Divers of climate change impacts on bird communities

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Drivers of climate change impacts on bird communities.

Pearce-Higgins, J.W.[1][*], Eglington, S.M.[1,2], Martay, B.[1], Chamberlain, D.E.[3]

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

[2]ECON Ecological Consultancy Ltd, Unit 7, The Octagon Business Park, Little Plumstead, Norwich, NR13 5FH, UK

[3]Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Via Accademia Albertina 13, 10123 Torino, Italy.

*Corresponding author; Telephone: +44 1842750050, Fax: +44 1842750030, email james.pearce-higgins@bto.org

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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.

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Introduction

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

Many of these studies have been conducted on well monitored bird populations, where three main trends in community change have been described. Firstly, long-distance migrants have declined more than resident or short-distance migrant species (Holmes & Sherry 2001; Sanderson *et al.* 2006; Yamaura *et al.* 2009). This has been attributed to a range of factors, but there is evidence that climate change may have driven at least some of this variation. For example, long-distance migrants now arrive later relative to spring temperatures on the breeding grounds than they used to, which may have population consequences (Both & Visser 2001; Møller *et al.* 2008; Saino *et al.* 2010; although see Johansson & Jonzén 2012), whilst their populations may also 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_1 modelled estimates of the intercept,

226　species-specific effect of density-dependence and mean weather effect size across all

227　species, respectively.

228

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

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

11

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

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

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

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

The interaction between mean monthly temperature and SSI was statistically significant ($P < 0.05$) for eight months, of which three remained significant after applying the Bonferroni correction (Fig. 3a). All of these significant effects, and the 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 signification 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 (Februrary$_t$) 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 $year_t$, 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

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).

567

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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 indicted 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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860   a)

