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14 **Drivers of climate change impacts on bird communities.**

15

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28

29 Word count: 7,995

30 **Abstract**

31 1. Climate change is reported to have caused widespread changes to species'
32 populations and ecological communities. Warming has been associated with declines
33 in long-distance migrants, reductions in habitat specialists and increases in southerly
34 distributed species. However, the specific climatic drivers behind these changes
35 remain undescribed.

36 2. We analysed annual fluctuations in the abundance of 59 breeding bird species in
37 England over 45 years to test the effect of monthly temperature and precipitation
38 means upon population trends.

39 3. Strong positive correlations between population growth and both winter and
40 breeding season temperature were identified for resident and short-distance migrants.
41 Lagged correlations between population growth and both summer temperature and
42 precipitation identified for the first time a widespread negative impact of hot, dry
43 summer weather, whilst resident populations appeared to increase following wet
44 autumns. Populations of long-distance migrants were negatively affected by May
45 temperature, consistent with a potential negative effect of phenological mismatch
46 upon breeding success. There was some evidence for non-linear relationships between
47 monthly weather variables and population growth.

48 4. Habitat specialists and cold-associated species showed consistently more negative
49 effects of higher temperatures than habitat generalists and southerly-distributed
50 species associated with warm temperatures, suggesting that previously reported
51 changes in community composition represent the accumulated effects of spring and
52 summer warming.

53 5. Long-term population trends were more significantly correlated with species'
54 sensitivity to temperature than precipitation, suggesting that warming had had a

55 greater impact on population trends than changes in precipitation. Months where there
56 had been the greatest warming were the most influential drivers of long-term change.
57 There was also evidence that species with the greatest sensitivity to extremes of
58 precipitation have tended to decline.

59 5. Our results provide novel insights about the impact of climate change on bird
60 communities. Significant lagged effects highlight the potential for altered species'
61 interactions to drive observed climate change impacts, although some community
62 changes were driven by more immediate responses to warming. In England, resident
63 and short-distance migrant populations have increased in response to climate change,
64 but potentially at the expense of long-distance migrants, habitat-specialists and cold-
65 associated species.

66

67 Keywords: birds, climate change, community specialisation index, community
68 temperature index, migrants, population trends, precipitation, temperature.

69

70

71

72 **Introduction**

73 Climate change is projected to have a significant effect upon the future rate of
74 biodiversity loss, the first consequences of which are already being detected (e.g.
75 Parmesan & Yohe 2003; Thomas *et al.* 2004). There is mounting evidence for
76 widespread changes to the distribution of species as a result of warming, with ranges
77 spreading polewards and upwards (Hickling *et al.* 2006; Chen *et al.* 2011). Impacts of
78 climate change have been detected on individual populations (e.g. Conrad, Woiwod &
79 Perry 2002; Both *et al.* 2006; Foden *et al.* 2007; Wake 2007), although few studies
80 have demonstrated increased risk of extinction in response to climate change (Cahill
81 *et al.* 2013). Some of the strongest signals of climate change have been apparent at the
82 community level (Morecroft & Speakman 2013), indicative of differential impacts of
83 climate change on populations of different species. These may be used to infer
84 potential variation in the sensitivity of different populations and species to future
85 climate change, and therefore are worthy of further investigation.

86

87 Many of these studies have been conducted on well monitored bird populations,
88 where three main trends in community change have been described. Firstly, long-
89 distance migrants have declined more than resident or short-distance migrant species
90 (Holmes & Sherry 2001; Sanderson *et al.* 2006; Yamaura *et al.* 2009). This has been
91 attributed to a range of factors, but there is evidence that climate change may have
92 driven at least some of this variation. For example, long-distance migrants now arrive
93 later relative to spring temperatures on the breeding grounds than they used to, which
94 may have population consequences (Both & Visser 2001; Møller *et al.* 2008; Saino *et*
95 *al.* 2010; although see Johansson & Jonzén 2012), whilst their populations may also
96 be affected by climate change on the wintering grounds (Newson *et al.* 2009a).

97 Variation in population trends have been attributed to differences in wintering
98 (Thaxter *et al.* 2010; Jones & Creswell 2010), and breeding location (Ockendon *et al.*
99 2012; Morrison *et al.* 2013), and habitat (Both *et al.* 2010), each of which may be
100 interpreted in relation to potential effects of climate change, as well as other factors.

101

102 Secondly, communities have become increasingly similar to each other
103 (homogenised) as a result of populations of generalist species increasing relative to
104 those of habitat specialists (Devictor *et al.* 2008a; Davey *et al.* 2012; Le Viol *et al.*
105 2012); findings which are apparent across a wide-range of taxa (Spear & Chown
106 2008; Winter *et al.* 2009). Whilst this may be attributable to a range of drivers
107 associated with land-use and management change (e.g. Devictor *et al.* 2008a; Doxa *et*
108 *al.* 2012), there is increasing evidence that generalist species with a broader niche
109 breadth may respond more positively to warming than specialists (Davey *et al.* 2012;
110 2013).

111

112 Thirdly, variation in population trends between species at individual locations has
113 been linked to the spatial association of each species to temperature. Populations
114 associated with warmer temperatures (which tend to have southerly distributions)
115 have increased in abundance relative to more northerly distributed species associated
116 with cooler temperatures (Devictor *et al.* 2008b; Jiguet *et al.* 2010; Lindström *et al.*
117 2013). This has led to detectable changes in communities of both birds and butterflies
118 across Europe, as measured by the community temperature index (Devictor *et al.*
119 2012), although some of the changes observed may also be linked to land-use change
120 (Clavero, Villero & Brotons 2011; Barnagaud *et al.* 2012).

121

122 Combined, there is good evidence that populations of long-distance migrants,
123 specialists and cold-associated bird species have declined in Europe (Sanderson *et al.*
124 2006; Devictor *et al.* 2012; Le Viol *et al.* 2012). However, there is a lack of
125 understanding about the extent to which such changes may be directly attributable to
126 climate change in Europe, or precisely which components of climate change may be
127 responsible. Given differential patterns of warming and precipitation change in
128 different seasons of the year (see Fig. 5), there is a clear need to understand more
129 precisely to which components of climate change species' populations are responding,
130 the likely ecological mechanisms driving these population responses, and how these
131 mechanisms vary between species.

132

133 To do this, we analysed long-term national population time-series data of birds in
134 England, in relation to variation in both temperature and precipitation measures
135 through the year. Importantly, this is an avifauna where both distribution and
136 community changes have previously been attributed to warming (e.g. Thomas &
137 Lennon 1999; Davey *et al.* 2012; Devictor *et al.* 2012). Specifically, we examined the
138 extent to which the observed community changes of declining long-distance migrants,
139 community homogenisation and increasing community temperature index may be
140 driven by variation in species' sensitivity to the weather variables by testing whether
141 species' population responses to temperature and precipitation varied with respect to
142 migratory strategy, habitat specialisation and thermal association. In order to identify
143 the seasons where long-term climate change is most likely to have driven recent
144 changes in bird populations, we then regressed long-term population trend against
145 species' sensitivity to temperature and precipitation in each month.

146

147 **Materials and Methods**

148 DATA

149 Data from the British Trust for Ornithology's (BTO) Common Bird Census (CBC)
150 and the BTO/Joint Nature Conservation Committee/Royal Society for the Protection
151 of Birds Breeding Bird Survey (BBS) were used to generate annual indices of
152 population change for England from 1966 to 2011. The CBC provided data from 1966
153 until 1994. Within the CBC, bird territories were mapped from observations made on
154 seven to ten visits per year to self-selected sites (Marchant *et al.* 1990). The BBS
155 involves two parallel 1km line-transects in 1km squares being surveyed during two
156 early morning surveys between early April and late June (Gregory & Baillie 1998;
157 Risely *et al.* 2012). These two methods produce differently structured data at the site
158 level, making combined analysis at this resolution across the entire time-period very
159 difficult. However, at the national level, despite the switch in methodology, the data
160 from the two surveys can be combined to produce joint trends for most species using
161 a log-linear model with a Poisson error distribution (Freeman *et al.* 2007). We
162 therefore analysed data for 59 species (listed in Appendix S1) with comparable trends
163 for England from both CBC and BBS that can be used to generate robust annual
164 estimates of abundance using well-established analytical protocols developed
165 specifically for this purpose (e.g. Gregory *et al.* 2005; Newson *et al.* 2009b). Trends
166 were fixed to one in the first year (1966) and indicate relative population changes
167 across species, so that each species contributes equally to the analysis.

168

169 Variation in the weather was described by monthly averages of temperature and
170 precipitation for England (<http://www.metoffice.gov.uk/climate/uk/datasets/>). For the
171 purposes of analyses, we focussed on mean monthly temperature (°C) and total

172 monthly precipitation (mm), although equivalent patterns in the data for temperature
173 were also produced using mean minimum and mean maximum monthly temperatures
174 (Appendix S2).

175

176 Given the strong spatial autocorrelations in weather variables and our use of national
177 summaries of bird populations, this paper describes large-scale population responses
178 to large-scale climatic variation. We do not consider how variation in the conditions
179 experienced at individual sites (e.g. Newson *et al.* 2014), or local adaptation, might
180 influence specific population responses.

181

182 STATISTICAL ANALYSIS

183 Annual variation in the population (n) growth rate of each species from year t to year
184 $t+1$ ($\ln(n_{t+1}/n_t)$) was modelled as a function of each of the monthly weather variables,
185 using a single model combining data from all species. Count (n_{t+1}) was modelled
186 using a Poisson error distribution and a log link function, with $\ln(n_t)$ specified as an
187 offset in order to generate the log-ratio of change. Count in the first year (n_t) was also
188 included as a predictor variable to account for potential density-dependence and
189 survey error (Freckleton *et al.* 2006). Species identity was specified as a random
190 effect, and a first-order autoregressive function accounted for potential temporal
191 autocorrelation in the data. The Kenward-Rogers correction was applied to ensure the
192 correct estimation of the degrees of freedom. This model was run for temperature and
193 rainfall separately.

