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

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Complementary results and analysis of the data for the four geographical sites, Intraspecific and intraspecific competition comparison, Realized growth rate for the three sites presented in the main text, Parameters of Equation 1, and model selection.

In the following, we first list the most appropriate models for the four geographical sites (S1-S4), as found through non-linear (GAM) regression analysis combined with AIC_c-based model selection (table S6);. Table S5 gives complementary information on the study sites and design. Of the environmental and climate variables tested (monthly temperature, Spring temperature [average for March, April, May], Winter temperature [average for December, January, February], Beech Crop Index [BCI], and winter index for the North Atlantic Oscillation [NAO for December, January, February] and for spring [MAM: March, April, May). Only the most relevant were added to the models, i.e., those with a significant effect on either or both tit populations. Using the models we derived the competition factors (α_{ij} 's, $i \neq j$, i = 1, 2; see Eqn. 1).

In the following analyses, i = 1 indicates GT variables and constants, whereas i = 2 indicates BT.

Table S1. Model formulation summary. Model selected for the four sites to explain population changes in great tits (GT) and blue tits (BT). Models are following Eqn. 3 (Eqn. 4 when a threshold formulation is required) as reparameterisation of Eqn. 1. In all models $N_1 = GT$ and $N_2 = BT$.

Study site	Species	Dependent variable	Intercept	Intraspecific term	Interspecific term	Threshold θ
PLOT B	GT	$\ln(N_{1,t+1})$	$a_{10}(\text{Temp}_{\text{April}, t})$	$(1+a_{11})\ln(N_{1,t})$	$a_{12}ln(N_{2,t})$	
	BT	$\ln(N_{2,t+1})$	a ₂₀ (Temp _{Spring, t})	$[1+b_{22}(\theta)]ln(N_{2,t})$	$a_{21}ln(N_{1,t})$	Temp _{Spring,t}
PLOT HP	GT	$\ln(N_{1,t+1})$	$a_{10}(\text{Temp}_{\text{Dec},t} + \text{Temp}_{\text{Apr},t})$	$(1+a_{11})\ln(N_{1,t})$	$a_{12}ln(N_{2,t})$	
	BT	$ln(N_{2,t+1})$	$a_{20}(MAM_{,t} + Temp_{Spring,t})$	$(1+a_{22})ln(N_{2,t})$	$a_{21}ln(N_{1,t})$	
Marley	GT	$\ln(N_{1,t+1})$	$a_{10}(\text{Temp}_{\text{May, t}})$	$(1+a_{11})ln(N_{1,t})$	$a_{12}ln(N_{2,t})$	
	BT	$ln(N_{2,t+1})$	a ₂₀ (Temp _{Jun, t})	$(1+a_{22})ln(N_{2,t})$	$a_{21}ln(N_{1,t})$	
Liesbos	GT	$\ln(N_{1,t+1})$	$a_{10}(\text{Temp}_{\text{May},t}, \text{BCI}_t)$	$(1+a_{11})\ln(N_{1,t})$	$a_{12}ln(N_{2,t})$	
	BT	$ln(N_{2,t+1})$	$a_{20}(\text{Temp}_{\text{Apr, t}})$	$(1+a_{22})ln(N_{2,t})$	$a_{21}ln(N_{1,t})$	

Temp= temperature for spring=Spring (March April and May), Mar=March, Apr=April, May=May, Jun=June, Dec=December; NAO= winter North Atlantic Oscillation Index, MAM= spring (March, April, May) NAO index; BCI= Beech Crop Index

S2. Analysis of the data of Plot B, Peerdsbos, Belgium [51.27° N, 04.48° E]

The Bürmann-test conducted indicated non-additive models for both GT (p = 0.043) and BT (p=0.044). However, the permutation test conducted confirmed a non-additive models only for BT (p=0.046) with an interaction between BT and average temperatures in spring (average March-April-May). The most appropriate model is given by the following set of equations showing a non-linear (threshold-type of) interaction between temperature and BT abundance for the BT model:

$$\ln(N_{1,t+1}) = a_{10}(\text{Temp}_{\text{April},t}) + (1+a_{11})\ln(N_{1,t}) + a_{12}\ln(N_{2,t})$$
(S2(a))

