation across a phylogeny and a pure Brownian model of evolution  
274 (Freckleton *et al.*, 2002); it ranges from 0 for phylogenetic independence to 1 for  
275 phylogenetic dependence. Importantly, we accounted for measurement error in  $\text{Acc}_{\text{TV}}$

276 values by incorporating within-species standard errors in our estimation of  $\lambda$  (Ives *et al.*,  
277 2007). We estimated  $\lambda$  values using the function `phylosig` in the R package `phytools`  
278 (Revell, 2012).

279

### 280 *Biological traits*

281 To test our four trait-based hypotheses, we obtained data on four biological traits of  
282 British birds: natal dispersal, adult survival, trophic level and species specialization  
283 index (SSI). We obtained natal dispersal estimates (in km) from Barbet-Massin *et al.*  
284 (2012). These estimates were obtained directly or extrapolated from published  
285 estimates of mean straight-line distance (in km) between the location birds were ringed  
286 in their year of birth and the location in which they were recovered at first breeding age  
287 (Paradis *et al.*, 1998). We chose adult survival – calculated as the average proportion of  
288 birds of breeding age surviving each year (Robinson 2005) – as our measure of life-  
289 history speed. We also considered body size and reproductive output as additional  
290 measures of life-history speed but, given the high inter-correlation among the three  
291 variables, we only kept adult survival. We generated a factor variable for trophic level by  
292 placing each species into one of 5 categories (modified from Huntley *et al.* 2004): (i)  
293 exclusively herbivorous species; (ii) herbivorous/insectivorous species, with  
294 predominantly herbivorous diet; (iii) herbivorous/insectivorous species, with  
295 predominantly insectivorous diet; (iv) insectivorous species and carnivorous species  
296 predominantly consuming herbivorous prey; (v) carnivorous species predominantly  
297 consuming carnivorous prey. Finally, we estimated species' habitat specialization using  
298 the species specialization index (SSI), a measure of evenness in habitat affinity

299 (Devictor *et al.*, 2008b). The higher the SSI, the more specialised a species. SSI values  
300 were calculated by Le Viol *et al.* (2012) for 99 of the species in our final dataset, based  
301 on the coefficient of variation in habitat affinity across 98 habitat categories in Europe  
302 (Le Viol *et al.*, 2012).

303

#### 304 *Trait models*

305 We examined whether biological traits could predict variation in climatic niche tracking,  
306 as measured by  $Acc_{TV}$ . Because shared natural history among our set of species  
307 unaccounted by the modelled traits may lead more phylogenetically-related species to  
308 respond more similarly, modelling individual species as statistically-independent units  
309 may lead to biased results. Therefore, we accounted for shared phylogenetic history in  
310 our trait models using phylogenetic generalised least squares (PGLS) models – as  
311 implemented in the R package CAPER (Orme *et al.*, 2011) – which incorporate  
312 covariances between species into the model's error term. To avoid under- or over-  
313 correcting for phylogenetic autocorrelation, we estimated the degree of phylogenetic  
314 dependence in model residuals by estimating the maximum-likelihood value of Pagel's  $\lambda$   
315 (Pagel, 1999) simultaneously with the other model parameters.

316 We constructed a PGLS model set including all possible combinations of the  
317 single and additive effects of natal dispersal, adult survival, trophic level and SSI, as  
318 well as an intercept-only model. We standardised all continuous predictors in each  
319 model (by subtracting the mean and dividing by the standard deviation); effect sizes  
320 obtained this way provide a measure of the importance of each predictor on the  
321 response (Schielzeth, 2010). All PGLS models assumed normally-distributed model

322 residuals; visual inspection of residuals vs fitted values plots and quantile-quantile plots  
323 confirmed that no model violated this assumption.

324 In order to derive reliable estimates of the sign and magnitude of the effect of  
325 each predictor based on the full set of potential trait models, we employed multimodel  
326 inference (Burnham & Anderson, 2004; Johnson & Omland, 2004). We first ranked all  
327 potential models using the Akaike Information Criterion correction for small sample  
328 sizes (AICc; Burnham and Anderson 2002). For each model in the full set, we quantified  
329 the probability that it was the best model given the data using AICc weights ( $AIC_w$ ), and  
330 its structural goodness-of-fit using adjusted  $R^2$ . Taking each predictor in turn, we then  
331 considered the full set of models in which the predictor appeared and calculated: i) its  
332 relative importance, by summing the  $AIC_w$  values across the model set ( $\sum AIC_w$ ), and ii)  
333 model-averaged coefficients and standard errors by averaging coefficients across all  
334 models in the set that included the focal variable, weighted by each model's  $AIC_w$   
335 (Johnson & Omland, 2004). For predictor coefficient averages,  $AIC_w$  values were  
336 recalculated over all models in which each predictor appeared, in order to make sure  
337  $AIC_w$  values used for weighting added up to 1.

338

## 339 **RESULTS**

### 340 **Climatic niches and climate redistribution**

341 When assessed against held out presence-absence data in  $t_1$ , our models showed  
342 excellent discrimination (AUC; mean  $\pm$  standard deviation =  $0.90 \pm 0.06$ ; see Fig. S1 in  
343 supporting information) and correlation (COR;  $0.60 \pm 0.20$ ). However, 18 (out of 112)  
344 species did exceed our simulation-based thresholds for acceptable error during model

345 calibration (AUC < 0.8; COR < 0.4), so we only considered the remaining 94 species in  
346 further analyses.

347 When projected on updated climate values in  $t_2$ , the mean discriminatory power  
348 and correlation of our models both decreased (AUC:  $0.86 \pm 0.08$ ; COR:  $0.53 \pm 0.17$ ; Fig.  
349 S1). We examined the pattern of grid square-wise mean predicted change in probability  
350 of presence ( $\Delta m_w$ ) across all species and found that the majority of grid squares across  
351 Great Britain were predicted to have a positive mean  $\Delta m_w$  (i.e. overall gains; see Fig.  
352 S2). Mean  $\Delta m_w$  values were highest in the highlands of Wales and western Scotland –  
353 where total precipitation increased most and standard moisture decreased least (Figure  
354 S3a, b) – and lowest in the Shetland Islands and south-eastern England – where mean  
355 temperatures increased most (Fig. S3c, d).

356

### 357 **Climatic niche tracking**

358 The degree of climatic niche tracking among the 94 British bird species was low overall  
359 ( $\text{Acc}_{\text{TV}}$ :  $0.52 \pm 0.20$ ; Fig. 3). When compared with our simulation results, the observed  
360 mean  $\text{Acc}_{\text{TV}}$  for British birds approached the value derived from scenarios where only  
361 10% of the virtual species' range changes were determined by climate (Appendix S1,  
362 Fig. S1). However, observed  $\text{Acc}_{\text{TV}}$  values varied considerably among bird species, with  
363 a number of species tracking their climatic niches closely and others shifting their  
364 ranges irrespective of or even opposite to climatic expectations (Fig. 3).