194

195 We considered also correcting for relatedness amongst species in our analysis, to
196 reduce the possibility of Type 1 errors arising from phylogenetic autocorrelation. The

197 inclusion of family identity as an additional random effect accounted for a negligible
198 amount of covariance (mean across all models = $2.98E^{-20} \pm 5.41E^{-21}$) compared to that
199 attributed to species (mean across all models = $0.011 \pm 7.99E^{-5}$). To further examine
200 similarity of response between species as a function of relatedness, we repeated all
201 analysis, but with species included as a fixed effect instead of a random effect, and
202 then conducted a Moran's I test on the species effects in relation to their phylogenetic
203 similarity. In only three cases was this test significant; models of the interaction
204 between STI and temperature in April_{t-1} ($P = 0.022$), July_{t-1} ($P = 0.025$) and April_t ($P =$
205 0.049). Given this lack of evidence for species population responses to temperature
206 and precipitation being phylogenetically conserved, and given the statistical
207 difficulties of accounting for phylogenetic independence within a single model that
208 includes multiple observations from the same species that are temporally
209 autocorrelated, we have not formally corrected for relatedness (see Kunin 2008).

210

211 For 11 % of tests, the inclusion of the autoregressive function led to a failure of model
212 convergence, in which case the function was deleted. To assess the extent to which
213 this may have reduced the comparability of these models with the remainder, we
214 repeated the analysis without the autoregressive function for all models, and
215 correlated the parameter estimates and standard errors from the two models for all
216 cases where both were estimated. Parameter estimates and standard errors were
217 virtually identical and highly correlated ($r > 0.993$ and 0.986 respectively),
218 demonstrating that the model outputs were comparable. Nevertheless, we highlight
219 these cases to the reader in case they are more susceptible to Type I error.

220

221 Whilst we used the mixed-model framework to estimate mean responses to each
222 weather variable across all species, it was necessary to account for species-specific
223 variation in the strength of density-dependence. Each model therefore included the
224 species * n_t interaction. The final model was specified as follows, with w as the
225 weather variable of interest, and a , b_o , and b_l modelled estimates of the intercept,
226 species-specific effect of density-dependence and mean weather effect size across all
227 species, respectively.

228

$$229 \quad \ln\left(\frac{n_{t+1}}{n_t}\right) = a + b_0 s n_t + b_1 w + \varepsilon$$

230

231 We tested the effect of monthly weather variables from April in the year before the
232 first survey (April_{t-1}) to June at the end of the second survey (June_{t+1}), a spread of two
233 years plus three months of the second survey that allowed for some investigation of
234 potential lagged effects of weather variables upon populations which have been
235 shown to be important for some species (e.g. Pearce-Higgins *et al.* 2010), without
236 over-inflating the number of variables considered (Fig. 1). These models provide a
237 description of the mean sensitivity of the bird community as a whole to weather at
238 different times of the year, and although not the main focus of this paper, are reported
239 in Appendix S3, alongside additional models that test for potential non-linear
240 relationships between weather variables and population growth through the inclusion
241 of an additional term $b_2 w^2$ in the model.

242

243 *Factors affecting variation in the sensitivity of different species.*

244 The effect of these weather variables is likely to differ between species in a manner
245 that can account for the observed changes in community composition. Therefore, the

246 focus of this paper is to test the extent to which species-specific responses to the
247 weather varied with migratory strategy, habitat specialisation (niche-breadth) and
248 thermal association. The pattern of these results indicate the likely processes
249 underpinning each of the observed community responses to climate change. Species
250 were classified as resident, short- and long-distance migrants from Thaxter *et al.*
251 (2010). Niche breadth was measured using the species specialisation index (SSI),
252 calculated from the coefficient of variation of species' density across habitats (Davey
253 *et al.* 2012). Thermal association was summarised using the species temperature index
254 (STI), calculated as the mean temperature across each species European breeding
255 range (from Devictor *et al.* 2012). This test was achieved by separately adding to each
256 model the each trait variable (t) plus its interaction with the relevant weather variable
257 as follows.

258

$$259 \quad \ln\left(\frac{n_{t+1}}{n_t}\right) = a + b_0 s n_t + b_1 w + b_2 t + b_3 t w + \varepsilon$$

260

261 The three traits were independent (correlation between SI and STI values across
262 species, $r = -0.20$, $n = 59$, $P = 0.11$; variation in STI, $F_{2,55} = 0.82$, $P = 0.44$ and SSI,
263 $F_{2,55} = 1.08$, $P = 0.35$, with migratory strategy).

264

265 *Variation in population trend with species' sensitivity to weather variables*

266 In order to assess the extent to which species population trends may be related to their
267 sensitivity to weather variables, and to directional shifts in those weather variables
268 through time (climatic change), we estimated linear national population trends from
269 the 45-years covered (1966-2011), from the slope of n_t against year. The interaction of
270 this trend with species-specific responses to weather in each month was then tested, in

271 the same way as described for other ecological traits above. For example, a positive
272 interaction with temperature in a particular month would show that species with a
273 positive relationship between temperature and population growth in that month have
274 generally shown a long-term increase. Similarly, species for which temperature had a
275 negative impact on population growth will have tended to decline in abundance. In
276 other words, we are testing the extent to which the effect of weather upon population
277 fluctuations result in long-term population trends as a result of climate change.

278

279 All analyses were undertaken using PROC GLIMMIX in SAS 9.2 (Littell *et al.* 1996).
280 Given the number of tests performed, we applied Bonferroni correction to highlight
281 those which are most likely to be statistically significant and meaningful ($P <$
282 0.00185), and focus primarily on those in the discussion of the results, although
283 record all of the weaker relationships for completeness. All parameter estimates,
284 standard errors and significance values of relationships shown graphically are
285 presented to the reader in Appendix S4.

286

287 **Results**

288 FACTORS AFFECTING VARIATION IN THE SENSITIVITY OF DIFFERENT 289 SPECIES

290 Monthly variation in the mean temperature effect upon populations was generally
291 similar between residents and short-distance migrants (Fig. 2a,b). Significant
292 interactions between migratory strategy and winter temperature were apparent in
293 February_{t-1} ($P = 0.0021$), December_t ($P = 0.0065$) and January_t ($P = 0.0005$), although
294 only the latter was below the Bonferroni threshold. These interactions are indicative
295 of a strong positive effect of winter temperature upon populations of resident species

296 counted in the following spring, the significance of which exceeded the Bonferroni
297 threshold for residents for December_t, January_t and February_t (Appendix 4). The same
298 relationships were apparent, but weaker, in short-distance migrants, and not apparent
299 in long-distance migrants (Fig. 2c). The strongest interaction between temperature and
300 migratory strategy was with May_t temperature ($P = 0.0003$), which was particularly
301 related to population growth in resident species (0.00915 ± 0.0035), but negatively in
302 long-distance migrants (-0.0203 ± 0.0066), although neither effect achieved
303 Bonferroni significance. The strong contrast for June_{t+1} temperature was between a
304 positive effect on long-distance migrants and negative impact on short-distance
305 migrants, neither of which achieved Bonferroni significance in isolation. Across
306 species, there was also evidence of a strong negative effect of summer temperature
307 with a one year lag (July_{t-1} and August_{t-1}) upon population growth (Appendix S3),
308 which was below the Bonferroni significance level for both short-distance and long-
309 distance migrants for July_{t-1}. Variation in the response of populations to precipitation
310 did not differ strongly with respect to migratory strategy (Fig. 2d-f), and broadly
311 reflected the general patterns across species of positive effects of wet spring weather
312 in year $t-1$, particularly resident and short-distance migrants in April_t, and of
313 precipitation in July and August in year_{t-1} upon population growth. Resident species
314 also showed strong positive effects of precipitation in October_t and November_t upon
315 population growth (Appendix S3, S4).

316

317 The interaction between mean monthly temperature and SSI was statistically
318 significant ($P < 0.05$) for eight months, of which three remained significant after
319 applying the Bonferroni correction (Fig. 3a). All of these significant effects, and the
320 results for the majority of other months, were for negative interactions between

321 temperature and SSI, indicating that habitat specialists experience greater negative
322 impacts of warming than generalists. Although there was some evidence that the
323 previously detected lagged negative effects of summer warming were more severe for
324 specialists (July_{t-1} $P = 0.003$, August_{t-1} $P = 0.019$), the strongest contrasts were with
325 respect to spring temperature (March_{t-1} $P = 0.0007$, April_t $P = 0.047$, March_t $P =$
326 0.0002 , May_{t+1} $P = 0.0006$). Warmer spring weather tended to increase populations of
327 generalists relative to specialists, both with and without a time lag. With respect to
328 monthly precipitation, correlations between population growth and the interaction
329 with SSI was significant for six months (Fig. 3b), of which those with May_{t-1} ($P =$
330 0.0006) and July_{t-1} ($P < 0.0001$) remained significant after applying the Bonferroni
331 correction. The latter re-enforces the suggestion that the negative effects of hot, dry
332 summer weather most strongly affect specialists.

333

334 The effect of STI on population responses to temperature were largely positive, such
335 that species with a high STI were more likely to have more positive relationships
336 between temperature and population growth (Fig. 4a), i.e. as expected, population
337 change of warm-climate species positively correlates with warmer conditions.
338 Thirteen of the interactions were significant ($P < 0.05$), including five which remained
339 after applying the Bonferroni correction. All related to spring or early summer
340 temperature (April_{t-1} $P < 0.0001$, April_t $P = 0.0002$, March_t $P = < 0.0001$, May_{t+1} $P = <$
341 0.0001 , June_{t+1} $P = < 0.0001$), and indicates that a greater number of individuals from
342 species with a high STI are recorded both in and following warm breeding seasons.
343 Ten of the interactions between STI and precipitation also reached significance ($P <$
344 0.05), with negative correlations with April_{t-1} ($P < 0.0001$), May_t ($P < 0.0001$) and

345 September_t ($P < 0.0001$), and a positive correlation with March_{t-1} ($P < 0.0001$)
346 remaining significant after applying the Bonferroni correction (Fig. 4b).

