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Testing for effects of climate change on competitive relationships and coexistence between two bird species

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36 **Summary**

37 Climate change is expected to have profound ecological effects, yet shifts in competitive abilities among
38 species are rarely studied in this context. Blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*)
39 compete for food and roosting sites; yet coexist across much of their range. Climate change might thus
40 change the competitive relationships and coexistence between these two species.

41 Analysing four of the highest quality, long-term datasets available on these species across Europe, we
42 extend the text-book example of coexistence between competing species to include the dynamic effects of
43 long-term climate variation. Using threshold time-series statistical modelling, we demonstrate that long-
44 term climate variation affects species demography through different influences on density-dependent and
45 density-independent processes. The competitive interaction between blue and great tits has shifted in one
46 of the studied sites, creating conditions that alter the relative equilibrium densities between the two species,
47 potentially disrupting long-term coexistence.

48 Our analyses show that long-term climate change can, but does not always, generate local differences in
49 the equilibrium conditions of spatially structured species assemblages. We demonstrate how long-term
50 data can be used to better understand whether (and how) e.g. climate change might change the
51 relationships between coexisting species. However, the studied populations are rather robust against
52 competitive exclusion.

53

54 **Keywords:** Intraspecific and interspecific competition; Climate variation; Statistical modelling;

55 Threshold modelling; Coexistence and competitive exclusion

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60 **1. Introduction**

61 Competition is defined as the negative effects which one organism has upon another by consuming, or
62 controlling access to, a resource that is limited in availability [1]. At the species level, competition may
63 lead to exclusion if one species experiences a greater competitive effect from another species than within
64 its own species [2, 3]. Theoretical [3] and empirical [4, 5] investigations have indicated the importance of
65 both competition and the environment in predicting species composition, diversity and niche overlap in
66 ecological communities. However, conclusive demonstrations of competitive exclusion are rare.

67 Climate fluctuations are known to affect the distribution, behaviour and phenology of plants and
68 animals [6]. Recent climatic changes have been reported to disrupt tight trophic interactions between
69 consumers and resources, in fish-plankton [7], insect-plant [8] and bird-insect systems [9], and climate
70 change is one of the largest current threats to biodiversity [10]. It has recently been hypothesised that
71 climate change may affect the coexistence of competing species [11] however few studies have so far
72 incorporated the climate effect in a classical competitive framework, e.g., those that do have dealt with
73 plant communities [12, 13]. To do so requires the analysis of long-term data on the dynamics of
74 competing species together with corresponding climate data. We do so here for the first time, to our
75 knowledge, using long-term data on competing bird species (tits).

76 It is important to differentiate between the effects that short- and long-term environmental changes
77 may have on species co-existence. Short-term environmental variation represents the fluctuations around
78 some stationary point (e.g., the annual variation in monthly temperature around the long-term mean for that
79 month) whereas long-term variation represents a change in position of this stationary point (e.g., an
80 increase or decrease in the long-term average temperature for a given month).

81 Here we study the effect of year-to-year variation in climatic condition on the competitive
82 interaction between two European tit species, the blue tit (*Cyanistes caeruleus*, BT) and the great tit (*Parus*
83 *major*, GT). During the breeding season GT and BT compete for food. Because BT consume smaller instar
84 of the same caterpillar species as eaten by the GT [14-16] they can pre-emptively consume available prey
85 and hence outcompete GT for food. Although this has an impact on GT reproductive success [17], it does

86 not have an effect on GT breeding numbers. During winter both GT and BT use cavities for night roosting.
87 When only large-holed nest boxes are available GT competitively exclude BT from the nest boxes, even
88 when these are superabundant, and hence outcompete BT. Providing small holed nest boxes, that can be
89 used by BT but not by GT, results in an increase BT numbers roosting in nest boxes [18, 19] and an
90 increase in BT breeding density implying that interspecific competition for cavities as roosting sites during
91 winter has an effect on BT breeding population size. We used data from four sites in Western Europe
92 (figure 1) where counts of breeding pairs of the two species have been collected for more than 15 years and
93 where both species were sufficiently numerous to test our hypotheses (see electronic supplementary
94 material, table S5). Finding suitable data series for these species represents a major challenge, due to
95 various anthropogenic habitat changes over time. For example, changes to forest structure and/or changes
96 in the number of nest boxes available in study plots have occurred in a number of the potential study
97 populations across Europe. The time series we investigated represented the few available lacking such
98 large-scale alterations, to avoid confounding results.