365

### 366 **Effect of phylogeny and traits on climatic niche tracking**



367 We limited our comparative analyses to 70 species with complete phylogenetic and trait  
368 information, as well as low calibration error (there was no significant difference in  $Acc_{TV}$   
369 distribution between this subset and the set of 94 species of Fig. 3;  $t_{144} = -0.54$ ,  $p =$   
370  $0.59$ ; Fig. S4). After accounting for uncertainty due to measurement error, the  
371 phylogenetic signal in  $Acc_{TV}$  values was not significantly different from 0 ( $\lambda = 0$ ;  $p = 1$ ).  
372 Although a low phylogenetic signal may suggest the use of PGLS models is  
373 unwarranted, the phylogenetic signal in the residuals of trait models was not null (upper  
374 95% confidence intervals of maximum-likelihood lambda values across trait models  
375 ranged from 0.17 – 0.29; Table 1). As a result, we proceeded by running phylogenetic  
376 trait models and present the results from these models below. However, we also ran  
377 non-phylogenetic generalised linear models (GLMs) for comparison. Given the minimal  
378 phylogenetic correction applied in PGLS models (Table 1), differences from GLMs were  
379 negligible (Tables S2, S3).

380 The best-supported trait model had a relatively low AICc weight ( $AIC_w = 0.283$ ;  
381 Tables 1, S2), indicating there was no overwhelming support towards any particular trait  
382 model (Johnson & Omland, 2004). Overall, models incorporating phylogeny and traits  
383 explained a very small portion of variation in  $Acc_{TV}$  values, up to a maximum adjusted  $R^2$   
384 of 0.14 (mean-adjusted  $R^2 \pm$  standard deviation:  $0.050 \pm 0.054$ ; Tables 1, S2).

385 Relative importance values supported adult survival as the most important trait  
386 predictor of  $Acc_{TV}$  ( $\sum AIC_w = 0.91$ ; Table 2), with model-averaged coefficients indicating a  
387 negative effect of adult survival on  $Acc_{TV}$  (Table 2). Furthermore, trophic level was also  
388 an important predictor of  $Acc_{TV}$  ( $\sum AIC_w = 0.57$ ); species with a mixed  
389 herbivorous/insectivorous diet had lower  $Acc_{TV}$  values compared to exclusively-

390 herbivorous and exclusively-carnivorous species (Table 2). We found no support for an  
391 effect of natal dispersal or SSI on  $Acc_{TV}$  (Tables 2, S4).

392

## 393 **DISCUSSION**

394 Evidence that species are responding individually to the same changes in climate  
395 (Chen *et al.*, 2011; Rapacciuolo *et al.*, 2014a) highlights the key role that biological traits  
396 play in determining distributional responses to climate change (Williams *et al.*, 2008;  
397 O'Connor *et al.*, 2012; Foden *et al.*, 2013). By comparing the redistribution of species'  
398 climatic associations with their recently-observed range gains and losses, we were able  
399 to test a number of hypotheses of the effect of biological traits on species' climatic niche  
400 tracking.

401 Overall, our results indicate that British breeding birds did not track their climatic  
402 niches closely and observed species' range shifts deviated substantially from climate  
403 change expectations over an approximately 30-year period. However, there was high  
404 heterogeneity among species in their degree of climatic niche tracking. A number of  
405 species, whose demographic rates are known to be significantly impacted by climate,  
406 did show a relatively high degree of climatic niche tracking. These included the Pied  
407 White Wagtail (*Motacilla alba*), whose first egg dates and juvenile survival rates  
408 increase with spring temperatures (Mason & Lyczynski, 1980; Crick & Sparks, 1999),  
409 the Merlin (*Falco columbarius*), whose regional declines have previously been linked  
410 with climate change drivers (Ewing *et al.* 2011), and the Blackcap (*Sylvia atricapilla*),  
411 whose overwinter survival rates have been improved by milder winter conditions  
412 (Plummer *et al.* 2015). In contrast, several other species appeared to have shifted

413 irrespective of, or even counter to, climate redistribution. Previous studies over similar  
414 timescales also found high heterogeneity in the degree of climatic niche tracking across  
415 bird species (Gregory *et al.*, 2005; Green *et al.*, 2008; Maggini *et al.*, 2011; La Sorte &  
416 Jetz, 2012). One possible explanation for this pattern is that some species' distributional  
417 responses may lag behind climate change (Menéndez *et al.*, 2006; Devictor *et al.*,  
418 2008a). Indeed, studies over longer timescales suggest that, given enough time, the  
419 overall degree of climatic niche tracking is generally higher (e.g. Tingley *et al.* 2009,  
420 2012). Alternatively, observed distribution changes of British breeding birds over our  
421 study period may not have been primarily driven by climate. For instance, population  
422 declines and range contractions in a number of British bird species are thought to be a  
423 consequence of changes in land-use (Thomas *et al.*, 2004; Eglinton & Pearce-Higgins,  
424 2012). This explains why species such as the Nightingale and the Turtle Dove – which  
425 have been hugely impacted by agricultural intensification and changing farming  
426 practices (Fuller *et al.*, 1995; Browne *et al.*, 2004) – displayed the lowest degree of  
427 climatic niche tracking. Lag effects and alternative drivers of change are only two of the  
428 potential explanations for mismatches between observations and climate-based  
429 predictions. Those and additional factors – such as changing biotic interactions – are  
430 undoubtedly required for a full attribution of observed range shifts. However, a full  
431 attribution of the drivers of recent range shifts was beyond the scope of our study, which  
432 instead focused on distinguishing species whose changes were consistent with climate  
433 predictions from species requiring additional processes. With this objective in mind, we  
434 believe that temporal validation plots and associated measures such as  $Acc_{TV}$  are a

435 useful tool and that their utility should increase as more temporal datasets of species'  
436 distribution shifts become available.

437 Models incorporating both species' traits and phylogeny explained only a small  
438 portion of the variation in climatic niche tracking among British breeding birds. This is in  
439 line with previous studies of the effect of traits on measures of the agreement between  
440 climate-based predictions and observations (McPherson & Jetz, 2007; Angert *et al.*,  
441 2011; Smith *et al.*, 2013). In general, species' responses to climate change are likely to  
442 be complex, idiosyncratic and difficult to predict given the multitude of interacting  
443 biological and environmental factors underlying them (Pimm 2009; Walther 2010;  
444 LaSorte and Jetz 2012). Our models were over-simplistic – limited to a number of  
445 hypotheses based on solid theoretical foundations – and should undoubtedly include  
446 additional processes. For instance, behavioural attributes such as activity times and  
447 nesting behaviour have been posited as important predictors of variation in climate  
448 change responses in mammals (McCain & King, 2014) and represent a fruitful direction  
449 for further theoretical and empirical work. Furthermore, an approach that directly tests  
450 the effects of species' biological traits on climatic niche tracking may be preferable or at  
451 least complementary with the indirect statistic on statistic approach we use here.  
452 However, it is not obvious how one would develop such direct approach without  
453 incurring a significant loss of information from the calculation of assemblage-level trait  
454 summaries (e.g. Douma *et al.*, 2012).