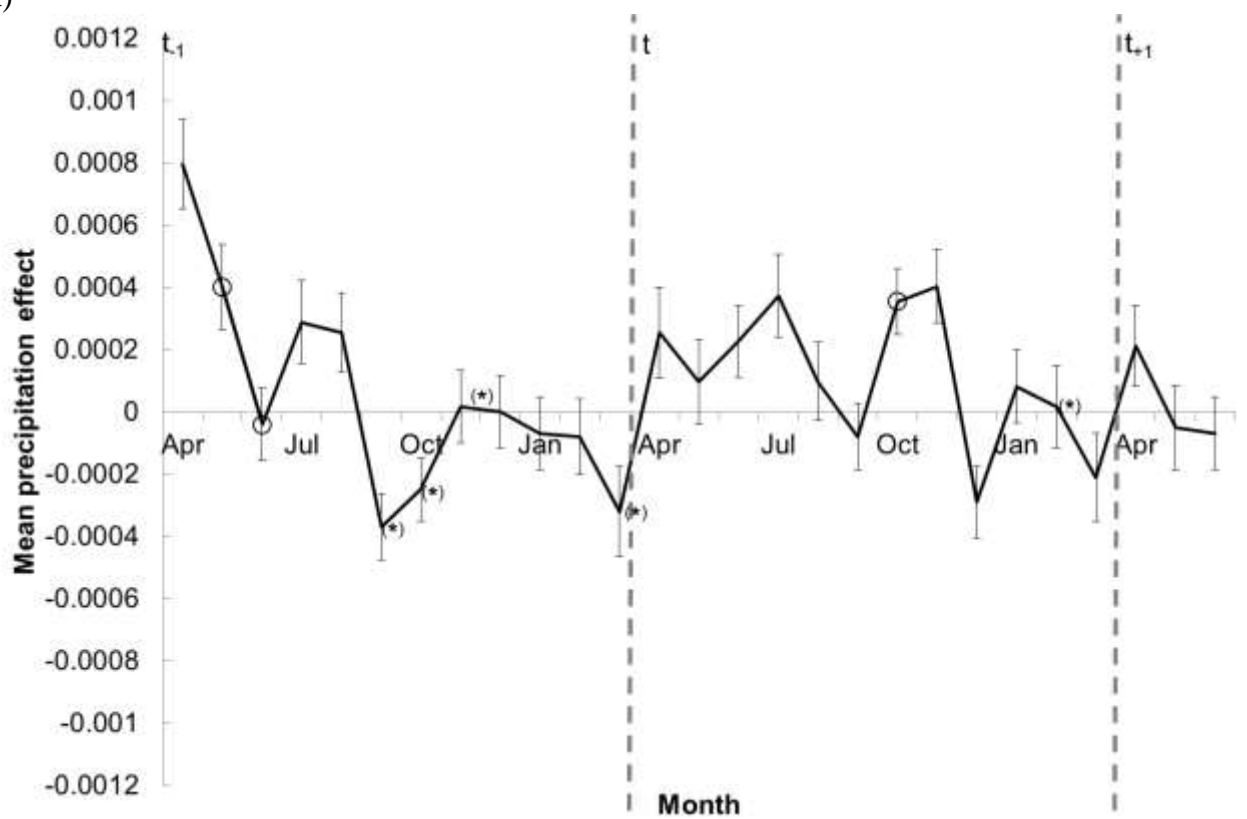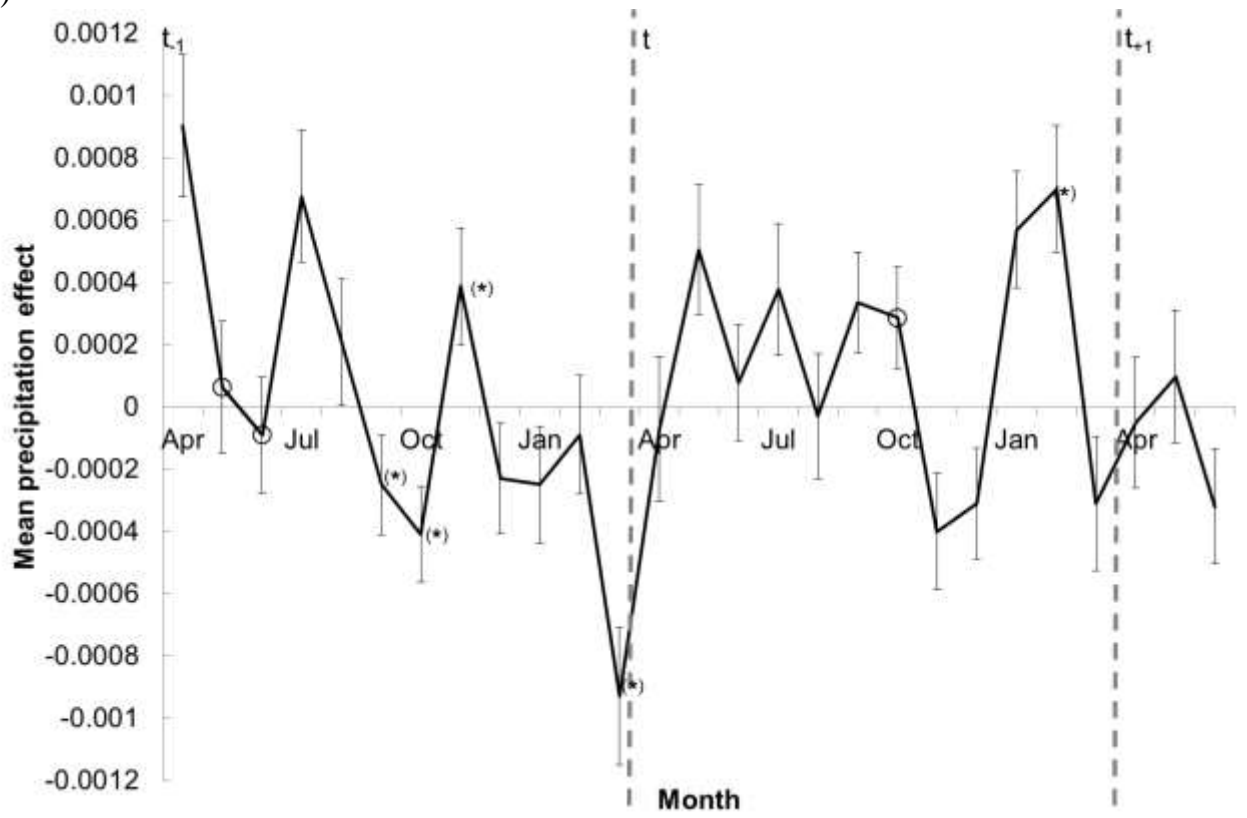
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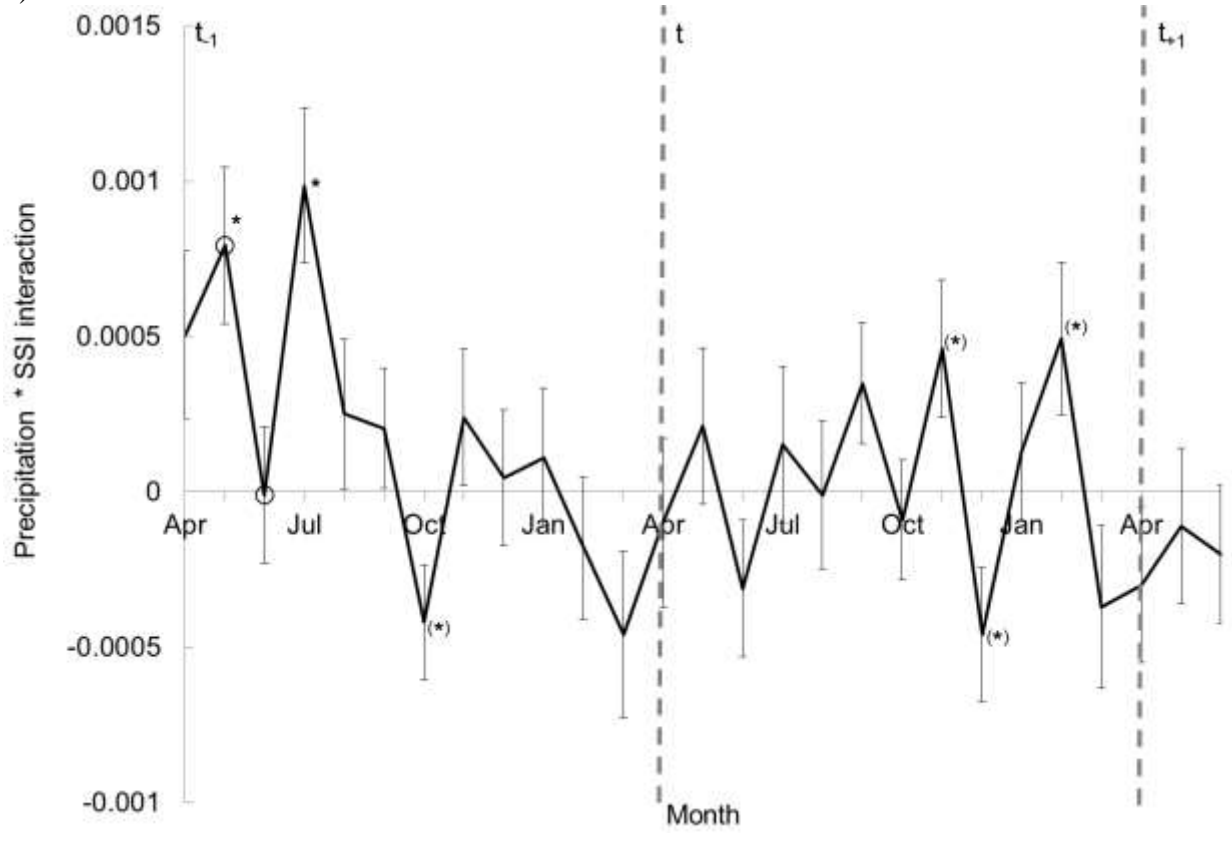