99 To assess the impact of climate change on the strength of competition between these two species
100 we estimate how the parameters of a competition model vary due to climate change (see Material &
101 Methods). For this, we use a discrete-time (annual reproduction) setting, assuming a Gompertz density-
102 dependent feedback framework, where intra- and interspecific competition affects each species' population
103 density, $N_{i,t}$ (where t indicates the year). While studying fish population, Myers et al. [20, 21] argued that
104 density dependence was best approximated by the discrete-time Gompertz model (i.e. log-linear
105 dependence on density). Such log-linear density dependence in the survival was later on demonstrated for
106 another population [22, 23]. Note that the log-transformation has fortunate effect that the addition of a
107 given number of individuals at low abundance will have larger effect than adding the same number of
108 individuals at high abundance. The Gompertz model is written:

$$109 \quad N_{i,t+1} = N_{i,t} \exp[r_i(1 - [\alpha_{ij} \ln(N_{i,t}) + \alpha_{ij} \ln(N_{j,t})]/K_i)], \quad (1)$$

110 where r_i is the maximum *per-capita* (intrinsic) growth rate for species i , K_i is the local equilibrium density
111 in the absence of heterospecifics and α_{ij} represents the per-capita effect of species j on the growth rate of

112 species i . Typically, K , r and α are considered constants for a given species, location and environmental
113 condition. However, if the environment changes, these parameters might also change. We therefore
114 estimate how these parameters vary with the environment at any given time, employing an appropriate
115 combination of additive and non-additive statistical models. Using Akaike's Information Criterion
116 corrected for small sample size (AICc) we select among competing models, which are flexible enough to
117 include terms that show whether model parameters vary with short- and/or long-term environmental
118 variation. Having selected the most appropriate model for each site, we assess the effect these changing
119 parameters values have on positive equilibrium densities when necessary (stable coexistence: if and only if
120 $\alpha_{ii} \cdot \alpha_{jj}$ is larger than $\alpha_{ij} \cdot \alpha_{ji}$).

121 The aims of this paper are therefore (1) to assess whether the strength of competition between great
122 and blue tits is changing over time, (2) to establish if this change, if any, is linked to any changes in
123 climatic variables and (3) to forecast the consequences of the change in the strength of competition for
124 species co-existence.

125

126 **2. Material and Methods**

127 The study was conducted on great tits (GT) and blue tits (BT) breeding populations from four sites in
128 Western Europe (figure 1). GT and BT are small cavity-nesting passerines that readily accept nest-boxes if
129 these are available in large numbers. In the semi-natural woodlands where the two species breed, nest
130 cavities are often a limiting resource due to forest management and nest-boxes are commonly provided by
131 researchers, volunteer bird-ringers and the general public. In the study, boxes with a large entrance hole (ca
132 32 mm) suitable for both tit species were provided in excess (>5 boxes per ha, ESM table S7), so that GT
133 breeding density was not limited by cavity availability. In Plot B small-holed nest-boxes (entrance hole ca.
134 26 mm; accessible to BT but not to GT) were also present throughout the study. The presence of small-
135 holed boxes reduces interspecific competition for roosting sites during winter and results in an increase of
136 BT breeding density [17]. During the breeding season boxes were checked at least once a week and the
137 number of pairs was recorded as the number of first clutches found in nest-boxes (figure 1, and ESM table

S7). Census data was collected annually for both species in all plots. We assumed that immigration and emigration rates were approximately equal (the simplest assumption in this case) and did not have an important effect on the dynamics we observed. For one of the Belgian populations we studied (PLOT HP) this has been tested. Plot HP was part of a regional study that included 7 study plots over a 15 year period, during which time all nestlings were banded, and many recaptured breeding. In all study plots and both for GT and for BT the exchange of immigrants among neighbouring sites was balanced [24].

Climate data were taken from regional weather stations located near the study sites (see ESM table S7). Monthly temperature, spring (average for March, April, May) and winter temperature (average for December, January, February) were calculated from these. We used the winter index for the North Atlantic Oscillation as a global index affecting all study populations (Winter NAO: December, January, February [25, 26] and spring NAO (MAM): March, April, May). We also used the Beech Crop Index [BCI] from the Netherlands as an environmental variable for PLOT B, PLOT HP and Liesbos (BCI is a measure for the amount of beech seeds present in the winter, and correlates with crop size of several other tree species fed on by tits, [27]). All these indices were shown to affect GT and/or BT population dynamics in different ways at the local population scale.

In three sites intra- and interspecific competition could be detected within and between the focal species (PLOT B and PLOT HP in Belgium, Marley Wood in the UK). In the remaining site, however, available data did not allow for adequately fitting models that included terms for both intraspecific and interspecific competition for both species (Liesbos in the Netherlands).