455 Together with the general challenges shared among studies of climate change  
456 responses, a number of factors specific to our study system may underlie the low  
457 explanatory power of our models. Although the British breeding bird data we use here

458 are among the highest quality datasets on spatiotemporal biodiversity changes, their  
459 temporal and spatial extents may not be sufficient to detect climatic niche tracking. First,  
460 a 30-year time interval may not be sufficient to detect substantial distributional  
461 responses to climate changes for most British breeding bird species. While this may be  
462 due to the aforementioned lag effects, it may also simply result from the fact that  
463 climatic conditions in Britain may not have changed sufficiently to generate a response  
464 for most species.  $Acc_{TV}$  estimates may be particularly prone to error for species  
465 experiencing lower magnitudes and extents of climate change. For instance, lower  
466 magnitudes and extents of climate change have been found to bias  $Acc_{TV}$  towards  
467 higher values by leading to intrinsically-lower mean deviations between predictions and  
468 observations (Rapacciuolo *et al.*, 2014b). Despite the low correlation of  $Acc_{TV}$  with both  
469 magnitude (measured as the range of  $\Delta m_w$  values;  $\rho = 0.12$ ) and extent of change  
470 (measured as the total number of observed gains and losses;  $\rho = 0.10$ ), we  
471 acknowledge that variation in these species-specific aspects of climate change  
472 exposure may still have impacted  $Acc_{TV}$  values. In general, we do caution against the  
473 use of temporal validation plots and  $Acc_{TV}$  for comparing among species and  
474 geographical areas with radically different climate change exposures. A second  
475 shortcoming of our particular study system is that Britain may not be a sufficient spatial  
476 extent to detect climate change responses for the species in our dataset, all of which  
477 have breeding ranges extending beyond Britain. Furthermore, Britain constitutes the  
478 northwestern boundary for many of these species' ranges and may not accurately  
479 reflect the entire spectrum of climatic conditions they can occupy. An important  
480 consequence of this is that the climatic niches we estimated are likely to be incomplete

481 for some species. We acknowledge that the failure to capture the full extent of species'  
482 climatic niches may be partially responsible for the deviations we identified between  
483 observed and predicted distribution changes. However, we preferred limiting our study  
484 to the standardised British data rather than incorporating additional European data on  
485 the species' ranges (e.g. EBCC Atlas of European Breeding Birds; Hagemeijer & Blair,  
486 1997) to avoid the perils of integrating data across different spatial and temporal scales  
487 (McPherson *et al.*, 2006; Bombi & D'Amen, 2012). These factors considered, the British  
488 breeding bird dataset we used here may appear as an unsuitable choice for testing  
489 hypotheses of the effect of traits on climatic niche tracking. However, it is one the few  
490 and, arguably, one of the highest-quality datasets that enables performing such tests. If  
491 hypotheses of climatic niche tracking are not testable using the best datasets currently  
492 available, they are in danger of not being testable at this time.

493 Our models did provide evidence that life-history speed and trophic level were  
494 the most important predictors of climatic niche tracking we considered. As  
495 hypothesised, species with lower adult survival were more likely to have tracked their  
496 climatic niches over the time period of our study. A likely explanation for this is that short  
497 generation times and higher rates of population growth lead to a higher likelihood of  
498 rapid expansion and subsequent establishment into newly-suitable areas (Angert *et al.*,  
499 2011; Anderson *et al.*, 2012; O'Connor *et al.*, 2012; Schloss *et al.*, 2012). Our result is in  
500 line with recent findings that life-history speed is positively correlated with population  
501 increase (Robinson *et al.*, 2014) and range expansion (Bradshaw *et al.*, 2014) in British  
502 birds. Conversely, our hypothesis that increasing trophic level would lead to lower  
503 climatic niche tracking due to increasing separation from direct climatic effects was only

504 partially supported. Species from both the lowest (i.e. exclusively-herbivorous species)  
505 and the highest (i.e. exclusively-insectivorous/carnivorous species) trophic levels  
506 tracked their climatic niches more closely than species from intermediate trophic levels  
507 (i.e. mixed herbivorous/insectivorous species). In addition to our original hypothesis, a  
508 number of processes may underlie this result. For instance, evidence from mammals  
509 suggests that carnivores may be better able to track their climatic niches than  
510 herbivores and omnivores due to their higher dispersal velocity (Schloss *et al.*, 2012)  
511 and wider range areas (Carbone *et al.* 2005). Furthermore, our measure of trophic level  
512 may have partially captured species' differences in ecological generalisation, with  
513 mixed-diet generalists potentially displaying a lower degree of climatic niche tracking  
514 due to their lower susceptibility to climate change (Foden *et al.*, 2013). Therefore,  
515 although we did not find evidence of an effect of natal dispersal or habitat specialisation  
516 on climatic niche tracking, it is possible that trophic level may have indirectly captured  
517 part of their hypothesised effects.

518         A further noteworthy result was that the phylogenetic signal in climatic niche  
519 tracking was not significantly different from zero, suggesting that biogeographic  
520 responses to climate change may be highly idiosyncratic among closely-related species.  
521 This pattern does not appear to be limited to British birds. A number of studies  
522 highlighted how congeneric species of birds and mammals are shifting their ranges in  
523 opposite directions (Moritz *et al.*, 2008; Tingley *et al.*, 2012; Rapacciuolo *et al.*, 2014a).  
524 Moreover, several studies reported that accounting for phylogenetic relatedness among  
525 species did not modify their conclusions on the effect of traits on the performance of  
526 climate-based species distribution models (Green *et al.*, 2008; Pöyry *et al.*, 2008;

527 Newbold *et al.*, 2009). However, one study did find a weak but significant phylogenetic  
528 signal to the predicted suitable future climate of European species (Thuiller *et al.*, 2011),  
529 which suggests that phylogeny remains an important factor to consider when assessing  
530 species' vulnerability to climate change. At first glance, our finding of an extremely low  
531 phylogenetic signal appears at odds with the conclusions of Bradshaw *et al.* (2014),  
532 who found a mid-range phylogenetic signal in the change in area of occupancy for 106  
533 British bird species (approximately 62 of which were shared with our 70-species subset;  
534 Bradshaw *et al.* 2014). However, our measure of climatic niche tracking  $Acc_{TV}$  was only  
535 weakly correlated with change in area of occupancy ( $\rho = 0.13$ ), as it was based on local  
536 rather than whole-range area changes. As a result, there is no real reason to expect  
537 congruence in phylogenetic signal among these two studies.