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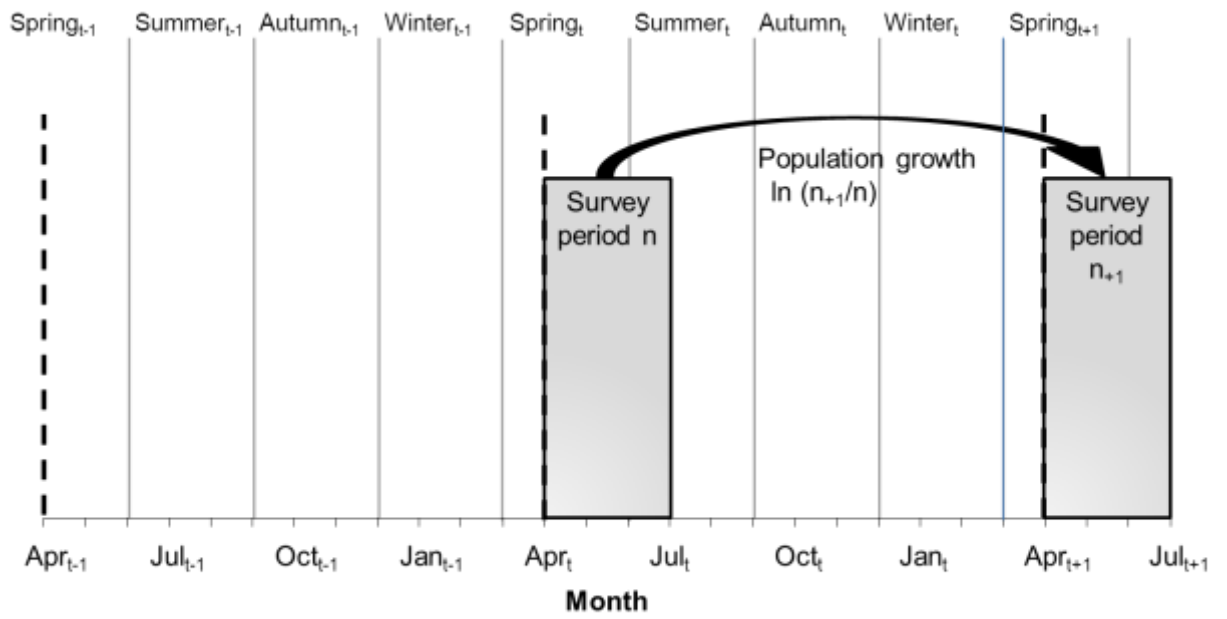