347

348 VARIATION IN POPULATION TREND WITH SPECIES' SENSITIVITY TO 349 WEATHER VARIABLES

350 There were strong and largely positive correlations between species' sensitivity to
351 temperature and population trend (Fig. 5a). A total of 16/27 relationships were
352 significantly positive, and a further two negative, whilst 11 positive interactions
353 remained significant after Bonferroni correction. The most consistent positive
354 relationships occurred in spring (April_{t-1}, March_{t-1} to May_t and March_t to June_{t+1}),
355 although positive effects of summer (July_{t-1} and to a lesser extent August_{t-1}), autumn
356 (November_{t-1}, November_t) and late winter (February_t) temperature upon population
357 growth were also apparent. The months where there was the strongest interaction
358 between species' sensitivity to temperature and population trend were not those where
359 temperature appeared to have the strongest mean impact across species (correlation
360 between y-axes of Fig. S3ai and Fig. 5a; $r = -0.20$, $P = 0.31$), but were those where
361 the amount of warming had been greatest (correlation between y-axis and z-axis of
362 Fig. 5a; $r=0.65$, $P = 0.00024$).

363

364 Species sensitivity to precipitation was correlated with population trend across 11 of
365 the months covered, although for only two of these (April_{t-1} and March_{t-1}) did these
366 achieve Bonferroni-corrected significance. Unlike temperature, there was no
367 correlation between the trend in precipitation and the interaction between population
368 growth and species' sensitivity to precipitation ($r = 0.14$, $P = 0.49$). Instead, mean
369 species' sensitivity to precipitation in that month (Fig. S3aii) was negatively

370 correlated with the relationship between precipitation sensitivity and long-term trend
371 ($r = -0.66$, $P = 0.00017$). This indicates that in months where species responses to
372 precipitation were largely positive, species with the most positive relationship
373 between precipitation and population growth tended to decline. Similarly, in months
374 where precipitation had largely negative effects upon population growth, species with
375 the most negative relationship between precipitation and population growth tended to
376 decline. In other words, species most sensitive to precipitation extremes were those
377 with the most negative population trends.

378

379 **Discussion**

380 We have presented important evidence identifying the key periods of the year in
381 which bird populations in England are affected by the weather, and how climate
382 change may have driven recent changes in bird communities.

383

384 Firstly, three main periods of sensitivity were apparent across species; the breeding
385 season (particularly June_t), winter (December_t to February_t) and summer (July_{t-1} and
386 August_{t-1}), although the importance of different months varied between species
387 groups. Positive relationships between winter temperature and population growth of
388 resident and short-distance migrants reflect negative effects of cold winter weather on
389 survival rates of many species, from small passerines, such as winter wren
390 *Troglodytes troglodytes* and treecreeper *Certhia familiaris* (Peach, du Feu &
391 McMeeking 1995; Robinson, Baillie & Crick 2007) to large waders such as northern
392 lapwing *Vanellus vanellus* and Eurasian golden plover *Pluvialis apricaria* (Peach,
393 Thompson & Coulson 1994; Piersma *et al.* 2005). Although for individual species, the
394 duration of snow cover or the number of frost days may provide better predictors of

395 survival or population change (e.g. Greenwood & Baillie 1991; Robinson, Baillie &
396 Crick 2007), our results suggest at the large scale, cold winters have a consistent
397 negative impact upon resident and short-distance migrant breeding bird populations in
398 England. Unsurprisingly, populations of long-distance migrants were unaffected by
399 winter temperature during year_t, but instead are strongly correlated with rainfall on
400 their wintering grounds (Peach, Baillie & Underhill 1991; Newson *et al.* 2009a;
401 Pearce-Higgins & Green 2014).

402

403 Positive effects of June breeding season temperature are probably mediated through
404 increased invertebrate food abundance, reduced thermoregulatory requirements and
405 increased foraging time (Pearce-Higgins & Green 2014) associated with warm
406 weather. These were most apparent in resident species, with strong relationships close
407 to the Bonferonni threshold apparent also in April_t and May_t. The strongly significant
408 negative effect of May_t temperature on long-distance migrant population trends, in
409 contrast to the positive effect on resident species, accounts for the less positive effect
410 of May_t temperature overall on bird populations (Fig. S3a). This contrast is consistent
411 with the proposed vulnerability of long-distance migrants to climate change on the
412 breeding grounds, as a result of phenological mismatch. Late arriving, long-distance
413 migrants that have failed to advance their arrival time have tended to decline in
414 abundance, particularly in seasonal habitats (Møller *et al.* 2008; Saino *et al.* 2009;
415 Both *et al.* 2010). Although the empirical evidence in support of detrimental impacts
416 of mismatches on migrant populations in the UK is so far weak (reviewed in Pearce-
417 Higgins & Green 2014), we would nevertheless expect May temperature to have
418 positive impacts on resident species likely to be feeding chicks, but a negative impact
419 on long-distance migrants likely to be incubating their eggs at this time, and therefore

420 unable to further adjust their breeding phenology to compensate for accelerated
421 environmental conditions.

422
423

424 Detrimental impacts of hot, dry summers on bird populations, were apparent, but
425 appeared to operate with a one-year lag. Thus, such conditions in year_{t-1} will result in
426 a population decline, not from year_{t-1} to year_t, but between year_t and year_{t+1}. This is the
427 effect previously identified for some upland birds as a result of negative impacts of
428 summer temperature upon their invertebrate prey (Pearce-Higgins *et al.* 2010;
429 Fletcher *et al.* 2013), and appears greatest in species that prey upon subsurface
430 invertebrates whose larvae are vulnerable to desiccation, such as Diptera, and
431 invertebrates which become less accessible in dry weather, such as Lumbricidae
432 (Pearce-Higgins 2010; Carroll *et al.* 2011). Our results suggest that lagged negative
433 impacts of hot, dry summer weather may affect more than just upland birds, and may
434 be ecologically more important than more direct effects of summer drought that
435 appear to affect post-fledging survival of thrushes (Robinson *et al.* 2004; Robinson,
436 Baillie & King 2012). These conclusions emphasise the importance of research to
437 identify the precise mechanisms which underpin these lagged effects, particularly as it
438 is likely to be through such lagged impacts affecting ecological interactions that
439 climate change may have the greatest impact on species' extinction risk (Cahill *et al.*
440 2013; Ockendon *et al.* 2014). The positive lagged relationship between precipitation
441 in April_{t-1} and population growth is less-clearly related to a specific mechanism, but
442 may also influence trophic interactions, such as through changes in plant growth. The
443 mechanisms underlying the positive effect of autumn_t precipitation upon population
444 growth, particularly apparent in October and November for resident species, was also

445 unclear, but may again occur through effects on other species, such as by influencing
446 prey availability during the winter.

447

448 Davey *et al.* (2012) suggested for Great Britain that increasing temperatures have
449 resulted in a reduction in community specialisation, a finding subsequently replicated
450 in Sweden (Davey *et al.* 2013). Our results are consistent with this observation, with a
451 generally negative interaction between mean monthly temperature and SSI (Fig. 3a).
452 Although these effects were not strongly tied to a particular month or season,
453 combined with the interactions for precipitation, they do suggest that negative effects
454 of hot, dry summers (July_{t-1} and August_{t-1}) may be most apparent in habitat
455 specialists, whilst the positive effects of spring temperature (March_{t-1}, April_t) may be
456 greatest for generalist populations. Interestingly, the strongest interactions were for
457 March_{t+1} and May_{t+1} temperatures, suggestive of a differential effect of breeding
458 season temperature upon the settlement or detectability of generalist and specialist
459 species. This is consistent with the observation that the strongest correlations between
460 temperature and community change are with breeding season temperature during the
461 year of the second survey (Davey *et al.* 2012, 2013). The meaning of more positive
462 effects of lagged May_{t-1} precipitation upon specialists than generalists (Fig. 3b) is
463 uncertain, but may be attributed to potential changes in vegetation growth and habitat
464 quality following wet springs that could enhance their breeding success and survival
465 (e.g. Robinson *et al.* 2004).

466

467 The analysis of interactions between species' responses to weather and thermal
468 association produced similar findings to those just described for habitat specialisation.
469 Thus, as expected from the large-scale increase in CTI observed across Europe

470 (Devictor *et al.* 2012), there was a tendency for positive interactions between STI and
471 temperature effects on population growth across a range of months (Fig. 4a). Effects
472 were strongest during the spring of the first survey (March_{t-1} – May_t, although
473 phylogenetic autocorrelation signalled the potential for a Type 1 error in the positive
474 interaction in April_t). This suggests that warmer breeding seasons tend to increase the
475 productivity of warm-adapted species, whilst warming during the spring of the second
476 survey (March_t, May_{t+1} and June_{t+1}), may lead such warm-adapted species to either
477 settle further north, or to be more detectable. Despite concerns over the role of land-
478 use change in also influencing changes in STI (Clavero, Villero & Brotons 2011;
479 Barnagaud *et al.* 2012), and potential uncertainty over the interpretation of CTI (for
480 example, whether changes are caused by increases in warm-associated species,
481 reductions in cold-associated species or both, or the fact that the breadth of the
482 temperature niche does not influence a species' contribution to CTI), our results are
483 consistent with the concept that changes in CTI track avian population responses to
484 warming.