538         Focusing on distribution changes consistent with climate change at the local  
539 scale can unveil patterns of species' sensitivity to climate change which may not be  
540 identified by examining range changes as a whole. We present here a promising  
541 approach for doing so, which uses temporal validation plots and time series of  
542 distribution data to assess how well climate-based models predict observed distribution  
543 gains and losses at individual sites. Though we are unable to provide strong empirical  
544 evidence that biological traits mediate climatic niche tracking in this study, we believe  
545 our approach may prove to be useful in this context as biodiversity datasets at broad  
546 temporal and spatial extents become increasingly available.

547

## 548 **DATA ACCESSIBILITY**



549 The species distribution data used in these analyses can be accessed via the National  
550 Biodiversity Network Gateway (1968–1972: <https://data.nbn.org.uk/Datasets/GA000600>;  
551 1988– 1991: <https://data.nbn.org.uk/Datasets/GA000147>). The climate data can be  
552 accessed via the Climate Research Unit (<http://www.cru.uea.ac.uk/cru/data/hrg/>). The  
553 bird phylogeny can be accessed from the relevant publications (Thomas, 2008; Cassey  
554 *et al.*, 2012). R code to generate temporal validation plots can be found at  
555 <https://github.com/giorap/tv-plots>.

556

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## 565 **REFERENCES**

566 Anderson, A.S., Reside, A.E., Vanderwal, J.J., Shoo, L.P., Pearson, R.G. & Williams,  
567 S.E. (2012) Immigrants and refugees: The importance of dispersal in mediating  
568 biotic attrition under climate change. *Global Change Biology*, **18**, 2126–2134.

569 Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J. & Chunco, A.J.  
570 (2011) Do species' traits predict recent shifts at expanding range edges? *Ecology*  
571 *Letters*, **14**, 677–689.

- 572 Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species-  
573 climate impact models under climate change. *Global Change Biology*, **11**, 1504–  
574 1513.
- 575 Auer, S.K. & King, D.I. (2014) Ecological and life-history traits explain recent boundary  
576 shifts in elevation and latitude of western North American songbirds. *Global  
577 Ecology and Biogeography*, **23**, 867–875.
- 578 Barbet-Massin, M., Thuiller, W. & Jiguet, F. (2012) The fate of European breeding birds  
579 under climate, land-use and dispersal scenarios. *Global Change Biology*, **18**, 881–  
580 890.
- 581 Bombi, P. & D’Amen, M. (2012) Scaling down distribution maps from atlas data: a test  
582 of different approaches with virtual species. *Journal of Biogeography*, **39**, 640–651.
- 583 Bradshaw, C.J.A., Brook, B.W., Delean, S., Fordham, D.A., Cassey, P., Early, R.,  
584 Herrando-pe, S., Sekercioglu, C.H., Arau, M.B., Cassey, P., Early, R. & Ch, S.  
585 (2014) Predictors of contraction and expansion of area of occupancy for British  
586 birds. *Proceedings of the Royal Society of London: Biological Sciences*, **281**,  
587 20140744.
- 588 Browne, S.J., Aebischer, N.J., Yfantis, G. & Marchant, J.H. (2004) Habitat availability  
589 and use by Turtle Doves *Streptopelia turtur* between 1965 and 1995: an analysis of  
590 Common Birds Census data. *Bird Study*, **51**, 1–11.
- 591 Buckley, L.B. (2010) The range implications of lizard traits in changing environments.  
592 *Global Ecology and Biogeography*, **19**, 452–464.
- 593 Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a  
594 practical information-theoretic approach*, Springer, New York.

- 595 Burnham, K.P. & Anderson, D.R. (2004) Multimodel Inference: Understanding AIC and  
596 BIC in Model Selection. *Sociological Methods & Research*, **33**, 261–304.
- 597 Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Ryu,  
598 H.Y., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O. & Wiens, J.J. (2013)  
599 How does climate change cause extinction? *Proceedings of the Royal Society of*  
600 *London: Biological Sciences*, **280**, 20121890.
- 601 Cassey, P., Thomas, G.H., Maurer, G., Hauber, M.E., Grim, T., Lovell, P.G. & Mikšík, I.  
602 (2012) Why are birds' eggs colourful? Eggshell pigments co-vary with life-history  
603 and nesting ecology among British breeding non-passerine birds. *Biological Journal*  
604 *of the Linnean Society*, **106**, 657–672.
- 605 Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range  
606 shifts of species associated with high levels of climate warming. *Science*, **333**,  
607 1024–1026.
- 608 Crick, H.Q.P. & Sparks, T.H. (1999) Climate change related to egg-laying trends.  
609 *Nature*, **399**, 423–424.
- 610 Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. (2008a) Birds are tracking climate  
611 warming, but not fast enough. *Proceedings of the Royal Society of London:*  
612 *Biological Sciences*, **275**, 2743–2748.
- 613 Devictor, V., Julliard, R. & Jiguet, F. (2008b) Distribution of specialist and generalist  
614 species along spatial gradients of habitat disturbance and fragmentation. *Oikos*,  
615 **117**, 507–517.
- 616 Dobrowski, S., Thorne, J., Greenberg, J., Safford, H., Mynsberge, A., Crimmins, S. &  
617 Swanson, A. (2011) Modeling plant ranges over 75 years of climate change in

- 618 California, USA: temporal transferability and species traits. *Ecological Monographs*,  
619 **81**, 241–257.
- 620 Douma, J.C., Witte, J.-P.M., Aerts, R., Bartholomeus, R.P., Ordoñez, J.C., Venterink,  
621 H.O., Wassen, M.J. & van Bodegom, P.M. (2012) Towards a functional basis for  
622 predicting vegetation patterns; incorporating plant traits in habitat distribution  
623 models. *Ecography*, **35**, 294–305.
- 624 Eglington, S.M. & Pearce-Higgins, J.W. (2012) Disentangling the relative importance of  
625 changes in climate and land-use intensity in driving recent bird population trends.  
626 *PLoS ONE*, **7**, 1–8.
- 627 Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans,  
628 R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle,  
629 B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.,  
630 Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-pereira, R., Schapire, R.E.,  
631 Soberón, J., Williams, S., Wisz, M.S. & Zimmermann, N.E. (2006) Novel methods  
632 improve prediction of species' distributions from occurrence data. *Ecography*, **29**,  
633 129–151.
- 634 Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression  
635 trees. *The Journal of Animal Ecology*, **77**, 802–13.
- 636 Foden, W.B., Butchart, S.H.M., Stuart, S.N., Vié, J.-C., Akçakaya, H.R., Angulo, A.,  
637 DeVantier, L.M., Gutsche, A., Turak, E., Cao, L., Donner, S.D., Katariya, V.,  
638 Bernard, R., Holland, R. a, Hughes, A.F., O'Hanlon, S.E., Garnett, S.T.,  
639 Sekercioğlu, C.H. & Mace, G.M. (2013) Identifying the world's most climate change  
640 vulnerable species: a systematic trait-based assessment of all birds, amphibians