$$ln(N_{2,t+1}) = \begin{cases} a_{20}(Temp_{Spring, t}) + a_{21}ln(N_{1,t}) & \text{if } Temp_{Spring, t} < \theta \\ \\ b_{20}(Temp_{Spring, t}) + (1+b_{22})ln(N_{2,t}) + b_{21}ln(N_{1,t}) & \text{otherwise} \end{cases}$$
(S2(b))

where for GT model a_{10} (Temp_{April,t}) = $a'_{10} + a_{13}$ Temp_{April,t}; and for BT model a_{20} (Temp_{Spring,t}) = $a'_{20} + a_{23}$ Temp_{Spring,t} and b_{20} (Temp_{Spring,t}) = $b'_{20} + b_{23}$ Temp_{Spring,t}. Parameter estimates are given in table S2 for GT and BT. The resulting zero-growth isoclines below and above the temperature threshold of 9.7 °C for Spring temperatures are given in figure 2A.

Species	Term	Point estimates	Std. Err.	\mathbf{R}^2	F-stat	p-value
Great tit	Full model			0.42	3.176	0.06
	$a'_{10} = r_1$	5.197	1.285		16.37	<0.001
	$1 + a_{11} = 1 - r_1/K_2$	-0. 105	0.218		0.23	0.639
	$a_{12} = -r_1 \alpha_{12}/K_1$	-0.277	0.229		1.469	0.247
	a ₁₃	0.171	0.059		8.532	0.011
Blue tit	Full model			0.88	16.59	<0.0001
	a' $_{20} = r_2$ (Temp _{Spring,t} < θ)	6.200	0.609		114.02	<0.001
	b' ₂₀ = r_2 (Temp _{Spring,t} $\geq \theta$)	4.646	0.816		10.75	0.026
	$1 + b_{22} = 1 - r_2/K_2 \text{ (Temp_{Spring,t} \ge \theta)}$	0.512	0.169		9.21	0.011
	$a_{21} = b_{21} = -r_2 \alpha_{21}/K_2$	-0.736	0.108		46.46	<0.0001
	$a_{23} = b_{23}$	-0.166	0.056		7.89	<0.05
	$a_{25} = b_{25}$ (outlier)	-0.542	0.114		22.42	<0.001

Table S2. Regression results and estimated parameter values for the model given by Eqn. S2. The basic statistical parameter estimates obtained for the model.

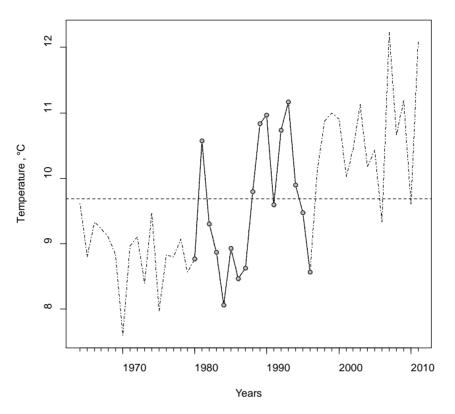


Figure S2. Illustration of spring temperature variation for 1964 to 2011 in PLOT B, Belgium. Population and temperature data at PLOT B were collected between 1980-1996 (grey dots). The horizontal dotted line corresponds to the temperature threshold θ of 9.7 °C. While long-term temperatures above the threshold are statistically associated with a higher BT equilibrium density, short-term annual variation in spring temperatures means that this attractor (equilibrium point) will fluctuate between years, with some recent spring temperatures being below the threshold.

S3. Analysis of the data of Plot HP, Ghent, Belgium [51.00° N, 03.70° E]

The Bürmann-test conducted indicated an additive model for both the great tit and the blue tit (p = ns). This result was confirmed by the permutation test (p = ns). The most appropriate model is given by the following set of equations:

$$ln(N_{1,t+1}) = a_{10}(Temp_{Dec,t} + Temp_{Apr,t}) + (1+a_{11})ln(N_{1,t}) + a_{12}ln(N_{2,t})$$
(S3(a))
$$ln(N_{2,t+1}) = a_{20}(MAM_{,t} + Temp_{Spring,t}) + (1+a_{22})ln(N_{2,t}) + a_{21}ln(N_{1,t})$$
(S3(b))

where $a_{10}(\text{Temp}_{\text{Dec},t} + \text{Temp}_{\text{Apr},t}) = a'_{10} + a_{13}\text{Temp}_{\text{Dec},t} + a_{14}\text{Temp}_{\text{Apr},t}$ and $a_{20}(\text{Temp}_{\text{Apr},t}) = a'_{20} + a_{23}\text{MAM}_{,t} + a_{24}\text{Temp}_{\text{Spr},t}$. According to this model for the two competing species, the effect of climate was found to be additive for great tit and for blue tit densities (on the log-scale). Parameter estimates are given in table S3 for GT and BT. The resulting zero-growth isoclines are given in figure 2B.