485

486 Finally, our results highlighted widespread correlations between long-term population
487 trends and species' sensitivity to temperature, compared to precipitation. Thus, recent
488 warming trends appear likely to have contributed to the observed changes in bird
489 communities previously described, including declines in long-distance migrants,
490 habitat specialists with a narrow niche breadth and cold-adapted species (Sanderson *et*
491 *al.* 2006; Davies *et al.* 2012; Devictor *et al.* 2012). Although there was no match
492 between the main periods of sensitivity to weather across species, and the periods of
493 greatest correlation between sensitivity and population trend, it did appear that species
494 whose populations had increased, tended to be those with positive relationships

495 between temperature and population growth in periods of greatest warming. In
496 particular, late winter and spring warming appears to have caused increases in
497 populations with significant positive relationships between February_t, March_t, May_{t+1}
498 and June_{t+1} temperatures and population growth. This potentially accounts for the
499 apparent effects of conditions during spring_{t+1} upon changes in both community
500 specialisation and CTI. Long-term population trends did not appear significantly
501 related to the periods of greatest contrast between species with differing migratory
502 strategies, including May_t and February_t. In addition, the effect of precipitation upon
503 long-term population trends was negatively correlated with mean precipitation effect,
504 such that species which showed the greatest sensitivity to precipitation (having the
505 most positive effects of precipitation upon population growth during periods where
506 most species respond positively to precipitation, or the most negative effects of
507 precipitation upon growth in months when most species respond negatively to
508 precipitation), were also those which tended to decline. Although further work is
509 required to fully attribute long-term population changes to climate change, our results
510 suggest that both warming and changes in precipitation extremes may have influenced
511 long-term avian population trends in the UK.

512

513 It is worth emphasising that the results presented here are for relatively common and
514 widespread bird species monitored by extensive surveys. Although these data have
515 previously formed the basis for assessing community level changes in response to
516 climate change (e.g. Davey *et al.* 2012; Devictor *et al.* 2012), no very rare species,
517 and few upland species, are sufficiently well covered by these surveys to be included
518 in our analysis. Thus, as these other species may be particularly sensitive to climate
519 change (Pearce-Higgins 2010), the results presented here may present a potentially

520 more positive overall assessment of climate change than would be apparent were the
521 entire avifauna assessed. In addition, we have also not considered other potentially
522 confounding non-climatic drivers of change that may also affect long-term population
523 trends. Although these may be more responsible for some of the long-term trends
524 observed than climate change (e.g. Eglington & Pearce-Higgins 2012), by including a
525 first-order autoregressive function in our models, we significantly reduced the risk
526 that our results may be due to Type I errors caused by other potential drivers of
527 change being correlated with the precipitation and temperature variables.

528

529 To conclude, we have found good evidence that increasing winter and spring
530 temperatures are likely to have improved climatic conditions for resident and short-
531 distance migrant species in England, accounting for some of the observed long-term
532 population increases in these species. A component of long-distance migrant
533 population declines may also have been caused by warming in the UK, such as
534 through increasing May temperatures, potentially through detrimental effects of
535 phenological mismatch upon breeding success (e.g. Both & Visser 2001; Both *et al.*
536 2006) and lagged effects of hot, dry summers. The effects of such summer conditions
537 were relatively widespread across species, particularly also affecting habitat
538 specialists with a narrow niche breadth (Fig. 3a), and cold-adapted species (Fig. 4a),
539 and may have been mediated through impacts on food resources reducing breeding
540 success in year, as has previously been observed in upland habitat specialists (Pearce-
541 Higgins 2010; Pearce-Higgins *et al.* 2010; Fletcher *et al.* 2013). Thus, our results add
542 weight to the increased recognition of the need to consider potential lagged effects of
543 climate change on species' interactions (Cahill *et al.* 2013; Ockendon *et al.* 2014).
544 Finally, our results are consistent with previous work demonstrating negative impacts

545 of warming on habitat specialists with a narrow niche breadth (Davey *et al.* 2012,
546 2013) and northerly-distributed species associated with cold climates (Devictor *et al.*
547 2012). These community-level changes appear to represent the accumulation of
548 consistent differential impacts of summer and spring warming. In summary, our
549 analysis has provided novel insights about the climatic drivers of recently observed
550 changes in bird communities in England than before, and strengthens the assertion
551 that such changes are indeed at least partially a response to climate change.

552

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561

562 *Data accessibility*

563 The annual population trend estimates for England used in this paper can be viewed at
564 <http://www.bto.org/about-birds/birdtrends> and are available through the BTO's
565 standard data request procedure (see [http://www.bto.org/research-data-services/data-
566 services/data-and-information-policy](http://www.bto.org/research-data-services/data-services/data-and-information-policy)).

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814 **Fig. 1.** Schematic illustrating the months and seasons over which weather data were
815 collated (only every third month is shown for reasons of space) against the survey
816 periods used to generate the population growth data. Vertical dashed lines indicate
817 census years.

818

819

820 **Fig. 2.** Monthly variation in the mean effect of temperature (a-c) and precipitation (d-
821 f) upon the population growth of bird species, plotted separately for resident (a, d),
822 short-distance migrants (b, e) and long-distance migrants (c, f). Statistically
823 significant ($P < 0.05$) interactions between weather variable effect and migratory
824 status are indicated by an asterisk, with those outside of parenthesis achieving the
825 Bonferroni threshold for significance. The significance of individual effects are given
826 in Appendix S4. Estimates from models in which the autoregressive function failed to
827 converge, are circled as they may be more prone to Type I error.

828

829 **Fig. 3.** Monthly variation in the mean interaction (\pm SE) between temperature (a) or
830 precipitation (b) and niche breadth (measured by the species specialisation index;
831 SSI), upon the population growth of bird species. A negative interaction means that
832 weather variables had a more negative, or less positive, impact on specialist than
833 generalist species. Statistically significant interactions ($P < 0.05$) are indicated by an
834 asterisk, with those outside of parenthesis achieving the Bonferroni threshold for
835 significance. Estimates from models in which the autoregressive function failed to
836 converge, are circled as they may be more prone to Type I error.

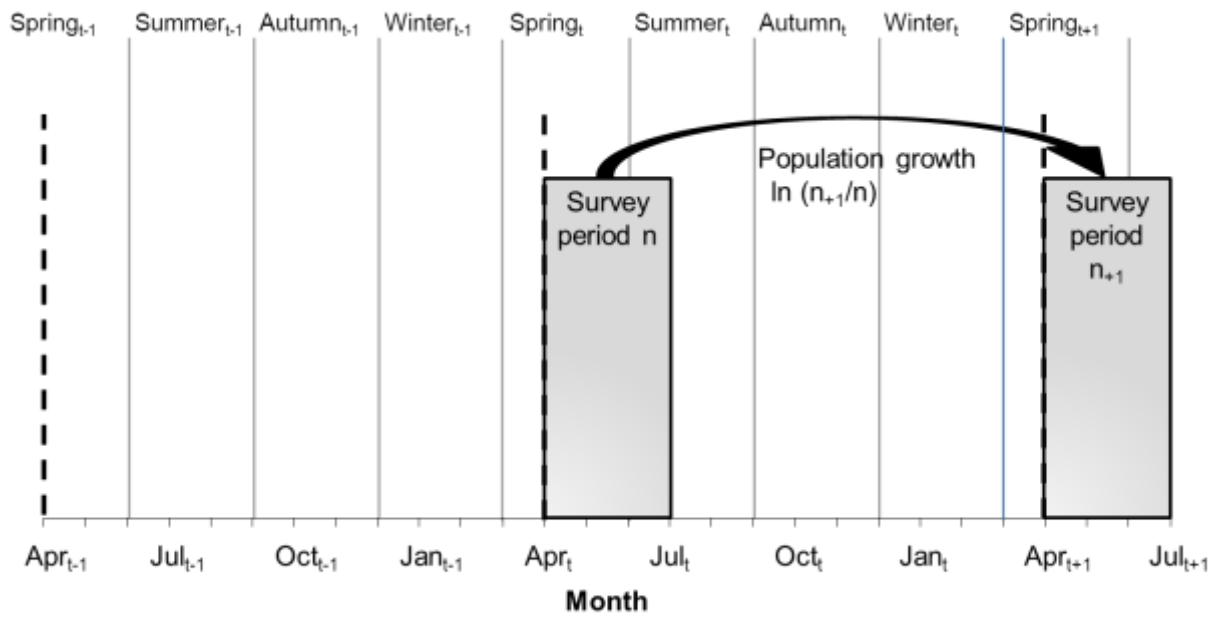
837

838 **Fig. 4.** Monthly variation in the mean interaction (\pm SE) between temperature (a) or
839 precipitation (b) and thermal association (measured by the species temperature index;
840 STI), upon the population growth of bird species. A negative interaction means that
841 weather variables had a more negative, or less positive, impact on warm-associated
842 than cold-associated species. Statistically significant interactions ($P < 0.05$) are
843 indicated by an asterisk, with those outside of parenthesis achieving the Bonferroni
844 threshold for significance. Estimates from models in which the autoregressive
845 function failed to converge, are circled as they may be more prone to Type I error.
846

847 **Fig. 5.** Monthly variation in the interaction between the relationship between weather
848 variables and population growth and 45-year population trends (solid line).
849 Statistically significant interactions ($P < 0.05$) are indicated by an asterisk, with those
850 outside of parenthesis achieving the Bonferroni threshold for significance. The single
851 circled estimate is from a model in which the autoregressive function failed to
852 converge, and may be more prone to Type I error. These are overlaid above the long-
853 term trend in weather variables (z-axis) for each month over the same period (grey
854 bars). Values vary slightly for the same month, depending on which year they refer to.
855 Error bars give standard errors.