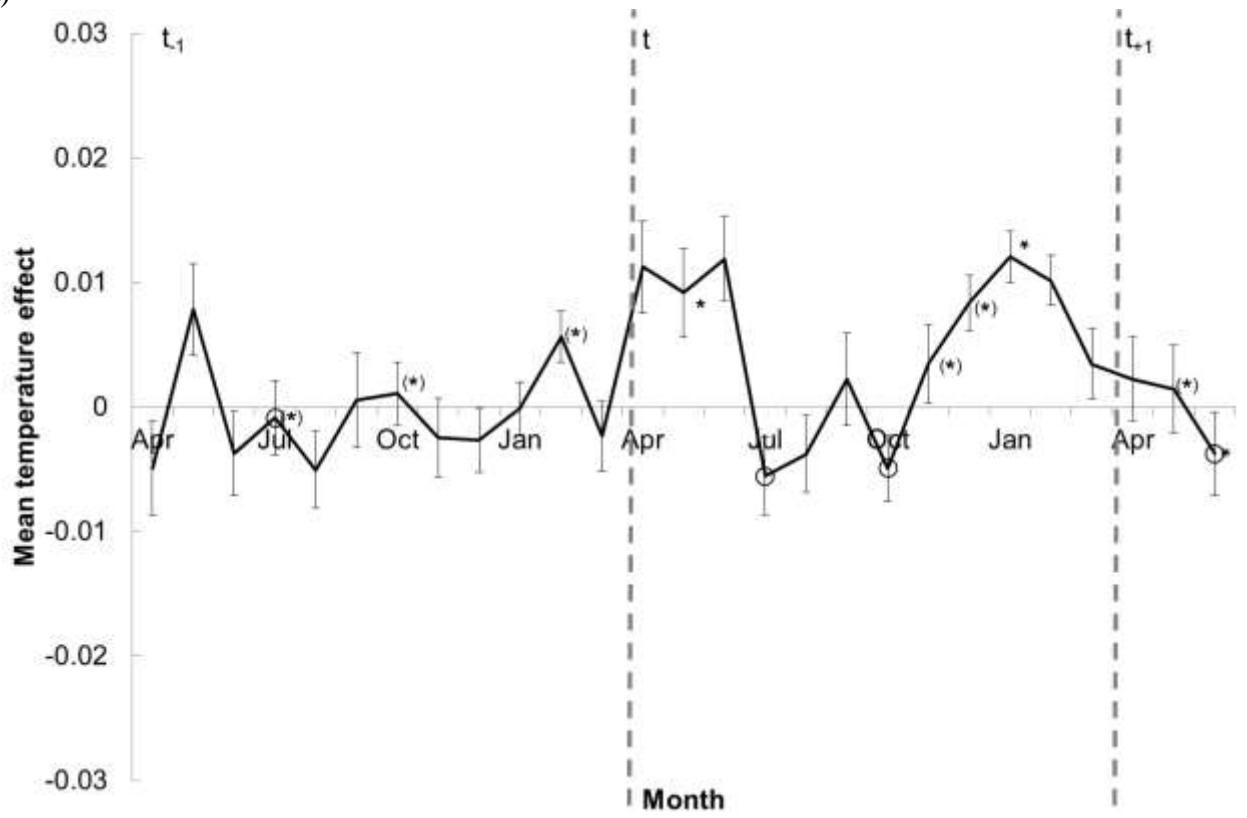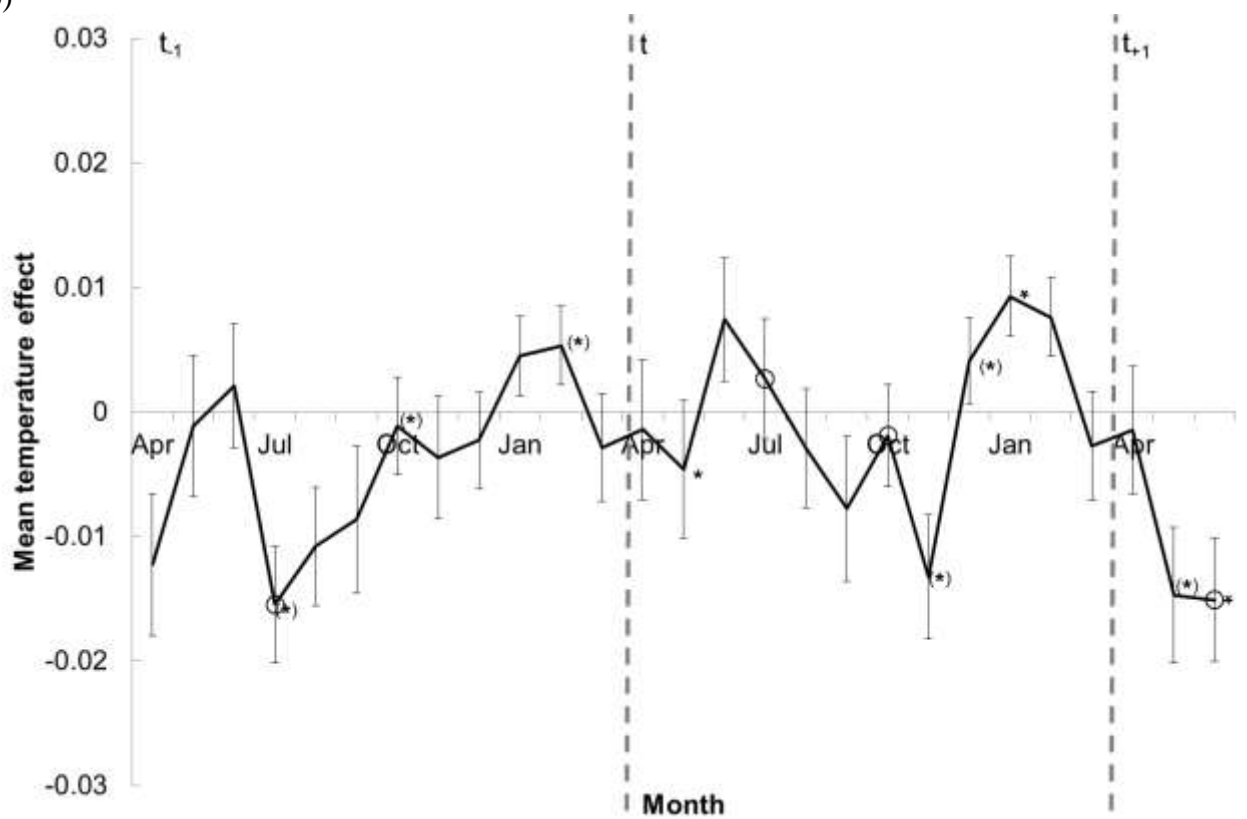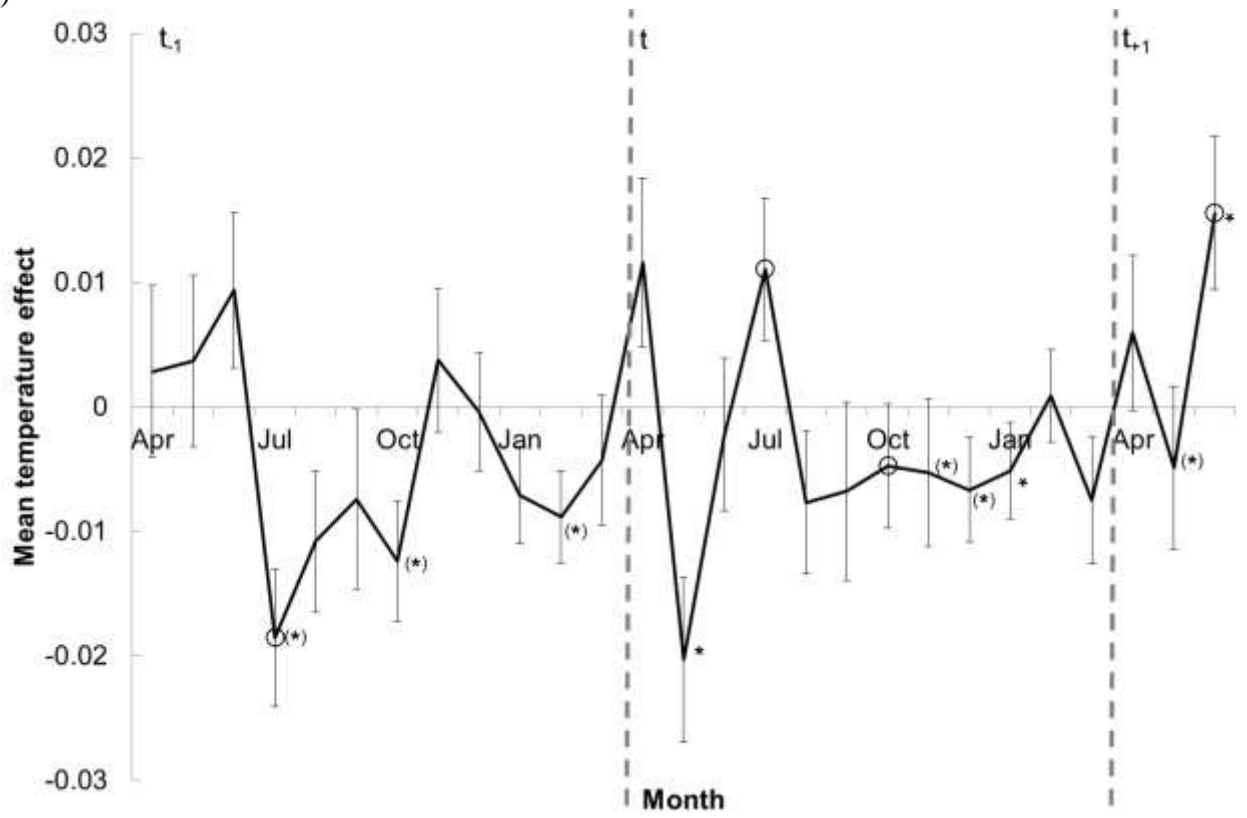