(a) Theoretical model

Model (1) can be re-parameterized as follows:

$$N_{i,t+1} = N_{i,t} \exp[a_{i0} + a_{ii}\ln(N_{i,t}) + a_{ij}\ln(N_{j,t})], \quad (2)$$

where $a_{i0} = r_i$, $a_{ii} = -r_i/K_i$, and $a_{ij} = -r_i\alpha_{ij}/K_i$. That is, the ecological parameters can be expressed as statistical parameters: $r_i = a_{i0}$, $K_i = -a_{i0}/a_{ii}$, and $\alpha_{ij} = a_{ij}/a_{ii}$. On the log-scale, and slightly rearranged, the model becomes:

$$\ln(N_{i,t+1}) = a_{i0} + (1+a_{ii})\ln(N_{i,t}) + a_{ij}\ln(N_{j,t}) \quad (3)$$

To account for possible non-linearities, we also considered a threshold model [28], after testing for additivity/non-additivity [29 see also below].

$$\ln(N_{i,t+1}) = \begin{cases} a_{i0} + (1+a_{ii})\ln(N_{i,t}) + a_{ij}\ln(N_{j,t}) & \text{if } E_t < \theta \\ b_{i0} + (1+b_{ii})\ln(N_{i,t}) + b_{ij}\ln(N_{j,t}) & \text{otherwise,} \end{cases} \quad (4)$$

The environmental variable E_t is used to partition the effect of position over a “low” or “high” environmental regime (for instance, if E interacts with N_i , $(1+a_{ii})$ will differ from $(1+b_{ii})$, as can a_{i0} from b_{i0} while a_{ij} will remain unchanged; $a_{ij} = b_{ij}$). The threshold level (θ) of covariate E that separates the two regimes, was chosen by minimizing the Generalized Cross Validation (GCV) score among models that spanned the restricted range of E .

Such a linear (or piece-wise linear) model formulation was used for our statistical modelling procedure. Coefficients $(1+a_{ii})$ and $(1+b_{ii})$ (the latter represented as a threshold-dependent parameter) were estimated as the full term within the parenthesis.

(b) Statistical modelling

All analyses were performed using software R 3.0.2 [30]. We developed a model incorporating inter- and intraspecific competition and environmental variables (to limit the number of degrees of freedom we used only one climate or environmental variable per model). We tested potential interactions between the explanatory variables using Bürmann’s expansion [29]. This non-parametric method yields a test for the null hypothesis that the variables have additive effects only, as well as tests for interactions between each pair of variables. Following this we apply a threshold non-additive formulation (as given by Eqn. 4) where the response changes according to whether the climate covariate is above or below some threshold level, θ . The threshold level (θ) is found by minimizing the Generalized Cross Validation (GCV) score over an interval defined by the 20 to 80 percentiles of the covariate. We then assess the significance of the

190 threshold effect identified through the above procedure using a non-parametric permutation test (see the
191 following section for more details).

192 The most appropriate model, given the data, was selected using the Akaike's Information Criterion
193 corrected for small sample size (AIC_c). The selected model was that with the lowest values of AIC_c , and
194 factors were considered to lead to a significant change in the model when they led to $\Delta AIC_c \geq 2$ (ESM
195 table S8). In summary, for each system and for any particular climatic or environmental covariate, we
196 tested for non-additivity (see below) and only if the test rejected non-additivity did we proceed to fit a
197 threshold model and test for threshold effects, so as to ensure that the non-additivity detected may be
198 adequately described by a threshold model. The AIC selection was then used to select the final model
199 among competing threshold models. Thus, the tests were used for the sole purposes of screening and
200 validating which climatic or environmental covariates may be appropriate threshold variables, and only
201 then was AIC used to rank the models.

202 203 **(c) Additivity, non-additivity and threshold modelling**

204 Two numerical and continuous covariates may interact with each other (in our case temperature and intra-
205 specific competition). A formal test has been developed to check the additivity assumption that is implicit
206 in linear regression modelling (Bürmann-test [29]). Once a threshold effect is detected through the above
207 procedure, we conduct a non-parametric permutation test to assess its statistical significance, with the null
208 hypothesis that there is no change of covariate effect in different regimes defined by the level of the
209 threshold variable. We randomly shuffle the threshold variable repeatedly, but keep the other variables
210 unchanged and refit the model to the shuffled dataset for a number of replications (e.g., $N=500$) to obtain a
211 sample of test statistics (e.g., log-likelihood). The p-value of the permutation test is then calculated as the
212 proportion of times when the test statistic from the shuffled dataset exceeds that from the original
213 (unshuffled) dataset. The null hypothesis of no threshold effect is rejected if the permutation p-value is less
214 than 0.05. A similar technique for testing threshold effects in spatial distribution change was adopted in
215 Liu et al [31].