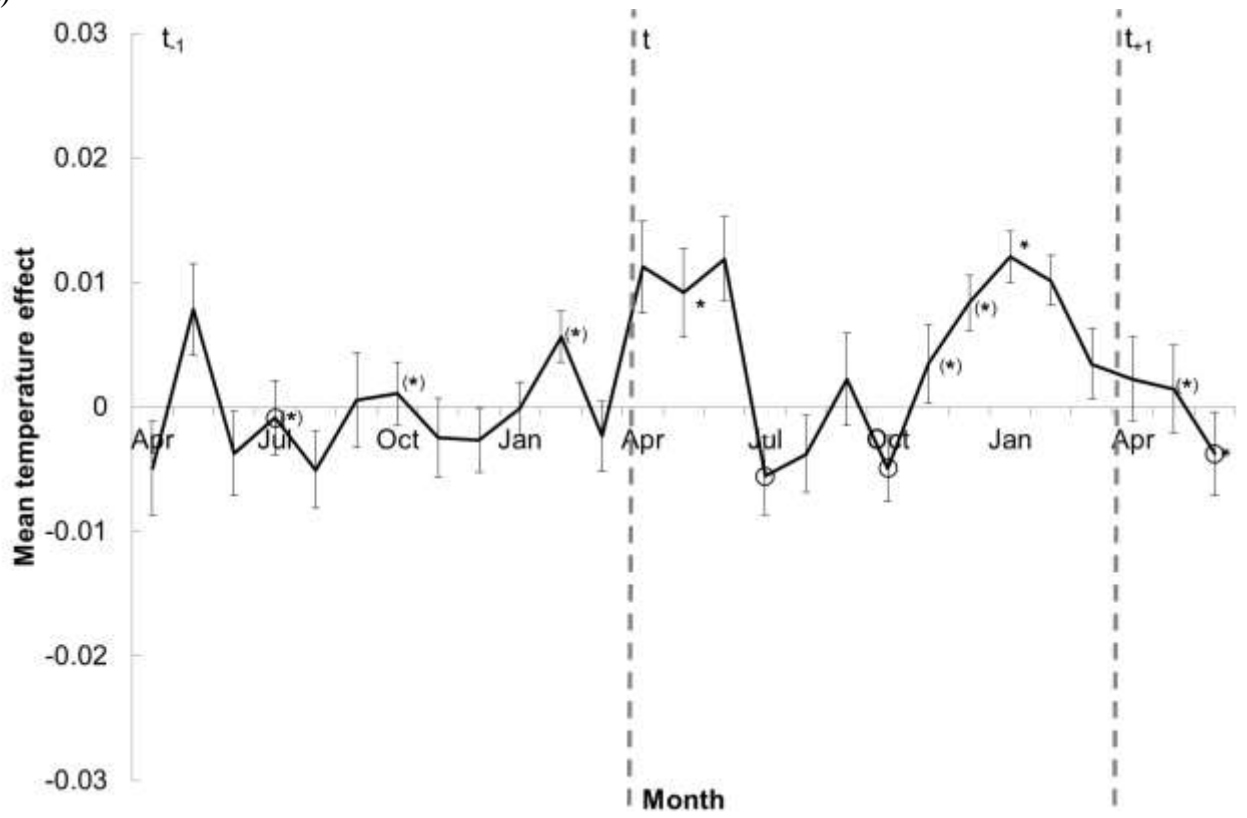
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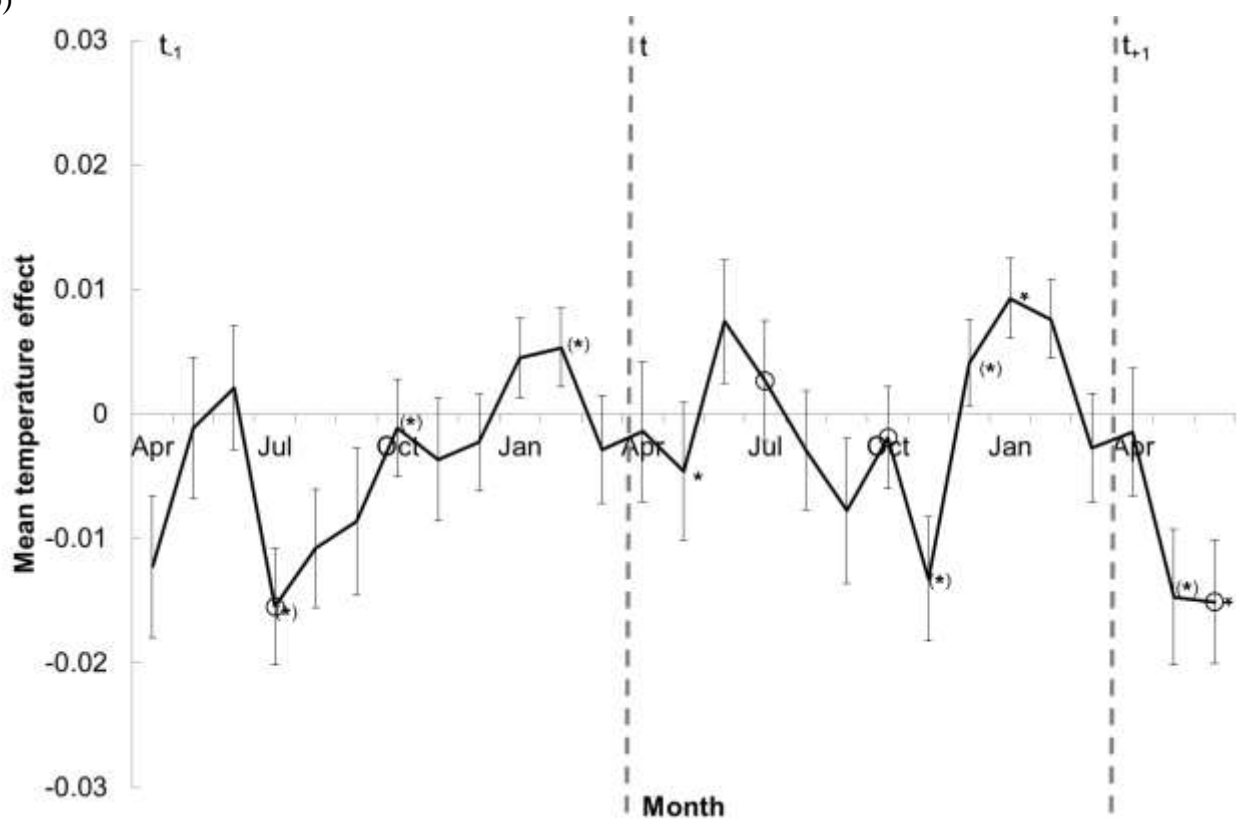


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860 a)