- 641 and corals. *PloS one*, **8**, e65427.
- 642 Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002) Phylogenetic analysis and  
643 comparative data: a test and review of evidence. *The American naturalist*, **160**,  
644 712–26.
- 645 Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R. &  
646 Carter, N. (1995) Population declines and range contractions among lowland  
647 farmland birds in Britain. *Conservation Biology*, **9**, 1425–1441.
- 648 Gibbons, D., Reid, J. & Chapman, R. (1993) *The New Atlas of Breeding Birds in Britain*  
649 *and Ireland: 1988–1991*, Poyser, London, UK.
- 650 Green, R.E., Collingham, Y.C., Willis, S.G., Gregory, R.D., Smith, K.W. & Huntley, B.  
651 (2008) Performance of climate envelope models in retrodicting recent changes in  
652 bird population size from observed climatic change. *Biology Letters*, **4**, 599–602.
- 653 Gregory, R.D., van Strien, A., Vorisek, P., Gmelig Meyling, a. W., Noble, D.G., Foppen,  
654 R.P.B. & Gibbons, D.W. (2005) Developing indicators for European birds.  
655 *Philosophical Transactions of the Royal Society of London: Biological Sciences*,  
656 **360**, 269–288.
- 657 Hagemeyer, W.J.M. & Blair, M.J. (1997) *The EBCC atlas of European breeding birds:*  
658 *their distribution and abundance*, T. & A.D. Poyser, London, UK.
- 659 Hanley, J.A. & McNeil, B.J. (1982) The meaning and use of the area under a receiver  
660 operating characteristic (ROC) curve. *Radiology*, **143**, 29–36.
- 661 Hofreiter, M. & Stewart, J. (2009) Ecological change, range fluctuations and population  
662 dynamics during the Pleistocene. *Current Biology*, **19**, R584–R594.
- 663 Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M. & Williams,

- 664 S.E. (2012) Predicting organismal vulnerability to climate warming: roles of  
665 behaviour, physiology and adaptation. *Philosophical Transactions of the Royal*  
666 *Society of London: Biological Sciences*, **367**, 1665–1679.
- 667 Huntley, B., Green, R.E., Collingham, Y.C., Hill, J.K., Willis, S.G., Bartlein, P.J., Cramer,  
668 W., Hagemerijer, W.J.M. & Thomas, C.J. (2004) The performance of models relating  
669 species geographical distributions to climate is independent of trophic level.  
670 *Ecology Letters*, **7**, 417–426.
- 671 Illán, J.G., Thomas, C.D., Jones, J. a, Wong, W.-K., Shirley, S.M. & Betts, M.G. (2014)  
672 Precipitation and winter temperature predict long-term range-scale abundance  
673 changes in Western North American birds. *Global Change Biology*, **20**, 3351–3364.
- 674 IPCC (2013) *Summary for Policymakers. Climate Change 2013: The Physical Science*  
675 *Basis. Contribution of Working Group I to the Fifth Assessment Report of the*  
676 *Intergovernmental Panel on Climate Change* (ed. by T.F. Stocker), D. Qin), G.-K.  
677 Plattner), M. Tignor), S.K. Allen), J. Boschung), A. Nauels), Y. Xia), V. Bex), and  
678 P.M. Midgley), Cambridge University Press, Cambridge, United Kingdom and New  
679 York, NY, USA.
- 680 Ives, A.R., Midford, P.E. & Garland, T. (2007) Within-species variation and  
681 measurement error in phylogenetic comparative methods. *Systematic biology*, **56**,  
682 252–270.
- 683 Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends*  
684 *in Ecology and Evolution*, **19**, 101–108.
- 685 Kharouba, H.M., Algar, A.C. & Kerr, J.T. (2009) Historically calibrated predictions of  
686 butterfly species' range shift using global change as a pseudo-experiment. *Ecology*,

- 687       **90**, 2213–2222.
- 688   Lennon, J.J., Greenwood, J.J.D. & Turner, J.R.G. (2000) Bird diversity and  
689       environmental gradients in Britain: a test of the species-energy hypothesis. *Journal*  
690       *of Animal Ecology*, **69**, 581–598.
- 691   Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009)  
692       The velocity of climate change. *Nature*, **462**, 1052–1055.
- 693   Maggini, R., Lehmann, A., Kéry, M., Schmid, H., Beniston, M., Jenni, L. & Zbinden, N.  
694       (2011) Are Swiss birds tracking climate change? *Ecological Modelling*, **222**, 21–32.
- 695   Mason, C.F. & Lyczynski, F. (1980) Breeding biology of the Pied and Yellow Wagtails.  
696       *Bird Study*, **27**, 1–10.
- 697   McCain, C.M. & King, S.R.B. (2014) Body size and activity times mediate mammalian  
698       responses to climate change. *Global Change Biology*, **20**, 1760–1769.
- 699   McPherson, J.M. & Jetz, W. (2007) Effects of species' ecology on the accuracy of  
700       distribution models. *Ecography*, **30**, 135–151.
- 701   McPherson, J.M., Jetz, W. & Rogers, D.J. (2006) Using coarse-grained occurrence data  
702       to predict species distributions at finer spatial resolutions—possibilities and  
703       limitations. *Ecological Modelling*, **192**, 499–522.
- 704   Menéndez, R., Megías, A.G., Hill, J.K., Braschler, B., Willis, S.G., Collingham, Y., Fox,  
705       R., Roy, D.B. & Thomas, C.D. (2006) Species richness changes lag behind climate  
706       change. *Proceedings of the Royal Society of London: Biological Sciences*, **273**,  
707       1465–70.
- 708   Mitchell, T.D. & Jones, P.D. (2005) An improved method of constructing a database of  
709       monthly climate observations and associated high-resolution grids. *International*

- 710 *Journal of Climatology*, **25**, 693–712.
- 711 Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C. & Beissinger, S.R. (2008)
- 712 Impact of a century of climate change on small-mammal communities in Yosemite
- 713 National Park, USA. *Science*, **322**, 261–264.
- 714 New, M., Hulme, M. & Jones, P. (1999) Representing Twentieth-Century Space – Time
- 715 Climate Variability . Part I: Development of a 1961 – 90 Mean Monthly Terrestrial
- 716 Climatology. *Journal of Climate*, **12**, 829–856.
- 717 Newbold, T., Reader, T., Zalut, S., El-Gabbas, A. & Gilbert, F. (2009) Effect of
- 718 characteristics of butterfly species on the accuracy of distribution models in an arid
- 719 environment. *Biodiversity and Conservation*, **18**, 3629–3641.
- 720 O'Connor, M.I., Selig, E.R., Pinsky, M.L. & Altermatt, F. (2012) Toward a conceptual
- 721 synthesis for climate change responses. *Global Ecology and Biogeography*, **21**,
- 722 693–703.
- 723 Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S. & Isaac, N. (2011) The
- 724 caper package: comparative analysis of phylogenetics and evolution in R. R
- 725 package version 0.4/r75.
- 726 Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**,
- 727 877–884.
- 728 Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. (1998) Patterns of natal and
- 729 breeding dispersal in birds. *Journal of Animal Ecology*, **67**, 518–536.
- 730 Phillimore, A.B., Hadfield, J.D., Jones, O.R. & Smithers, R.J. (2010) Differences in
- 731 spawning date between populations of common frog reveal local adaptation.
- 732 *Proceedings of the National Academy of Sciences of the United States of America*,