216 Once non-additivity is detected, it is necessary to somehow model it appropriately. In such
 217 circumstances one modelling approach is to partition one of the two interacting covariates in two levels,
 218 below and above a certain threshold. In other words, the model formulation (threshold non-additive
 219 formulation) is composed of two additive formulations where the response changes according to an
 220 environmental force (e.g., temperature) above or below this threshold level. In this procedure there is no *a*
 221 *priori* knowledge of where the threshold may be. This is overcome by carrying out a grid search
 222 throughout the entire range of the interacting covariate, and selecting the threshold that produces the best
 223 model, where the best model is that which minimizes the GCV (Generalized Cross Validation) score. In
 224 short, the GCV is a measure of the predictive squared error of the model [32]. Low values indicate the best
 225 compromise between model complexities (i.e. number of parameters) and fit to the observed data. To
 226 conduct this analysis, we used a linear version (L.C. Stige, pers. comm.) of the univariate threshold GAM
 227 function [28] developed by Kung-Sik Chan. This approach has previously been successfully used in
 228 several studies [e.g., 32].

229

230 **(d) Dynamical properties**

231 Point estimates for population parameters [r_i , K_i], theoretical equilibrium densities [N_i^*] and eigenvalues
 232 [λ_i] for the three study plots with statistical support for interspecific competition were calculated.
 233 Eigenvalues are derived from the Jacobian matrix (\mathbf{B}) of the linearized system evaluated around the
 234 interior equilibrium, with elements

$$b_{ij} = \left. \frac{\partial f(N_i)}{\partial N_j} \right|_{N_i=N_i^*}$$

$$b_{ii} = \exp\left(r_i \left[\frac{1 - \ln(N_i^*) a_{ii} + \ln(N_j^*) a_{ij}}{K_i} \right]\right) (K_i - r_i a_{ii}) / K_i$$

$$b_{jj} = \exp\left(r_j \left[\frac{1 - \ln(N_i^*) a_{ii} + \ln(N_j^*) a_{ij}}{K_i} \right]\right) (r_i a_{ij} N_i^*) / (K_i N_j^*)$$

235

236 where $f(N_i)$ is given as equation (1) and $\mathbf{N}^* = \exp(\mathbf{A}^{-1}\mathbf{K})$ gives the 2 by 1 vector containing species specific
 237 equilibrium population densities.

238

3. Results

Parameterization of model (1) for the four different time series (table 1) documented the existence of both intra- and interspecific competition between GT and BT in three of the four sites and predicted coexistence of GT and BT in all study plots. Parameter estimates for r_i , K_i , α_{ij} as given in Eqn. 1 are presented in table 1 and ESM table S6 for each of the four sites. The results of the analyses of the community models (for both GT and BT) with respect to possible effects of temperature on competitive coexistence are reported below for each study site (figure 2, tables 1, ESM table S1).

In PLOT B (Peerdsbos, Belgium) the best models selected included intraspecific and interspecific terms; for BT the model also included a threshold effect related to spring temperatures (March to May). The parameter for the interspecific term a_{12} , expressing the effect of BT numbers on GT per-capita growth rate (Eqn. 3, ESM table S2) is not significantly different from 0. This indicates a non-significant per-capita interspecific effect on the growth rate of GT (α_{ij} , Eqn. 1). In contrast, the term a_{21} , expressing the effect of GT numbers on BT per-capita growth rate, is highly significant (Eqn. 3, ESM table S2). Furthermore, as shown by the Bürrmann and permutation tests, long-term climate change had a biologically important effect on population and community dynamics, as demonstrated by a threshold type response of model parameters associated with a change in the relevant climate variable (Eqn. 4, ESM table S2). For BT all parameters of Eqn. 1 changed with spring temperature: in the context of this analysis we emphasise that r_2 decreased (6.20 to 4.65) while K_2 increased (ESM table S6), resulting in a reduction of intraspecific competition. On the other hand interspecific competition as expressed by α_{12} (the effect of GT numbers on BT) increased. When spring temperatures were warmer than the estimated threshold temperature of 9.7°C , $\alpha_{12} = 1.51$; in years in which spring temperatures were below the threshold level $\alpha_{12} = 0.74$ (table 1, ESM tables S1, S2 and S6). Therefore, spring temperature affected both intra- and interspecific competition for BT in Plot B but in opposite directions. GT intrinsic growth rate (r_1) increases with increasing temperature. The net result is that colder springs ($\text{Temp}_{\text{Spring},t} < \theta$) are associated with GT having higher equilibrium

264 densities than BT ($N^*_{GT} > N^*_{BT}$), while this relative abundance ranking is switched during warmer springs
265 ($\text{Temp}_{\text{Spring},t} \geq \theta$; $N^*_{BT} > N^*_{GT}$) (table 1). The zero-growth isoclines are shown in figure 2A).