Species	Term	Point estimates	Std. Err.	\mathbf{R}^2	F-stat	p-value
Great tit	Full model			0.55	12.50	<0.0001
	$a'_{10} = r_1$	3.768	0.510		54.57	<0.0001
	$1 + a_{11} = 1 - r_1/K_1$	0.262	0.107		5.998	<0.05
	$a_{12} = -r_1 \alpha_{12}/K_1$	-0.373	0.078		22.96	<0.0001
	a ₁₃	-0.108	0.033		10.50	<0.01
Blue tit	a ₁₄	-0.082	0.031		7.118	<0.05
	Full model			0.79	38.29	<0.0001
	$a'_{20} = r_2$	2.241	0.562		15.86	<0.001
	$1 + a_{22} = 1 - r_2/K_2$	0.616	0.101		37.05	<0.0001
	$a_{21} = -r_2 \alpha_{21}/K_2$	-0.324	0.115		7.947	<0.01
	a ₂₃	0.057	0.020		8.197	<0.01
	a ₂₄	-0.127	0.046		7.734	<0.01

Table S3. Regression results and estimated parameter values for the model given by Eqn. S3. The basic statistical parameter estimates obtained for the model.

S4. Analysis of the data of Marley, UK [51.78° N, 01.33° W]

The Bürmann-test conducted indicated an additive model for both the great tit and the blue tit (p = ns). This result was confirmed by the permutation test (p = ns). The most appropriate model is given by the following set of equations:

$$ln(N_{1,t+1}) = a_{10}(Temp_{May,t}) + (1+a_{11})ln(N_{1,t}) + a_{12}ln(N_{2,t})$$
(S4(a))
$$ln(N_{2,t+1}) = a_{20}(Temp_{Jun,t}) + (1+a_{22})ln(N_{2,t}) + a_{21}ln(N_{1,t})$$
(S4(b))

where $a_{10}(\text{Temp}_{\text{May},t})$ is given as the following linear model: $a_{10}(\text{Temp}_{\text{May},t}) = a'_{10} + a_{13}\text{Temp}_{\text{May},t}$ and $a_{20}(\text{Temp}_{\text{Jun},t})$ given as $a_{20}(\text{Temp}_{\text{Jun},t}) = a'_{20} + a_{23}\text{Temp}_{\text{Jun},t}$. According to this model for the two competing species the effect of climate was found to be additive for great tit density (on the log-scale). Parameter estimates are given in table S4 for GT and BT. The resulting zero-growth isoclines are illustrated in figure 2C.

Table S4. Regression results and estimated parameter values for the model given by Eqn. S4. The basic statistical parameter estimates obtained for the model.

Species	Term	Point estimates	Std. Err.	\mathbf{R}^2	F-stat	p-value
Great tit	Full model			0.38	12.13	<0.0001
	$a'_{10} = r_1$	2.156	0.336		41.20	<0.0001
	$1 + a_{11} = 1 - r_1/K_1$	0.526	0.101		27.30	<0.0001
	$a_{12} = -r_1 \alpha_{12}/K_1$	-0.121	0.080		2.265	0.138
	a ₁₃	0.112	0.035		10.54	<0.05
Blue tit	Full model			0.61	30.92	<0.0001
	$a'_{20} = r_2$	1.587	0.365		18.89	<0.0001
	$1 + a_{22} = 1 - r_2/K_2$	0.775	0.087		79.17	<0.0001
	$a_{21} = -r_2 \alpha_{21}/K_2$	-0.203	0.109		3.474	0.067
	a ₂₃	0.070	0.038		3.463	0.068

S5. Analysis of the data of Liesbos, Netherlands [51.58° N, 04.67° E]