- 733           **107**, 8292–8297.
- 734   Pocock, M.J.O. (2011) Can traits predict species' vulnerability? A test with farmland  
735           passerines in two continents. *Proceedings of the Royal Society of London:*  
736           *Biological Sciences*, **278**, 1532–8.
- 737   Pöyry, J., Luoto, M., Heikkinen, R.K. & Saarinen, K. (2008) Species traits are  
738           associated with the quality of bioclimatic models. *Global Ecology and*  
739           *Biogeography*, **17**, 403–414.
- 740   R Core Team (2014) *R: A language and environment for statistical computing*, R  
741           Foundation for Statistical Computing, Vienna, Austria.
- 742   Rapacciuolo, G., Maher, S.P., Schneider, A.C., Hammond, T.T., Jabis, M.D., Walsh,  
743           R.E., Iknayan, K.J., Walden, G.K., Oldfather, M.F., Ackerly, D.D. & Beissinger, S.R.  
744           (2014a) Beyond a warming fingerprint: individualistic biogeographic responses to  
745           heterogeneous climate change in California. *Global Change Biology*, **20**, 2841–  
746           2855.
- 747   Rapacciuolo, G., Roy, D.B., Gillings, S., Fox, R., Walker, K. & Purvis, A. (2012) Climatic  
748           associations of British species distributions show good transferability in time but low  
749           predictive accuracy for range change. *PLoS ONE*, **7**, e40212.
- 750   Rapacciuolo, G., Roy, D.B., Gillings, S. & Purvis, A. (2014b) Temporal validation plots:  
751           quantifying how well correlative species distribution models predict species' range  
752           changes over time. *Methods in Ecology and Evolution*, **5**, 407–420.
- 753   Revell, L.J. (2012) phytools: An R package for phylogenetic comparative biology (and  
754           other things). *Methods in Ecology and Evolution*, **3**, 217–223.
- 755   Ridgeway, G. (2013) gbm: generalized boosted regression models. R package version

- 756           2.1.
- 757   Ridgeway, G. (1999) The state of boosting. *Computing Science and Statistics*, **31**, 172–
- 758           181.
- 759   Robinson, R.A., Morrison, C.A. & Baillie, S.R. (2014) Integrating demographic data:
- 760           towards a framework for monitoring wildlife populations at large spatial scales.
- 761           *Methods in Ecology and Evolution*, **5**, 1361–1372.
- 762   Rowe, K.C., Rowe, K.M.C., Tingley, M.W., Koo, M.S., Patton, J.L., Conroy, C.J.,
- 763           Perrine, J.D., Beissinger, S.R., Moritz, C., Jd, P., Sr, B. & Moritz, C. (2014)
- 764           Spatially heterogeneous impact of climate change on small mammals of montane
- 765           California. *Proceedings of the Royal Society of London: Biological Sciences*, **282**,
- 766           20141857.
- 767   Schielzeth, H. (2010) Simple means to improve the interpretability of regression
- 768           coefficients. *Methods in Ecology and Evolution*, **1**, 103–113.
- 769   Schloss, C.A., Nuñez, T.A. & Lawler, J.J. (2012) Dispersal will limit ability of mammals
- 770           to track climate change in the Western Hemisphere. *Proceedings of the National*
- 771           *Academy of Sciences*, **109**, 8606–8611.
- 772   Sharrock, J. (1976) *The atlas of breeding birds of Britain and Ireland*, Poyser,
- 773           Berkhamsted, UK.
- 774   Smith, A.B., Santos, M.J., Koo, M.S., Rowe, K.M.C., Rowe, K.C., Patton, J.L., Perrine,
- 775           J.D., Beissinger, S.R. & Moritz, C. (2013) Evaluation of species distribution models
- 776           by resampling of sites surveyed a century ago by Joseph Grinnell. *Ecography*, **36**,
- 777           1–15.
- 778   La Sorte, F.A. & Jetz, W. (2012) Tracking of climatic niche boundaries under recent

- 779 climate change. *The Journal of Animal Ecology*, **81**, 914–925.
- 780 Stewart, J.R. (2008) The progressive effect of the individualistic response of species to  
781 Quaternary climate change: an analysis of British mammalian faunas. *Quaternary*  
782 *Science Reviews*, **27**, 2499–2508.
- 783 Thomas, G.H. (2008) Phylogenetic distributions of British birds of conservation concern.  
784 *Proceedings of the Royal Society of London: Biological Sciences*, **275**, 2077–2083.
- 785 Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox,  
786 R., Clarke, R.T. & Lawton, J.H. (2004) Comparative losses of British butterflies,  
787 birds, and plants and the global extinction crisis. *Science*, **303**, 1879–81.
- 788 Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B. & Araújo, M.B.  
789 (2011) Consequences of climate change on the tree of life in Europe. *Nature*, **470**,  
790 531–534.
- 791 Tingley, M.W., Koo, M.S., Moritz, C., Rush, A.C. & Beissinger, S.R. (2012) The push  
792 and pull of climate change causes heterogeneous shifts in avian elevational  
793 ranges. *Global Change Biology*, **18**, 3279–3290.
- 794 Tingley, M.W., Monahan, W.B., Beissinger, S.R. & Moritz, C. (2009) Birds track their  
795 Grinnellian niche through a century of climate change. *Proceedings of the National*  
796 *Academy of Sciences of the United States of America*, **106**, 19637–19643.
- 797 Turner, M.G. (2010) Disturbance and landscape dynamics in a changing world.  
798 *Ecology*, **91**, 2833–2849.
- 799 Le Viol, I., Jiguet, F., Brotons, L., Herrando, S., Lindstrom, a., Pearce-Higgins, J.W.,  
800 Reif, J., Van Turnhout, C. & Devictor, V. (2012) More and more generalists: two  
801 decades of changes in the European avifauna. *Biology Letters*, **8**, 780–782.

802 Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A. a & Langham, G. (2008) Towards  
803 an integrated framework for assessing the vulnerability of species to climate  
804 change. *PLoS Biology*, **6**, 2621–2626.

805 Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H. & Guisan, A. (2008)  
806 Effects of sample size on the performance of species distribution models. *Diversity  
807 and Distributions*, **14**, 763–773.