266 In PLOT HP (Ghent, Belgium) the best models selected by AICc include both intraspecific (a_{i0})
267 and interspecific (a_{ij}) interaction terms for both species. Both estimates for the interspecific terms a_{12} and
268 a_{21} (Eqn. 3) are significantly different from 0 (table S3). While March temperature was found to be
269 important in driving population fluctuations of both GT and BT, there were no associated temporal
270 thresholds in this climate variable, with coexistence (and parameter values) maintained across the observed
271 range of climate fluctuations all else equal. The resulting zero-growth isoclines are shown in figure 2B,
272 with parameter estimates and equilibrium conditions outlined in table 1 and ESM table S3.

273 In Marley Wood (UK) the best model includes both intraspecific and interspecific terms for GT
274 (ESM tables S4 and S8). However, another, almost equally good model includes only the intraspecific term
275 (ESM table S8). A similar result is found for BT where the best model includes both intraspecific and
276 interspecific terms (ESM tables S4 and S8) with an equivalent model including only the intraspecific term
277 (ESM table S8). The parameters for the interspecific terms a_{12} and a_{21} (Eqn. 3) are not significantly
278 different from 0 (ESM table S4). Both tit species were affected by temperature (May and June for GT and
279 BT, respectively). There was no threshold effect of climate fluctuations on these populations. The resulting
280 zero-growth isoclines are shown in figure 2C with parameter estimates and equilibrium conditions outlined
281 in table 1 and ESM table S4.

282 In Liesbos (Netherlands) the best model includes only the intraspecific terms for GT (ESM table
283 S1). The second best includes both inter and intra-specific terms and is presented in ESM table S5. The
284 parameter for the interspecific term a_{12} is not significantly different from 0 (Eqn. 3, ESM table S5). For
285 BT, the best model includes both intraspecific and interspecific terms (ESM tables S5 and S8). However,
286 competing models include either only the intra- or the inter-specific term (ESM tables S8). The parameter
287 for the interspecific term a_{21} is not significantly different from 0 (and positive see ESM table S5),
288 suggesting there is no evidence for competition between these species at this site (therefore zero-growth
289 isoclines are not shown). Both species were affected by temperature (May and April for GT and BT,

290 respectively). Great tit numbers were also affected by the Beech Crop Index, but no threshold effect of
291 climate fluctuations on these populations was detected (tables 1 and ESM table S5).

292 All species pairs were found to be at a locally stable equilibrium (table 1). Under observed
293 conditions, population growth rates were close to 1. Recent climate change (warmer springs) has not
294 qualitatively changed these patterns, but has altered the relative abundances (equilibrium densities) of BT
295 and GT in one area.

296

297 **4. Discussion**

298 Using the best available long-term population time-series coupled with environmental covariates, we have
299 demonstrated local differences in the responses of two sympatric competitors to short- and long-term
300 climate change. While there is considerable spatio-temporal heterogeneity in our data – both within patch
301 local conditions and variation in temperature across time – short-term climate fluctuations (temperatures
302 during spring) were found to drive population fluctuations in all four study sites, whereas competition
303 between Blue and Great tits was detected in three of the four sites. In PLOT B (Peerdsbos, Belgium), long-
304 term climate fluctuations also modified density independent and density dependent population processes to
305 affect the long-term equilibrium behaviour of the system. The non-linear effect of long-term changes in
306 spring temperature interacted with population processes to swap the relative abundances of GT and BT in
307 PLOT B, Belgium: GT have higher abundance in cooler springs, while BT are predicted to be more
308 abundant in warmer springs. These changes in mean density, if maintained, may result in trophic cascades
309 [33] or in extreme cases, extinction cascades [34], leading to further restructuring of the local foodweb.
310 The distribution and (a)symmetry of pairwise competition values has strong effects on patterns of species
311 loss in competitive communities [35, 36] and food webs [37], thus any climate induced shifts in
312 competition, as observed here, can be expected to filter through the whole ecosystem, driving direct and
313 indirect changes across multiple trophic levels. The equilibrium densities are system attractors, with short-
314 term fluctuations (driven by, e.g., annual temperature variation) around these points. The threshold effect
315 identified in PLOT B leads to a change in the local equilibrium point when spring temperature is above the