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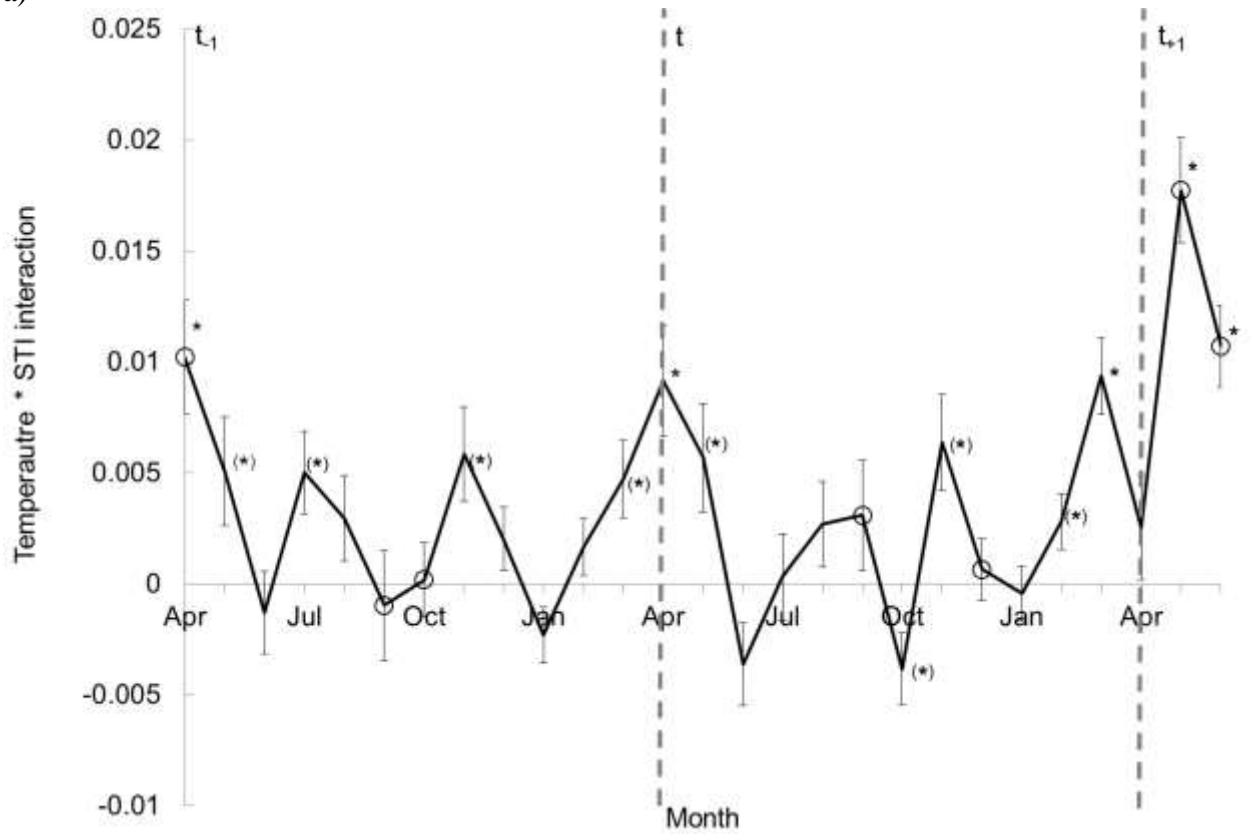