The Bürmann-test conducted indicated only additive models for both species (p = ns) confirmed by the permutation test (p = ns). No evidence for interspecific competition was detected from the data. The most appropriate models are given by the following equations:

$$ln(N_{1,t+1}) = a_{10}(Temp_{May,t}, BCI_t) + (1+a_{11})ln(N_{1,t}) + a_{12}ln(N_{2,t})$$
(S5(a))
$$ln(N_{2,t+1}) = a_{20}(Temp_{Apr,t}) + (1+a_{22})ln(N_{2,t}) + a_{21}ln(N_{1,t})$$
(S5(b))

where $a_{10}(\text{Temp}_{\text{May,t}}, \text{BCI}_t)$ is given as the following linear model: $a_{10}(\text{Temp}_{\text{May,t}}, \text{BCI}_t) = a'_{10} + a_{13}\text{Temp}_{\text{May,t}} + a_{14}\text{BCI}_t + a_{15}\text{BCI}_t$ (BCI being a factor variable, there is 2 constant calculated a_{14} and a_{15} depending on the level of BCI), and $a_{20}(\text{Temp}_{\text{Apr,t}}) = a'_{20} + a_{23}\text{Temp}_{\text{Apr,t}}$. According to this model for the two competing species the effect of climate was found to be additive for great and blue tits densities (on the log-scale). Parameter estimates are given in table S5 for GT and BT. It was not possible to draw isoclines due to the lack of interspecific competition.

Table S5. Regression results and estimated parameter values for the model given by Eqn. S5. The basic statistical parameter estimates obtained for the model.

Species	Term	Point estimates	Std. Err.	\mathbf{R}^2	F-stat	p-value
Great tit	Full model			0.19	2.336	0.055
	$a'_{10} = r_1$	3.288	0.522		39.65	<0.0001
	$1 + a_{11} = 1 - $	0.136	0.182			0.293
	r_1/K_1	0.100	0.102		1.128	0.200
	$a_{12} = -r_1 \alpha_{12}/K_1$	-0.055	0.105		0.276	0.602
	a ₁₃	0.066	0.034		3.694	0.060
	a_{14}	0.124	0.084		2.187	0.145
	a ₁₅	0.232	0.097		5.726	<0.05
Blue tit	Full model			0.15	3.048	<0.05
	$a'_{20} = r_2$	1.997	0.641		9.716	<0.01
	$1 + a_{22} = 1 - $					
	r_2/K_2	0.141	0.131		1.151	0.288
	$a_{21} = -r_2 \alpha_{21}/K_2$	0.179	0.161		1.228	0.273
	a ₂₃	0.104	0.047		4.858	<0.05

Study site	Species	r	К	α _{ij}
PLOT HP	GT	3.73 ± 0.27	5.10 ± 0.14	0.50 ± 0.05
	BT	2.17 ± 0.31	5.88 ± 0.66	0.66 ± 0.19
PLOT B	GT	5.47 ± 0.58	4.77 ± 0.35	0.26 ± 0.10
	BT, < θ	6.07 ± 0.17	6.08 ± 0.17	0.70 ± 0.04
	BT, ≥ θ	4.25 ± 1.04	9.59 ± 2.60	1.54 ± 0.62
Marley	GT	2.17 ± 0.12	4.60 ± 0.36	0.27 ± 0.10
	BT	1.56 ± 0.14	7.19 ± 1.48	0.94 ± 0.41
Liesbos	GT	3.30 ± 0.23	3.85 ± 0.19	0.08 ± 0.06
	BT	1.96 ± 0.36	2.28 ± 0.36	-0.22 ± 0.10

Table S6. Bootstrap procedure on Equation 1

Intervals around each parameter estimate represent \pm SD from a bootstrap procedure. We created 1000 bootstrap samples and estimated the parameters for the corresponding model in each sample and use them to estimate a, r and K.

The parameters were not considered to be significantly different from 0 if the (0.025, 0.975) quantile intervals spanned 0 (*). Note that results of the bootstrap may differ from those obtained in tables S2-S5.. GT= great tits and BT = blue tits.