316 threshold temperature in any year. However, if the temperature drops below the threshold in subsequent
317 years, the equilibrium point will also change correspondingly (ESM Fig. S2). The populations tracking
318 these shifting equilibria may struggle to match them in the short term, through under- or over-
319 compensatory dynamics, until longer-term changes in conditions settle down and populations fluctuate
320 around a new, more persistent equilibrium point (see also, e.g., [38-40] for further illustration and
321 discussion of this point).

322 Our results generate two important questions: (1) why do we observe an effect of spring
323 temperatures on community dynamics in only one of four study plots? and (2) what mechanism(s) can
324 cause this change?

325 To answer the first question, while we cannot provide a specific mechanism, it is useful to
326 underline a number of differences between PLOT B and the other three plots. Nest boxes were provided in
327 excess in all sites (ESM table S7) with a range of 5.3 (Liesbos) to 14.4 (PLOT B; 9.6 large-holed and 4.8
328 small-holed) nest boxes per hectare. PLOT B has the highest density (availability) of nest-boxes, which
329 might suggest the lowest levels of intra- and interspecific competition for this resource. This aspect is not
330 necessarily reflected in our parameter estimates: PLOT B has neither the highest K_i estimates nor the
331 lowest α_{ij} estimates in the sites we considered. However, PLOT B was part of a long-term experiment to
332 test for the effects of differences in intra- and interspecific competition between GT and BT in Antwerp
333 [17]. The experimental treatment in PLOT B provided a surplus of large-holed nest boxes (diameter 32
334 mm; used by both GT and BT) and a surplus of small-holed nest boxes (diameter 26 mm; used by BT
335 only). In the other three study sites only large holed nest boxes were available. The presence of small-
336 holed boxes results in a BT density that is 1.5-2 times higher than in their absence [18, 41]. Furthermore, in
337 plots with small-holed nest boxes and increased BT density (as in PLOT B) BT nestling and adult female
338 body mass (and hence probability of survival) is lower than in plots without small-holed nest boxes and
339 low BT density [17]. Experimental manipulations indicate that values for r increased when small-holed
340 boxes were present [17]. This is confirmed in our analysis with r_i values calculated for PLOT B of 6.20 and
341 4.65 being much larger than in PLOT HP (2.24), Marley (1.59) and Liesbos (2.00), where only large-holed

342 nest boxes were present (table 1). Finally local recruitment rates and dispersal are also impacted by the
343 presence of small-holed nest boxes [17]. All these differences between PLOT B and the other three plots
344 will likely translate into differences in how changing spring temperatures impact upon the interactions
345 between GT and BT. In their comparison between 24 long-term studies of GT and BT across Europe,
346 Visser et al. [42] found that the most rapid change in lay date of GT and BT was in PLOT B. Matthysen et
347 al. [43] showed that with increasing temperatures GT and BT not only advanced lay date but also strongly
348 reduced the proportion of breeding pairs that initiate second clutches, effects that again can impact GT and
349 BT in different ways.

350 Temperature dependent rates of caterpillar growth represent one possible mechanism involved in
351 the observed effect of spring temperature on the interaction between GT and BT in PLOT B. During warm
352 springs, the caterpillar food peak advances, tracked in parallel by both species [42, 43]. This in itself
353 should not induce a change in competition, but in warm springs the caterpillar food peak also becomes
354 narrower [44]. Several studies have shown differential use of prey sizes and prey categories by this species
355 pair. In general BT eat smaller prey than GT and if the time period during which BT have a competitive
356 advantage (because younger instar are smaller) is shortened, this would intensify competition [14, 15].

357 We used data on the number of each species observed in nest boxes, raising the question of the
358 significance of our result for the overall population (breeding in cavities and in nest boxes). In all areas we
359 studied nest boxes were present in surplus. GT and BT used natural cavities exceptionally where breeding
360 success is generally lower than in nest boxes [45]. As nest sites are typically a limiting factor for
361 population growth in managed forests over most of Europe [45, 46], we speculate that competition for nest
362 sites in areas without nest boxes is likely to have a similar effect.