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825 **TABLES**

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 827 **Table 1:** Summary of model selection for phylogenetic generalised least squares  
 828 (PGLS) models of climatic niche tracking ( $Acc_{TV}$ ) as a function of biological traits in  
 829 British birds. Traits considered were adult survival (Surv), trophic level (Troph), natal  
 830 dispersal (Disp), and habitat specialization (species specialization index; SSI).

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Acc <sub>TV</sub> PGLS models																
	Model rank															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Surv	•	•	•	•	•	•	•	•								
Troph	•	•			•			•				•		•	•	•
Disp		•	•			•		•		•			•	•		•
Spec					•	•	•	•			•		•		•	•
<b>ΔAIC</b>	0.0	1.4	1.5	1.6	2.4	3.3	3.6	3.7	4.3	5.6	6.4	6.5	7.7	8.7	8.9	11.2
<b>LL</b>	17.4	17.9	13.1	12.0	17.4	13.3	12.1	18.0	9.6	10.0	9.6	12.9	10.0	13.0	12.9	13.0
<b>AIC<sub>w</sub></b>	0.28	0.14	0.13	0.13	0.09	0.05	0.05	0.05	0.03	0.02	0.01	0.01	0.00	0.00	0.00	0.00
<b>λ<sub>upper</sub></b>	0.12	0.12	0.17	0.15	0.12	0.17	0.15	0.13	0.20	0.28	0.21	0.20	0.29	0.24	0.20	0.25
<b>R<sup>2</sup></b>	0.14	0.14	0.07	0.05	0.12	0.06	0.04	0.13	0.00	0.00	0.00	0.04	0.00	0.02	0.02	0.01

832 *Notes:* the variables included in each model are shown with the symbol •. Models are  
 833 ranked in order of increasing AICc differences ( $\Delta AIC$ ). The log likelihood (LL) and  
 834 Akaike weights ( $AIC_w$ ) indicate the relative likelihood of a model given the data,  $\lambda_{upper}$   
 835 represents the 95% upper confidence interval for the maximum-likelihood value of  
 836 phylogenetic dependence in the model residuals (all maximum-likelihood  $\lambda$  means were  
 837 0), and  $R^2$  indicates the proportion of the total variation in  $Acc_{TV}$  explained by the model  
 838 predictors. All models were built using 70 species with reliable climatic niche tracking  
 839 measures complete phylogenetic and trait information.

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852 **Table 2:** Summed AIC weight ( $\sum AIC_w$ ) and model-averaged coefficient for each trait  
 853 predictor of climatic niche tracking ( $Acc_{TV}$ ) in British birds across the full set of  
 854 phylogenetic generalised least squares (PGLS) models. The standard error for each  
 855 coefficient estimate is indicated in brackets. Average coefficients with confidence limits  
 856 not overlapping zero are shown in boldface.

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Acc <sub>TV</sub> PGLS models		
	$\sum AIC_w$	Model-averaged coefficient
(Intercept)	–	<b>0.722 (0.252, 1.192)</b>
Survival	0.91	<b>-0.069 (-0.121, -0.017)</b>
Trophic level	0.57	–
2	–	<b>-0.473 (-0.882, -0.064)</b>
3	–	<b>-0.463 (-0.920, -0.006)</b>
4	–	-0.333 (-0.736, 0.070)
5	–	-0.327 (-0.783, 0.130)
Dispersal	0.40	0.031 (-0.021, 0.083)
Specialization	0.25	-0.012 (-0.074, 0.049)

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859 *Notes:* Trophic levels are coded as follows: 2 = herbivorous/insectivorous species with  
 860 predominantly-herbivorous diet, 3 = herbivorous/insectivorous species with  
 861 predominantly-insectivorous diet, 4 = insectivorous species and carnivorous species  
 862 mostly consuming herbivorous prey; 5 = carnivorous species mostly consuming  
 863 carnivorous prey. All models were built using 70 species with reliable climatic niche  
 864 tracking measures and complete phylogenetic and trait information.

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872 **FIGURE LEGENDS**

873 **Figure 1:** The approach of temporal validation (TV) plots exemplified using  
874 observations and model predictions for the Firecrest (*Regulus ignicapillus*). (a)  
875 Observed changes in the distribution of the Firecrest between  $t_1$  and  $t_2$ , including  
876 observed gains (blue), losses (red), stable presences (dark grey), and stable absences  
877 (light grey). (b) Weighted changes in modelled probability of presence ( $\Delta m_w$ ) for the  
878 Firecrest between  $t_1$  and  $t_2$ .  $\Delta m_w$  values are derived by projecting in  $t_2$  a model  
879 calibrated using presence-absence and climate data in  $t_1$ . Bluer and redder colours  
880 indicate increases and decreases in probability of presence, respectively. (c) TV plot of  
881 the agreement between  $\Delta m_w$  values from the climate-based SDM and observed  
882 changes for the Firecrest. Shown are the model temporal validation curve (thick black) –  
883 the sum of the plotted gain function (blue curve) and loss function (red curve) – and  
884 confidence intervals of  $\pm 2$  standard errors of the mean (orange). The dashed black line  
885 represents the ideal expectation for a perfect temporal validation curve. The rug plots  
886 show model values at observed sites; colours shown correspond to colours in panel (a).