Table S7. Study sites and data information

Study Site	Coordinates	Site	Nestbox	Unused	Der	sity	Sample	Period		Climate data
	(longlat.)	surface (ha)	numbers	nestboxes (% ± S.D.)	GT	BT	frequ.	(years)	Weather station	(longlat.)
PLOT B, Belgium	51.27° N, 04.48° E	12.5	180	55 ± 8	6.2	3.9	1/we	1980-1996	Uccle	50.8°N, 4.3°E
PLOT HP, Belgium	51.00° N, 03.70° E	27	191	69 ± 6	2.4	1.3	1/we	1964-2011	Uccle	50.8°N, 4.3°E
Marley, UK	51.78° N, 01.33° W	26.7	218	62 ± 12	3.2	3.2	1/we	1947-2010	Radcliffe	51.77°N, 01.77°W
Liesbos, Netherlands	51.58° N, 04.67° E	19	100	36±14	3.3	2.1	1/we	1955-2011	De Bilt	52.1°N, 5.2°E

Density: maximum density observed in number of pairs per ha for GT (great tit) and BT (blue tit).

PLOT HP, mixed deciduous forest composed mainly of beech (*Fagus sylvatica*), 184 large-holed nestboxes/27 ha PLOT B, mixed deciduous forest composed mainly oak, 120 large-holed and 60 small-holed nestboxes (for BT only)/12.5 ha [1].

Marley, mixed-oak/ash (Quercus spp./Fraxinus excelsior) woodland, 214 large-holed nestboxes /26.7 ha [2].

Liesbos, deciduous wood with oak Quercus robur L. as the predominant tree species, density 100 large-holed nestboxes/19 ha [3, 4].

Study site	Species	Model formulation	AICc
PLOT B	GT	GT + BT+Temp _{apr}	-42.7
		GT + BT	-37.6
	BT	$BT^*(Temp_{Spring} \ge \theta)) + GT + Temp_{Spring}$	-63
		$BT^*(Temp_{Spring} \ge \theta)) + GT + NAO + Temp_{Spring}$	-62
		$BT^*(Temp_{Spring} \ge \theta)) + GT + NAO$	-57
PLOT HP	GT	GT + BT + Temp _{dec} + Temp _{mar}	-142.5
		$GT + BT + Temp_{dec}$	-137.7
		$GT + BT + Temp_{mar}$	-134.6
		$\mathbf{GT} + \mathbf{BT}$	-132.9
	BT	BT + GT + MAM + Temp _{apr}	-135.6
		BT + GT + MAM	-130.2
		$BT + GT + Temp_{apr}$	-129.7
		BT + GT	-128.4
Marley	GT	$\mathbf{GT} + \mathbf{BT} + \mathbf{Temp}_{may}$	-159.8
,		$GT + Temp_{may}$	-159.7
		$GT + BT + Temp_{jun}$	-156.9
		$GT + BT + Temp_{spr}$	-154.3
		GT + BT	-151.7
	BT	BT + GT+ Temp _{jun}	-149.5
		$BT + GT + Temp_{apr}$	-98.37
		$BT + Temp_{jun}$	-148.1
		BT + GT	-148.1
Liesbos	GT	GT + BT + Temp _{may} + BCI	-147.1
		$GT + Temp_{may} + BCI$	-149.3
		GT + BT + BCI	-145.6
	BT	BT+ GT + Temp _{apr}	-123.8
		$GT + Temp_{apr}$	-124.9
		$BT + Temp_{apr}$	-124.8
		BT + GT	-121.1

The model selected by AICc is indicated in bold. Models are presented in order from most to least complex, which does not always reflect the relative AICc rankings.

GT= great tit; BT = blue tit; Temp= temperature for spring=Spring (March April and May), mar=March, apr=April, may=May, jun=June, dec=December; NAO= winter North Atlantic Oscillation Index, MAM= spring (March, April, May) NAO index; BCI= Beech Crop Index

References

1. Dhondt, A. A., Adriaensen, F. 1999 Experiments on competition between Great and Blue Tit: Effects on Blue Tit reproductive success and population processes. *Ostrich.* **70**, 39-48.

2. Minot, E. O., Perrins, C. M. 1986 Interspecific interference competition - nest sites for blue and great tits. *J. Anim. Ecol.* **55**, 331-350.

3. Both, C. 1998 Density dependence of clutch size: habitat heterogeneity or individual adjustment? *J. Anim. Ecol.* **67**, 659-666.

4. Both, C. 1998 Experimental evidence for density dependence of reproduction in great tits. *J. Anim. Ecol.* **67**, 667-674.