363 Blue tits and great tits represent a species pair that has received considerable ecological interest
364 over the years. Surprisingly, few field studies that have tracked these species in forest habitats across
365 Europe have been able to maintain a relatively constant study site, with changes to, e.g., forest structure
366 and/or the number of nest boxes over time restricting the length and number of population time-series that
367 are amenable to long-term investigation. Analysing those long-term data that are available and relevant, we

368 have shown for the first time that climate change can affect the outcome of competitive interactions
369 between coexisting species in the field. Specifically we have provided an example where the relative
370 abundances of each species are expected to change as a consequence of long-term climate change. It
371 follows that climate change might have profound community effects resulting from changing competitive
372 relationships between competing species [33-36, 47, 48]. Previous work on population dynamics, species
373 interactions and environmental variation has tended to focus on the assumptions that the environment may
374 fluctuate around some mean value and affect maximum population growth rate additively [but see refs 3,
375 12, 13, 38, 49]. Here we have extended this view by demonstrating that changing climate can indeed
376 change equilibrium conditions, moving the system to a new state where a previously less abundant species
377 becomes relatively more abundant (BT). Such variation of competitive relationships may result in changes
378 in relative fitness for the competing species (e.g., nestling survival) across environments as, for instance,
379 demonstrated for Flycatchers [50]. Our results highlight the need for future research – both empirical and
380 theoretical – that considers how both short- and long-term environmental variation impact upon the form
381 and outcome of species interactions.

382

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508 **Figure legends:**

509

510 **Figure 1.** Data and location of the available long-time series on breeding density of Great and Blue tits in
511 Europe. Census data (A, C, E, G) were collected annually for both species in all plots. Data are presented
512 in number of breeding pairs over time (years) of both species: blue tits (blue lines-square symbols) and
513 great tits (red lines-dot symbols). On the location maps (B, D, F, H) the dots present the location of the
514 different study sites (ESM table S7).

515

516

517 **Figure 2.** Zero-growth isoclines for sympatric populations of great tits (GT, bold red lines) and blue tits
518 (BT, blue lines). Big black dots show estimated stable equilibrium points ($\ln(N^*)$ in Table 1) and small
519 light blue dots show the census data. The dotted ellipses correspond to the standard deviation around the
520 equilibrium calculated by bootstrap methods (ESM Table S6). α is α_{ij} . In PLOT B, BT population shows a
521 threshold interaction with an environmental variable (mean temperature conditions in spring; panel A). For
522 BT, there is a different isocline (and equilibrium state) for temperatures below (blue line) and above (blue
523 dotted line) the threshold of mean spring temperature of 9.7 °C. The blue arrow indicates the direction of
524 the change of the BT isocline with an increase of temperature over the threshold and the big red dot the
525 corresponding new equilibrium point. In PLOT HP, the equilibrium is unaffected by the environmental
526 variables modelled (panel B). At Marley, the community equilibrium point is unaffected by the
527 environmental variables modelled (panel C).

528

529

530 **Table 1.** Derivation of population dynamical stability properties. Point estimates for population parameters
531 $[r_i, K_i]$ (in log normal scale), equilibrium densities in number of breeding pairs $[N_i^*]$ and eigenvalues $[\lambda_i]$
532 for the three study plots with statistical support for interspecific interactions (α_{ij}). All systems are feasible
533 $[all N_i^* > 0]$ and locally stable (all $|\lambda_i| < 1$), i.e., populations will return to equilibrium following a small
534 perturbation. Plot B shows a shift in relative abundances of the two species across the temperature
535 threshold (θ), but no change in feasibility or local stability conditions. We created 1000 bootstrap samples
536 and estimated the parameters for the corresponding model in each sample. By definition the system is
537 locally stable when $(\alpha_{11} \cdot \alpha_{22} > \alpha_{12} \cdot \alpha_{21})$. In our case $(\alpha_{11} \cdot \alpha_{22} = 1)$ and $(1 > \alpha_{12} \cdot \alpha_{21})$. Models formulations are
538 summarised in ESM table S1.