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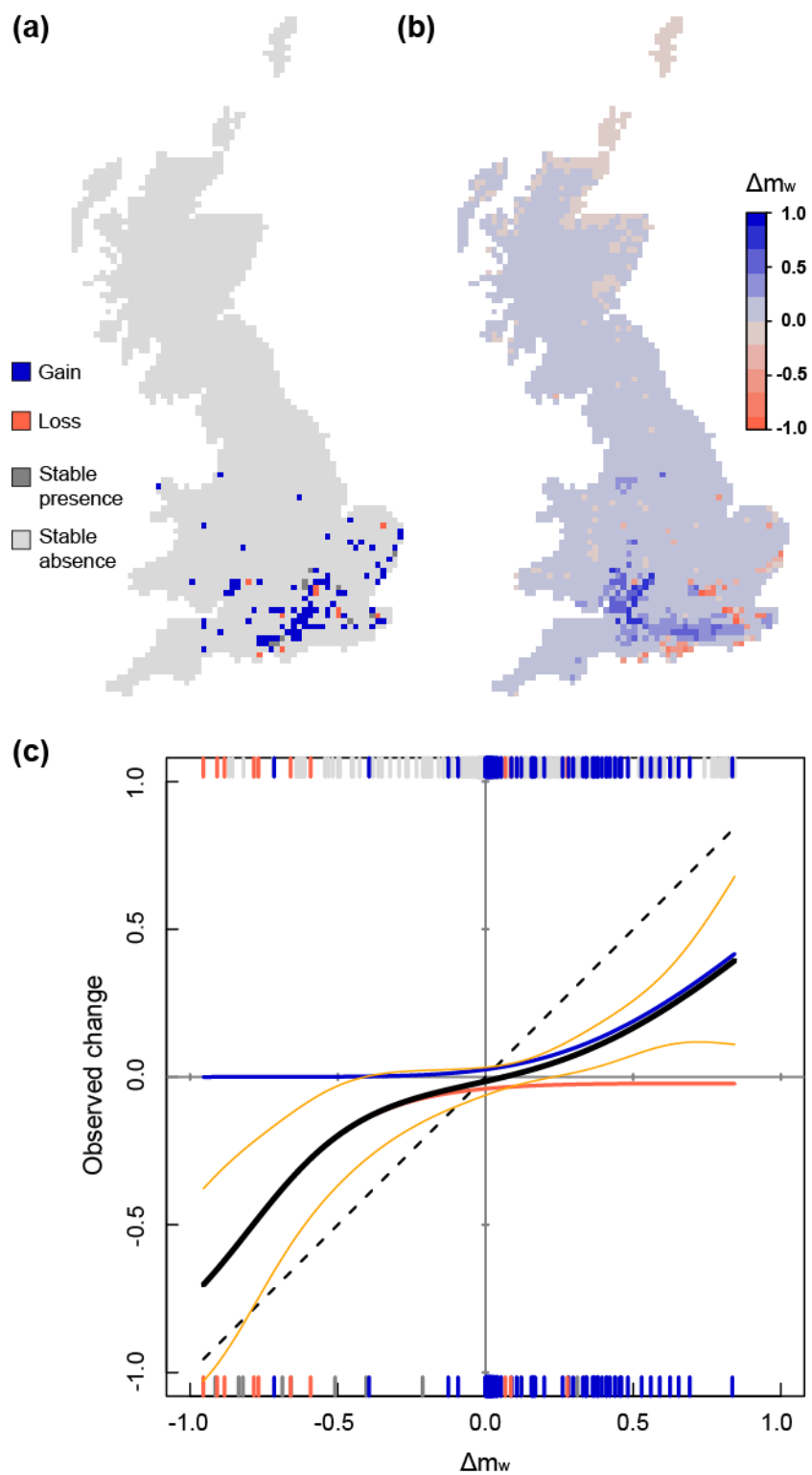
888 **Figure 2:** Measuring climatic niche tracking using temporal validation accuracy ( $\text{Acc}_{\text{TV}}$ ).  
889 Shown is a plot of observed range changes as a function of weighted changes in  
890 modelled probability of presence ( $\Delta m_w$ ) for the Firecrest (analogous to Fig. 1c).  $\text{Acc}_{\text{TV}}$  is  
891 the mean absolute distance between the modelled  $y$  values (points) and the ideal  $y$   
892 values (dashed black line), weighted by the corresponding absolute  $\Delta m_w$  values at each  
893 observed site (tick marks), subtracted from 1. Data points from the Firecrest model were  
894 rarefied for ease of visualisation.

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**Figure 3:** Distribution of  $Acc_{TV}$  values across 94 species of British breeding birds.  $Acc_{TV}$  is a measure of climatic niche tracking; values of 1 indicate perfect niche tracking. The dashed line indicates the median  $Acc_{TV}$  across all species (0.583).  $Acc_{TV}$  values for species with high errors during model calibration were excluded from this analyses (see Methods section).

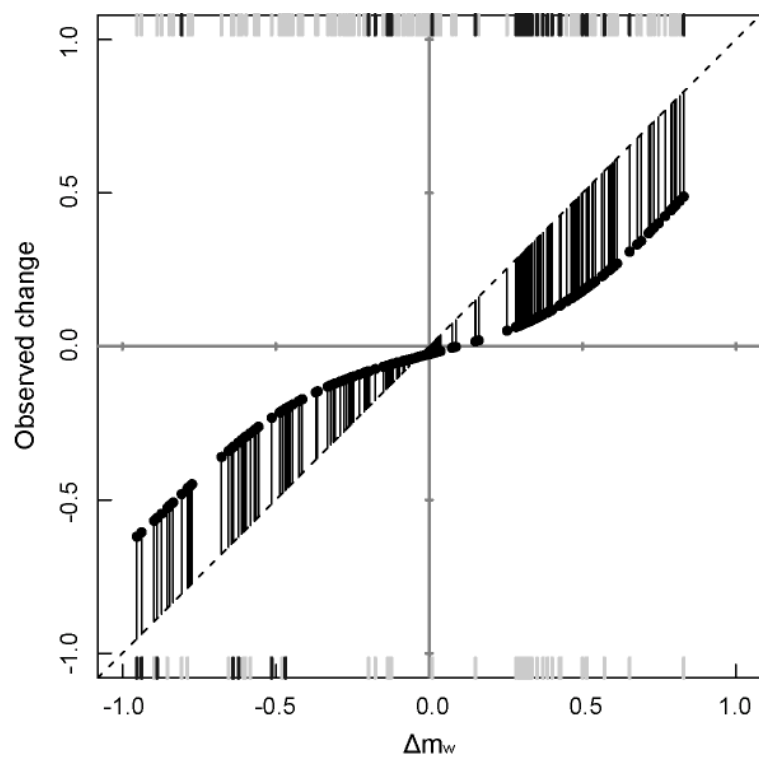


918 **FIGURES**



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920 **Figure 1**



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922 **Figure 2**

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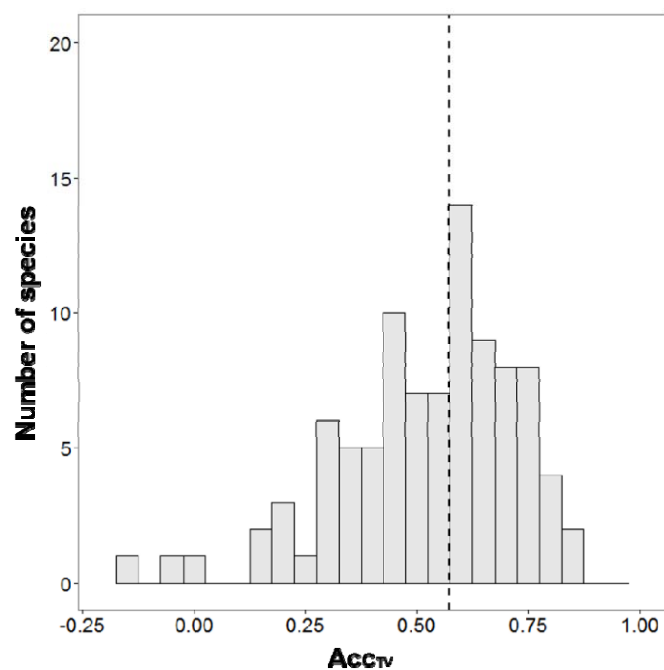
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936 **Figure 3**