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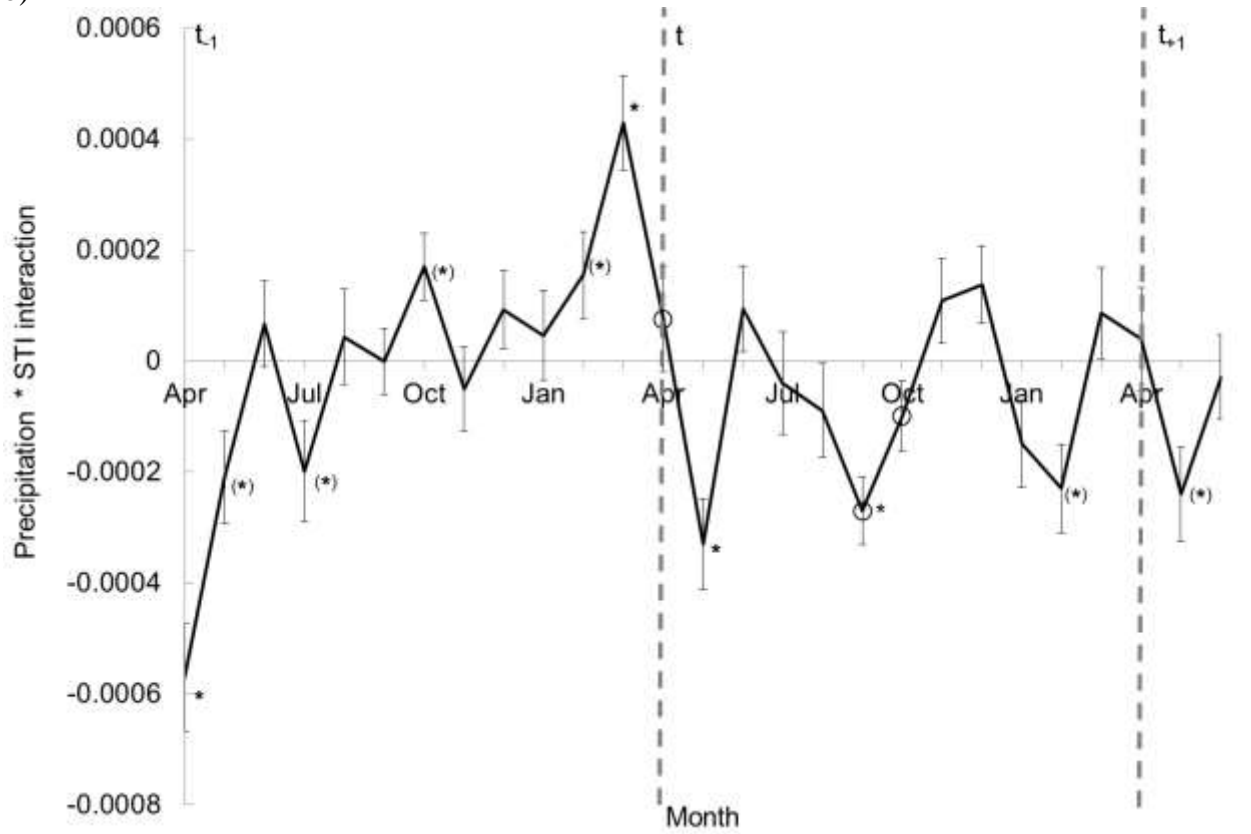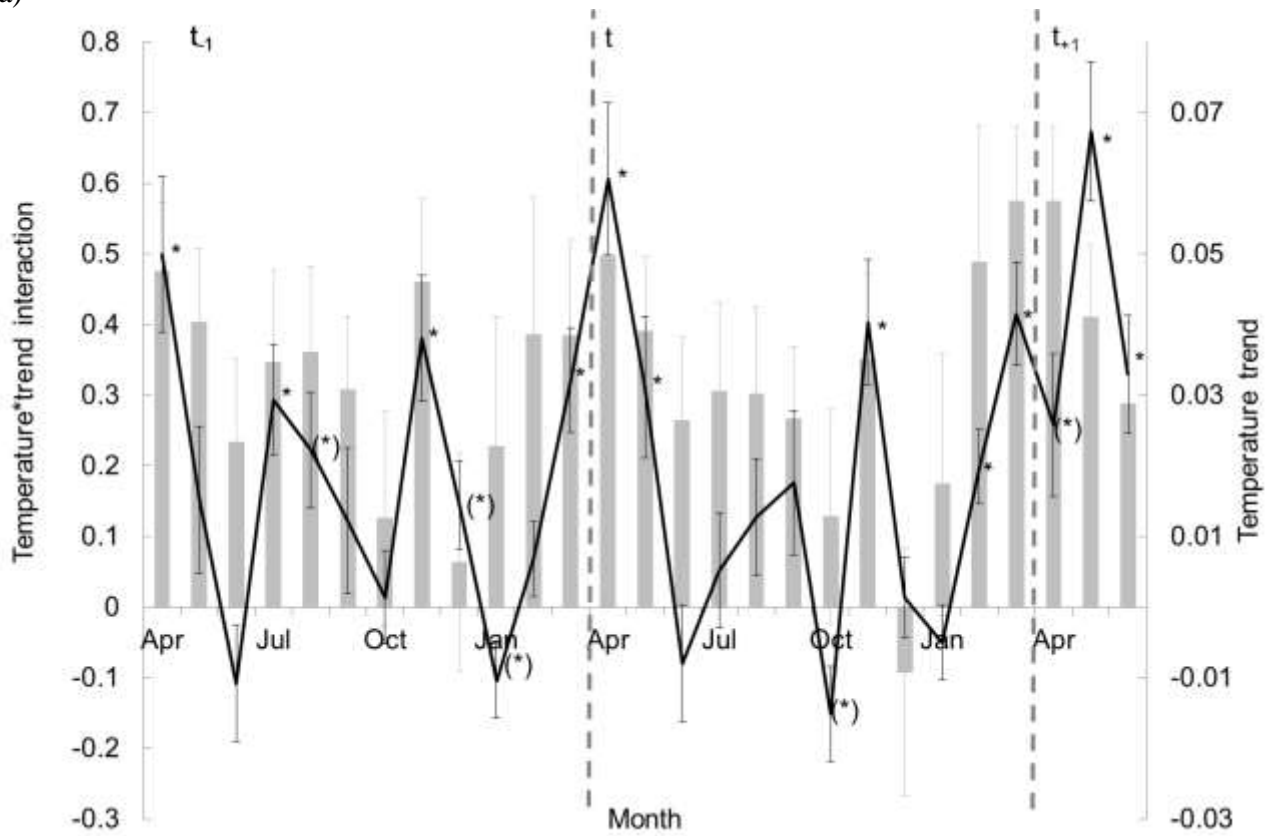