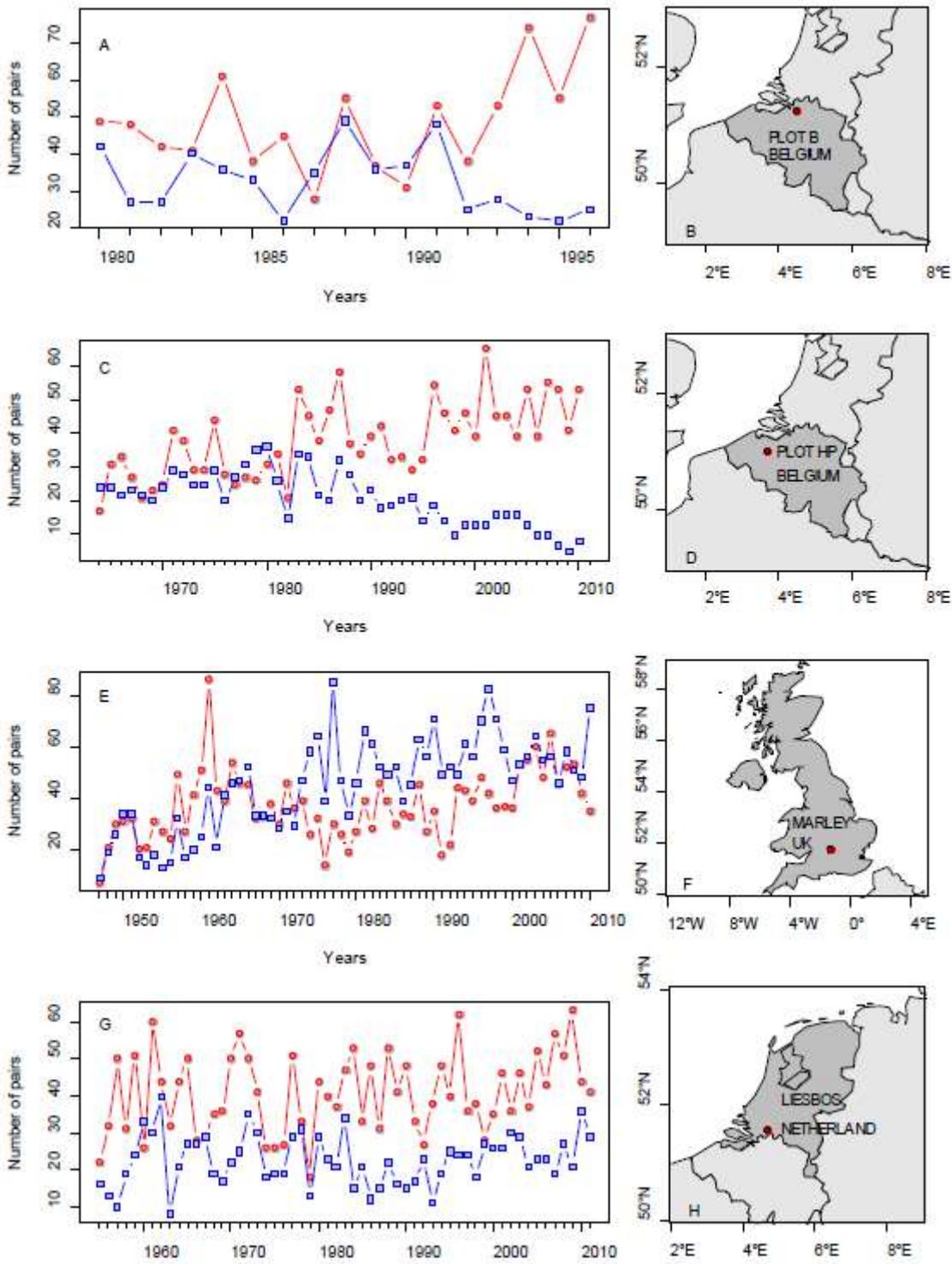
539

Location	Species i	r_i	K_i	α_{ij}	N_i^*	λ_i	significance of $1 > \alpha_{12} \cdot \alpha_{21}$	Interpretation
Plot HP	GT	3.77	5.11	0.51	43.27	0.83	$p < 0.001$	Stable coexistence
	BT	2.24	5.84	0.84	14.22	0.05		
Plot B	GT ($Temp_{Spring} < \Theta$)	5.20	4.70	0.25	47.45	-0.51	$p < 0.001$	Stable coexistence
	BT ($Temp_{Spring} < \Theta$)	6.20	6.21	0.74	28.98	0.40		
	GT ($Temp_{Spring} \geq \Theta$)	5.20	4.70	0.25	41.49	0.75	$p < 0.001$	Stable coexistence (tending towards unstable, see text)
	BT ($Temp_{Spring} \geq \Theta$)	4.65	9.51	1.51	49.49	-0.34		
Marley	GT	2.16	4.55	0.25	35.76	0.85	$p < 0.001$	Stable coexistence
	BT	1.59	7.05	0.90	45.64	0.45		
Liesbos	GT	3.29	3.81	0.06	36.94	0.14	$p < 0.001$	Stable coexistence
	BT	2.00	2.32	-0.21	21.59	0.14		

540

541

Figure 1



542

543