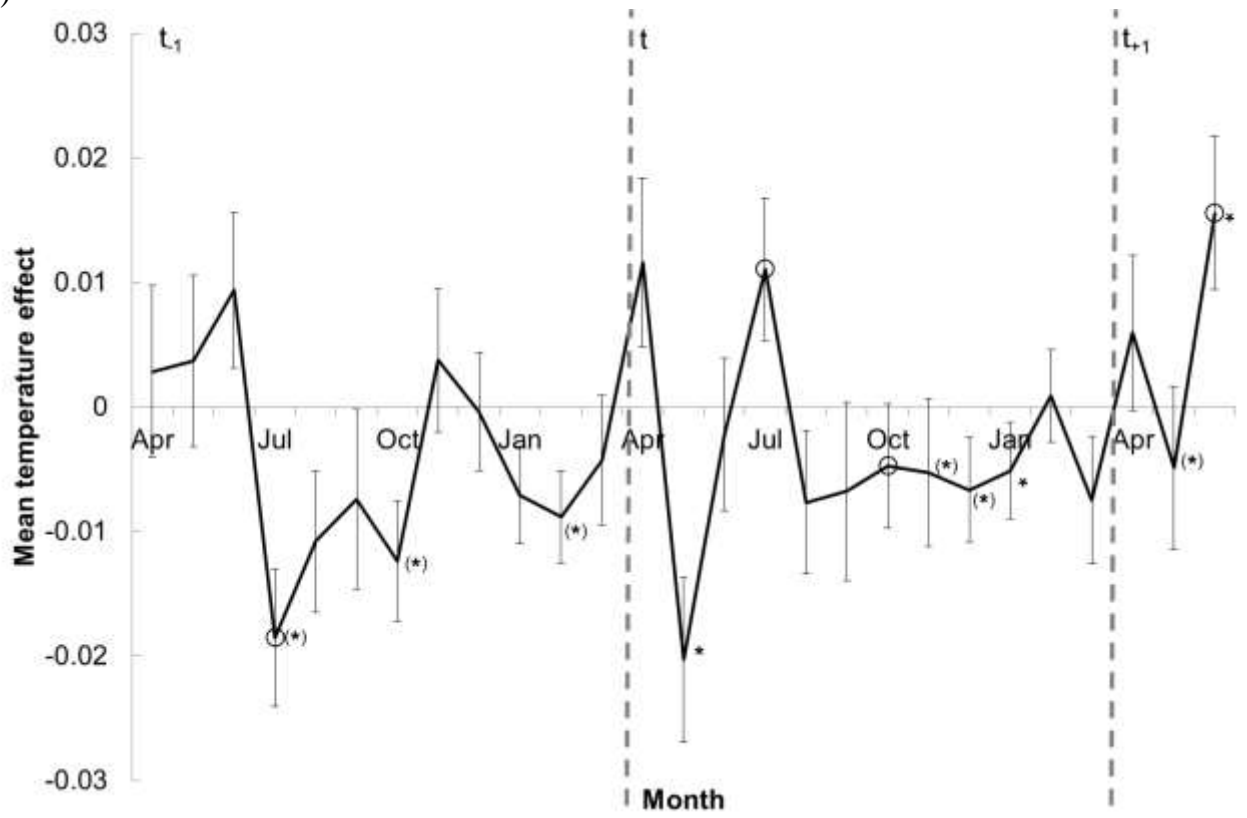


861 b)
862

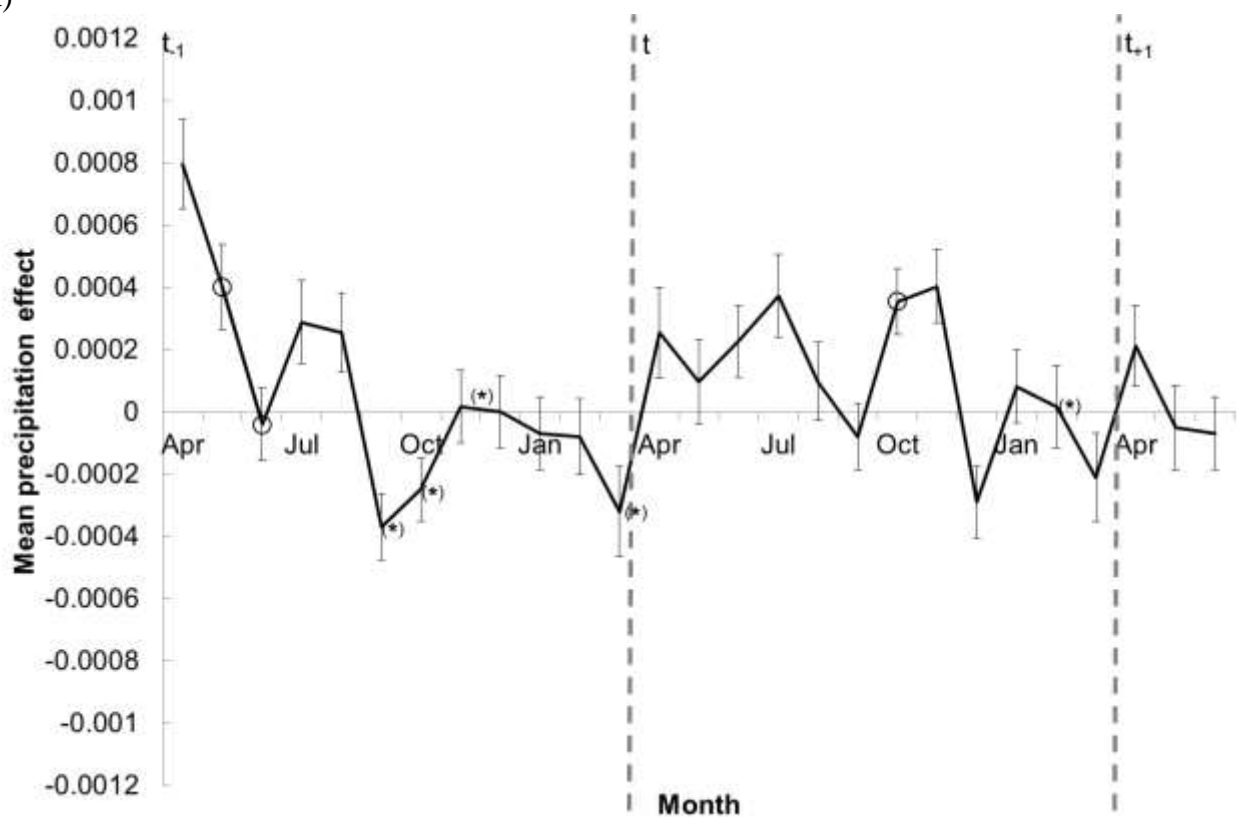


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865 c)

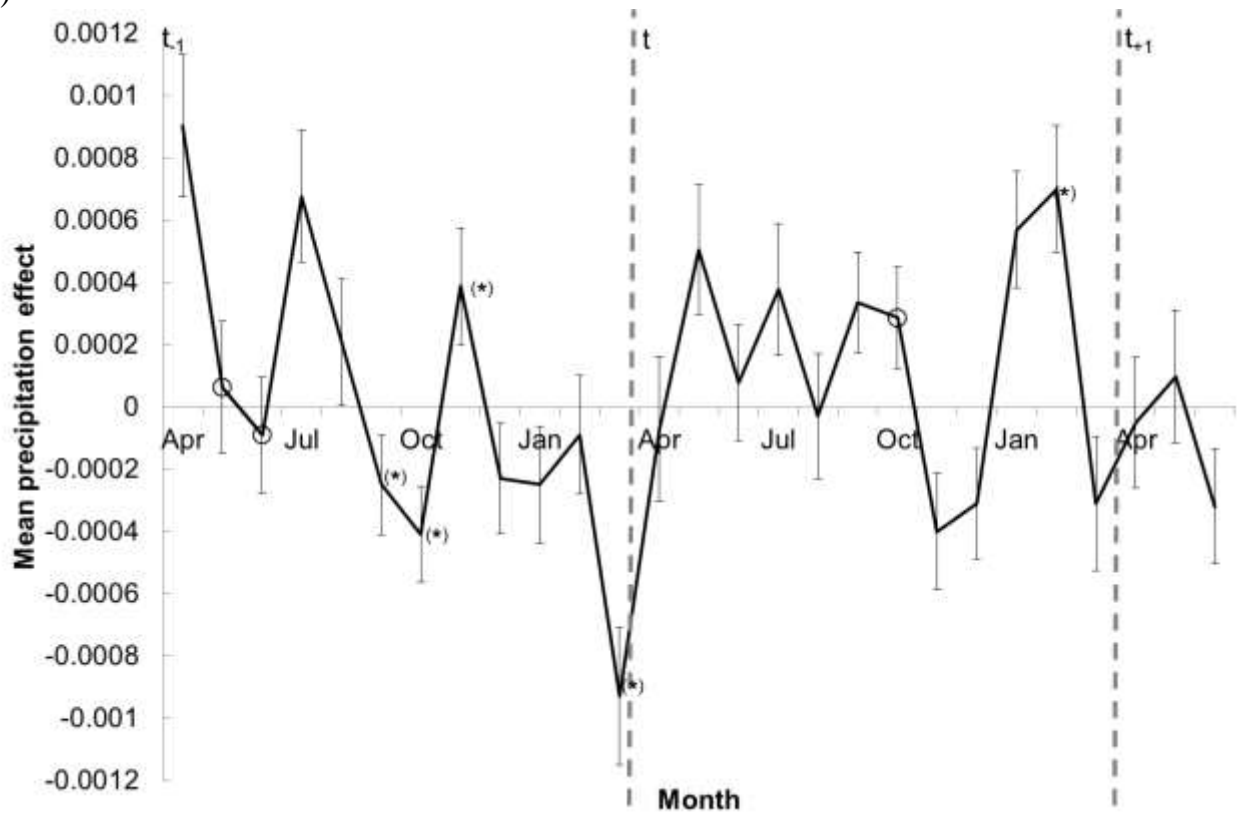


866 d)
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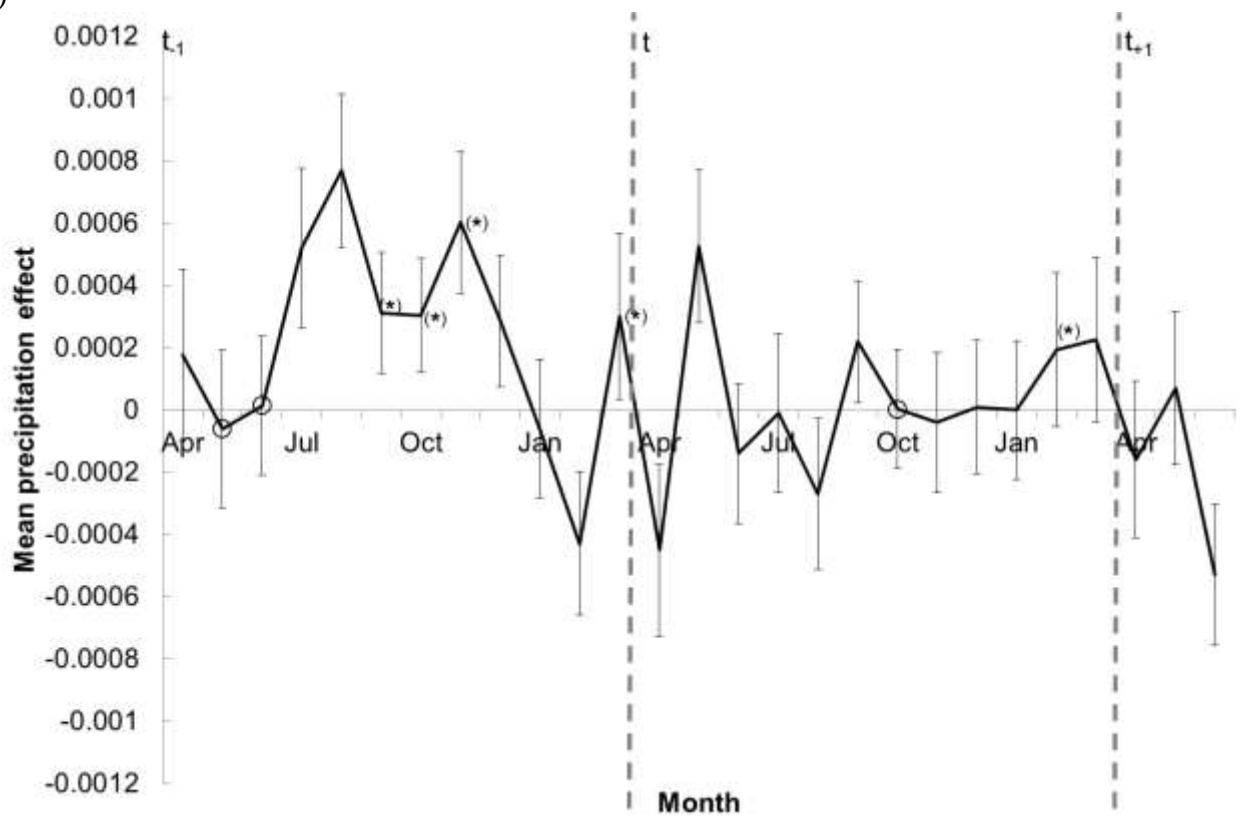


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872 e)