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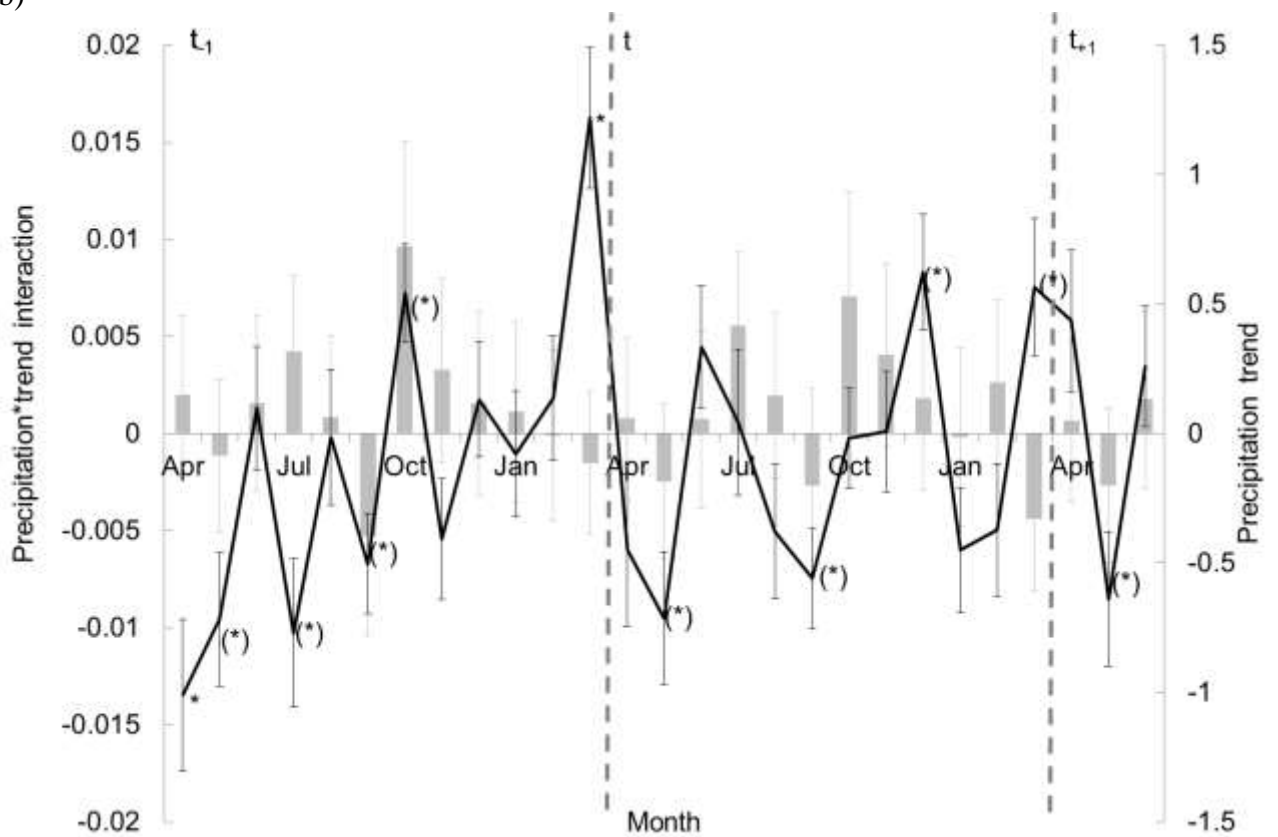879   b)