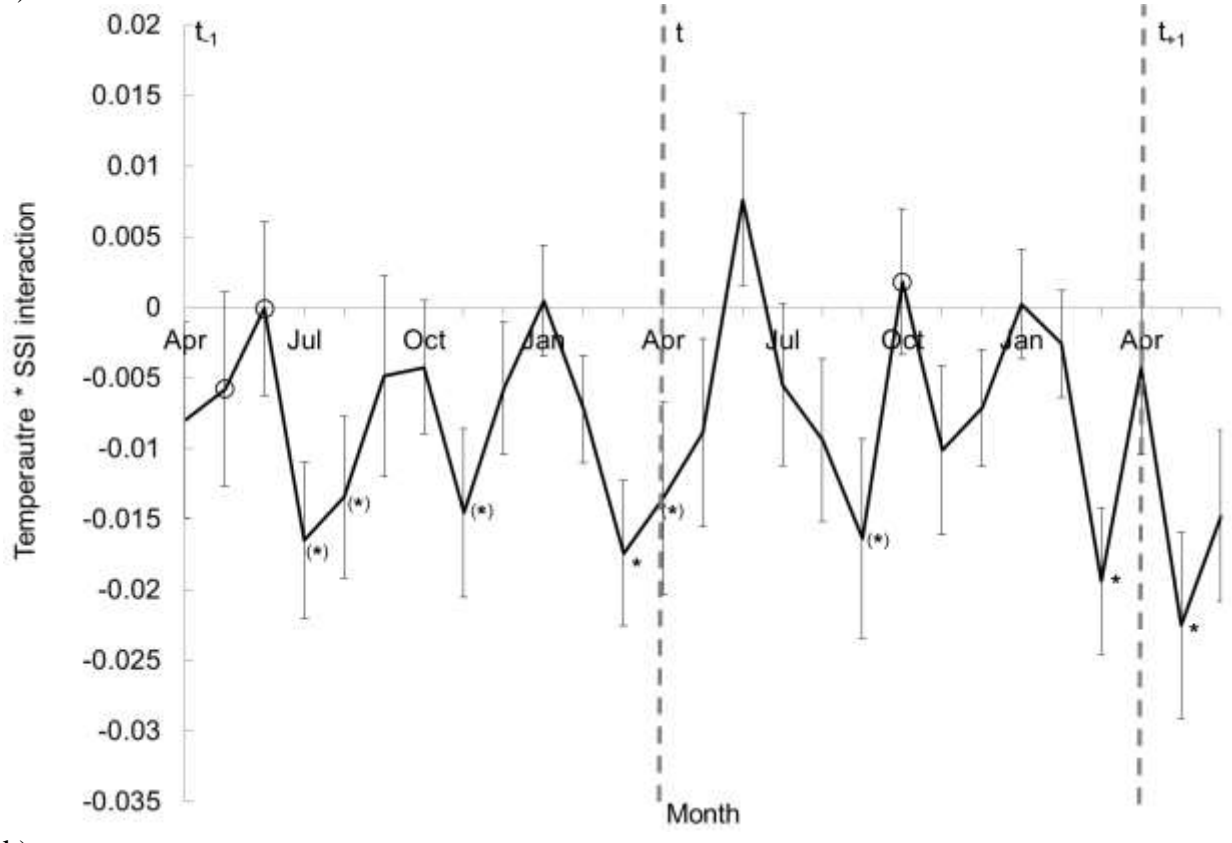


873 f)
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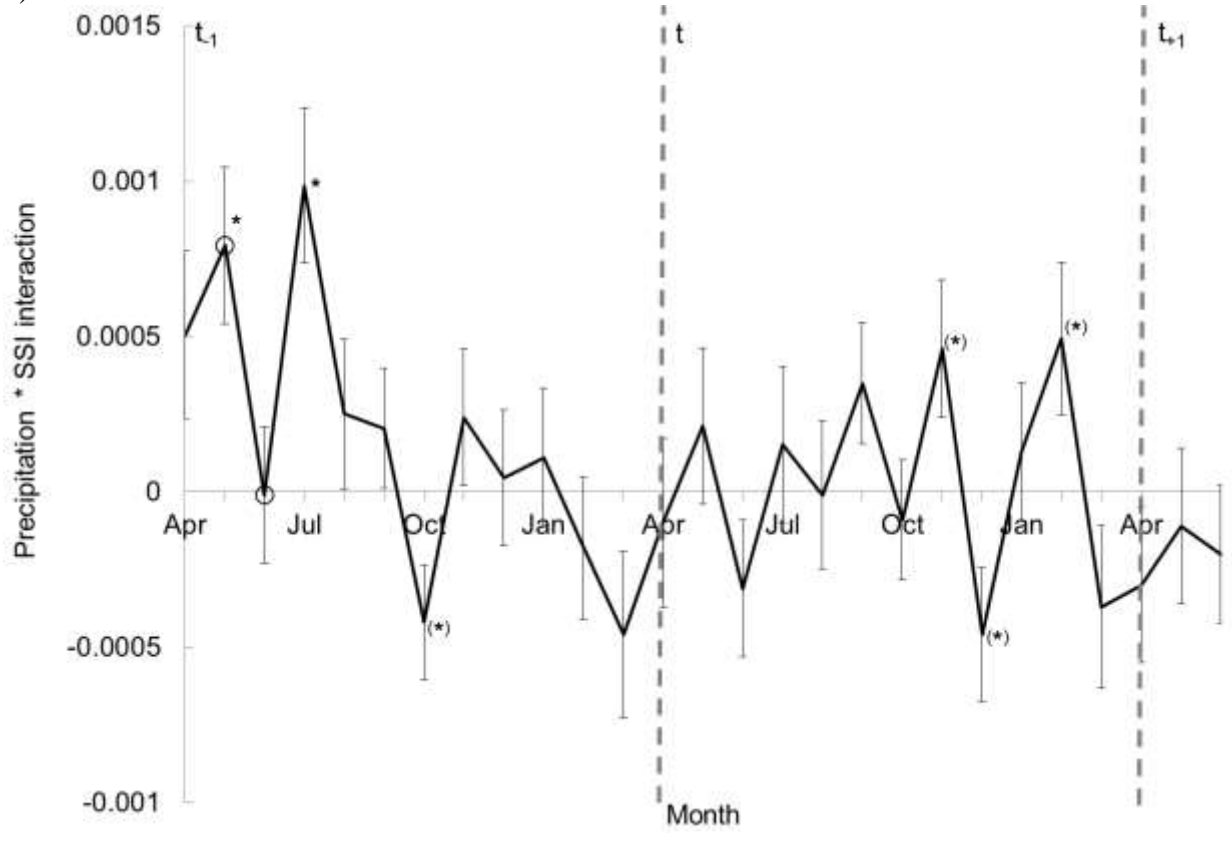


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877 a)



878 b)
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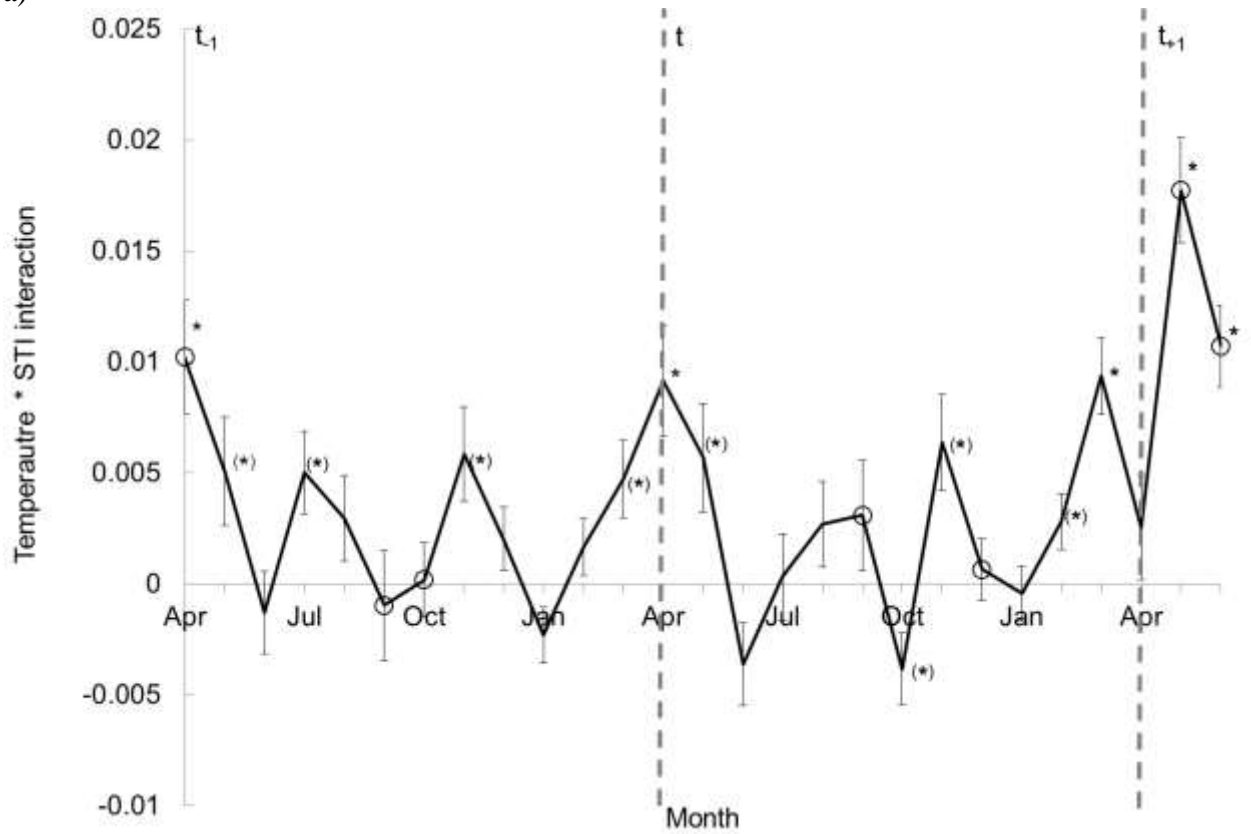


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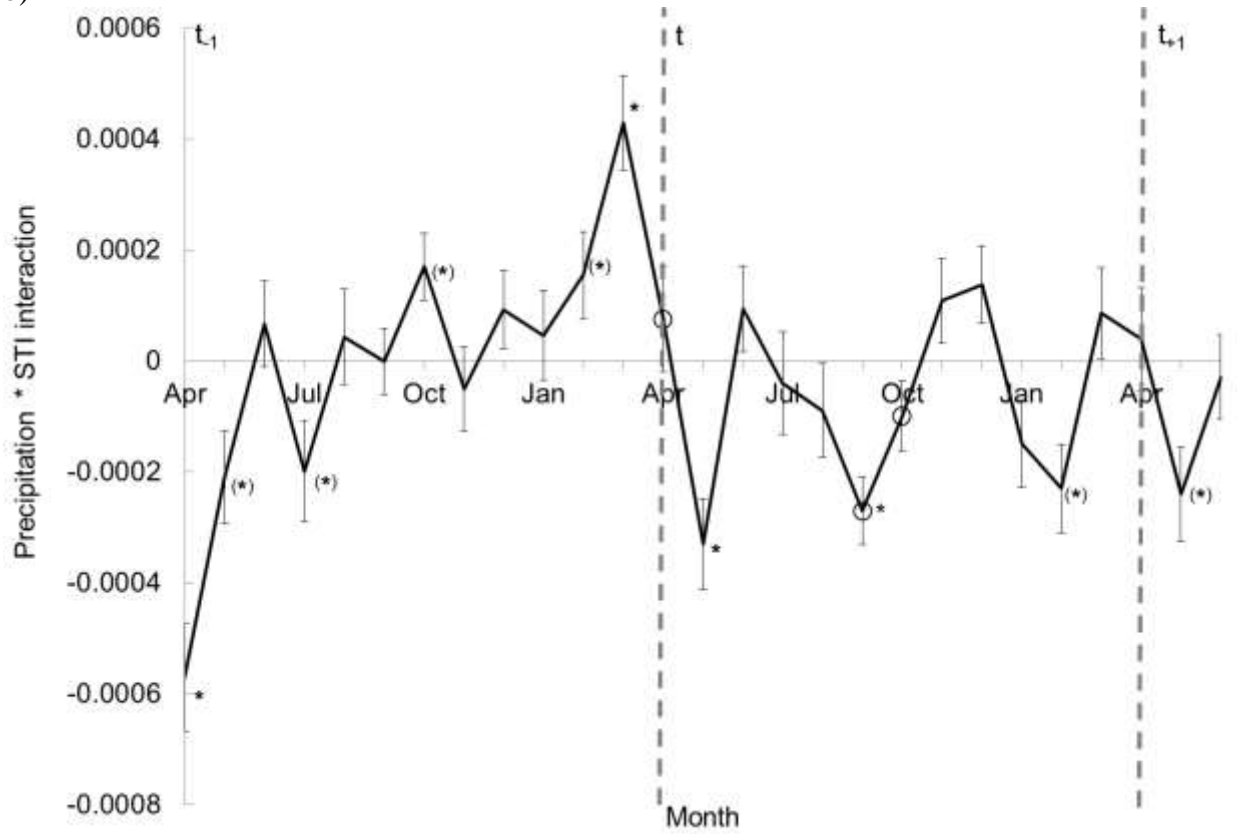
a)



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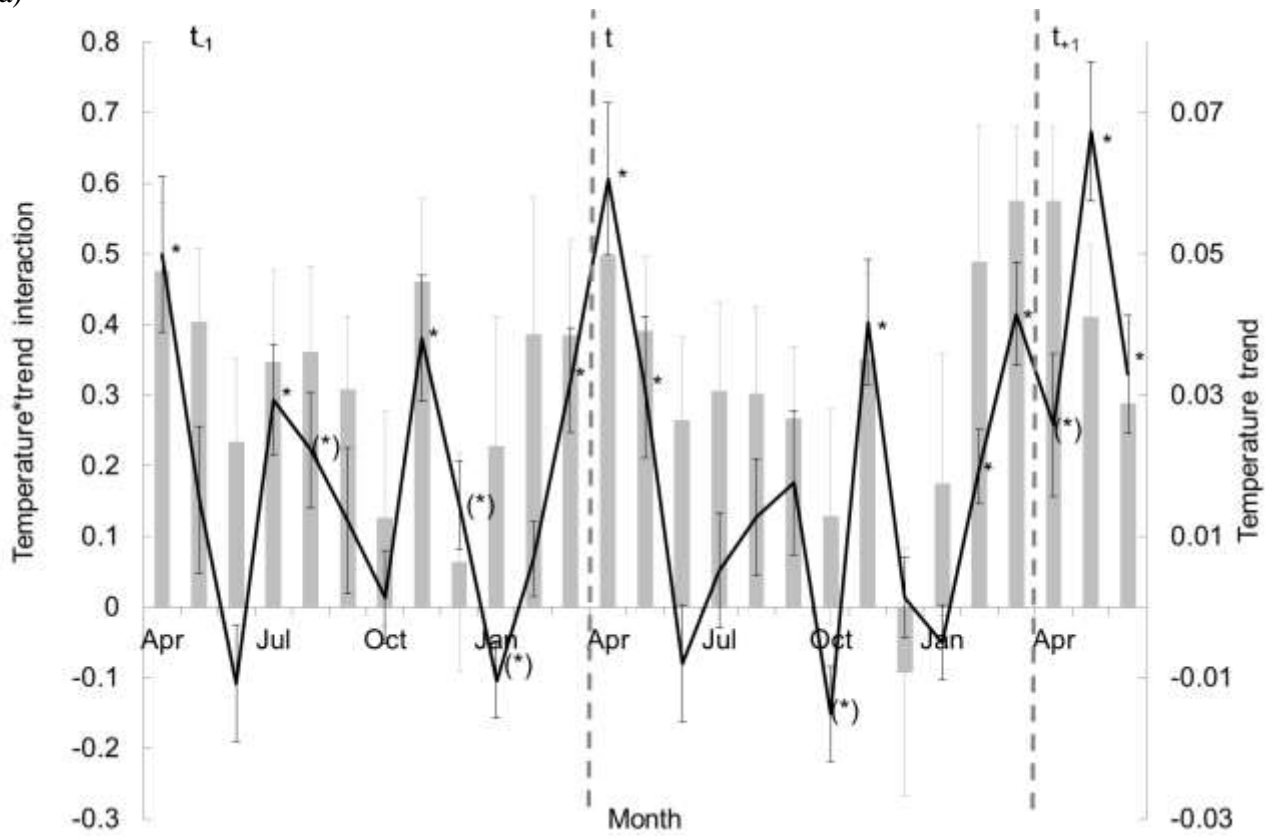
b)



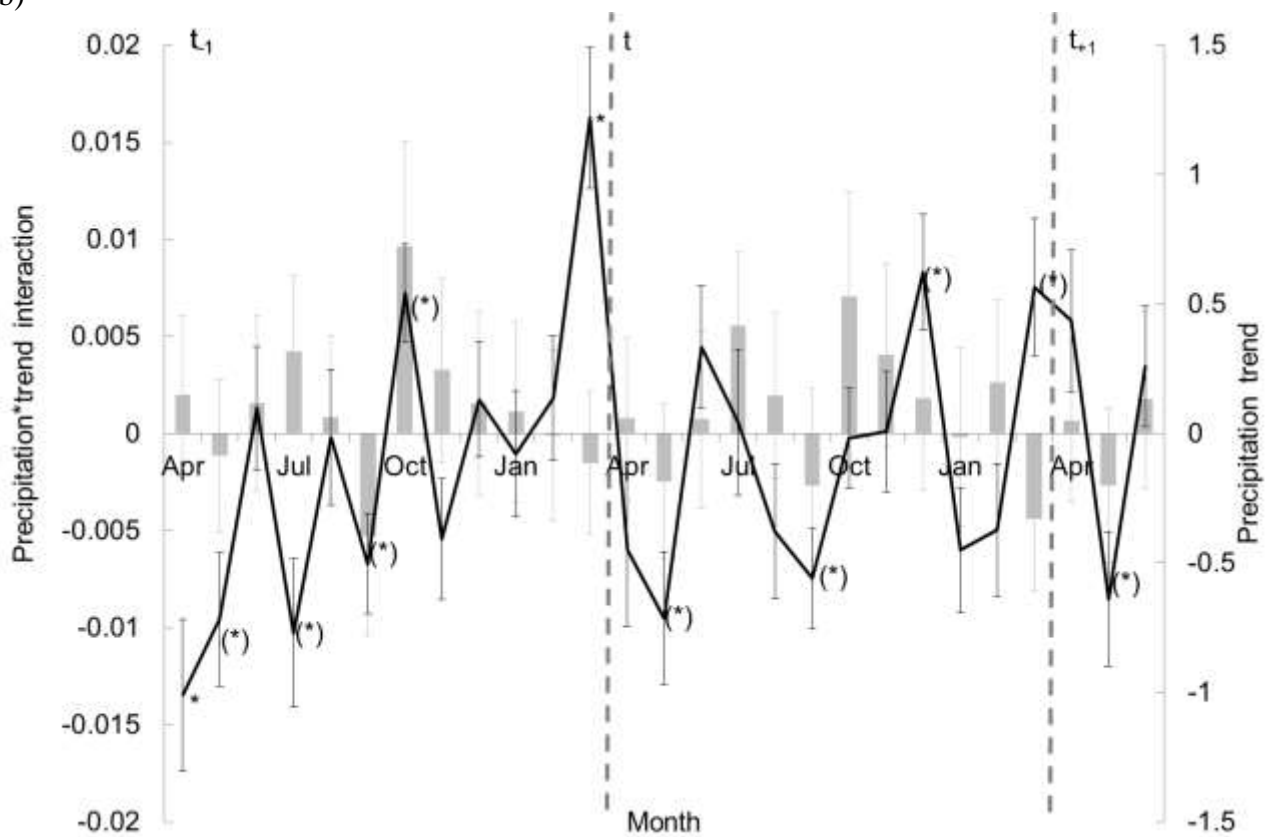
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890 a)



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892 b)



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