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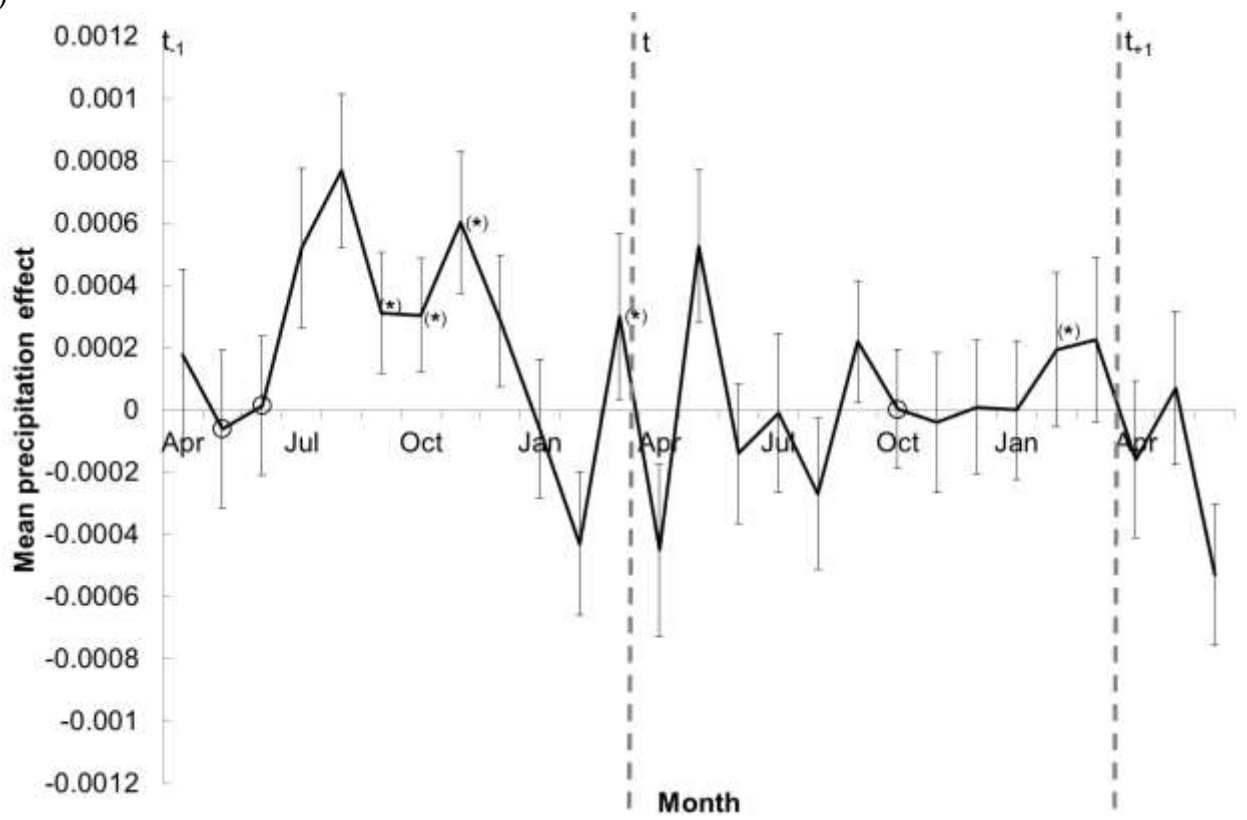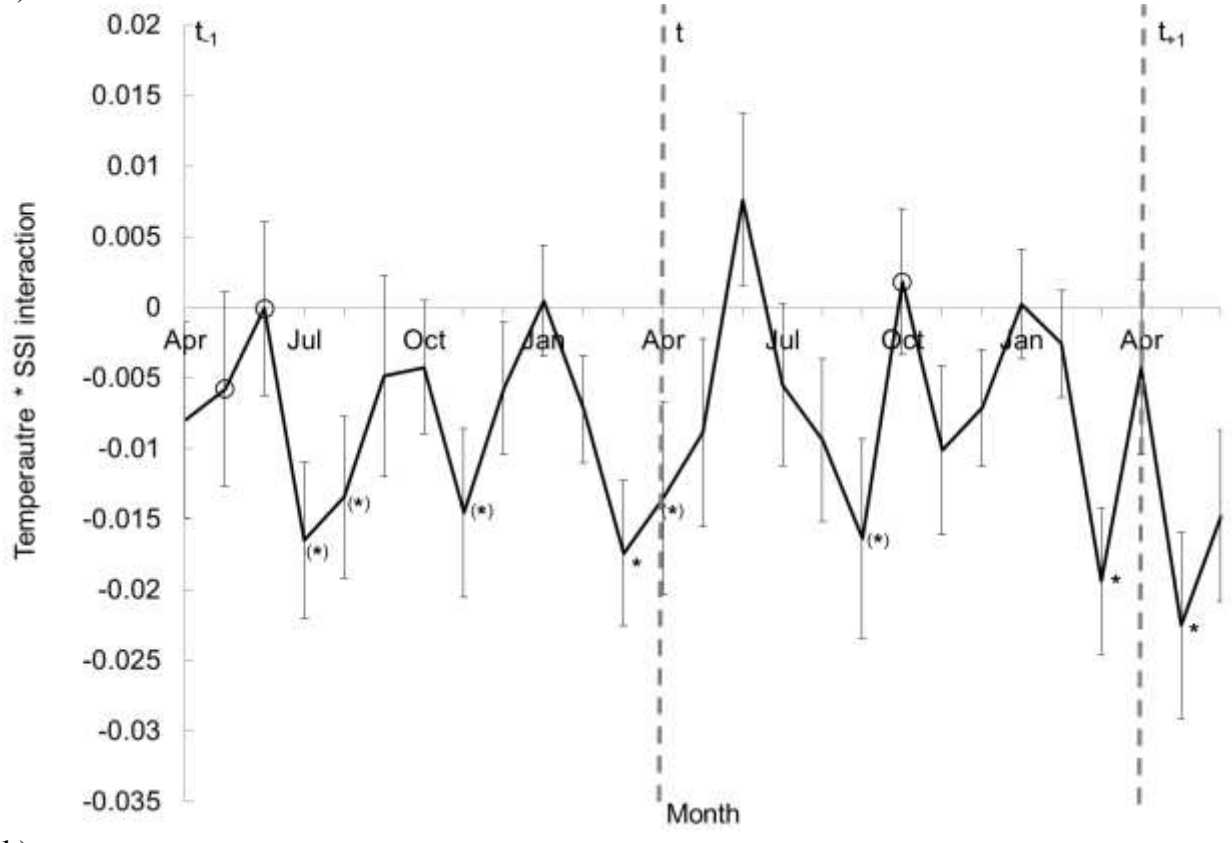
884
885   a)

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887   b)

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890   a)

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892   b)

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