Climate of the Past Discussions

Cascading climate effects and related ecological consequences during past centuries

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Cascading climate effects and related ecological consequences

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Abstract

The interface between climate and ecosystem structure and function is incompletely understood, partly because few ecological records start before the recent warming phase. Here, we analyse an exceptional 100-yr long record of the great tit (*Parus major*) population in Switzerland in relation to climate and habitat phenology. Using path analysis, we demonstrate an uninterrupted cascade of significant influences of the large-scale atmospheric circulation (North-Atlantic Oscillation, NAO, and North-sea – Caspian Pattern, NCP) on habitat and breeding phenology, and further on fitness-relevant life history traits within animal populations. We then apply the relationships of this analysis to reconstruct the circulation-driven component of fluctuations in great tit breeding phenology and population dynamics on the basis of new seasonal NAO and NCP indices back to 1500 AD. According to the path model, the multi-decadal oscillation of the atmospheric circulation likely led to substantial variation in habitat phenology, and consequently, tit population minima during the "Maunder Minimum" (1650–1720) and the Little Ice Age Type Event I (1810–1850). The warming since 1975 was not only related with a quick shift towards earlier breeding, but also with the highest productivity since 1500, and thus, an unprecedented increase of the population. A verification of the structural equation model against two independent data series corroborates that the retrospective model reliably depicts the major long-term NAO/NCP impact on ecosystem parameters. The results suggest a complex cascade of climate effects beginning at a global scale and ending at the level of individual life histories. This sheds light on how large scale climate conditions substantially affect major life-history parameters within a population, and thus influence key ecosystem parameters at the scale of centuries.

1 Introduction

Assessing the mechanisms of long-term, large-scale ecological consequences of climate fluctuations requires quantification of causal pathways from conditions at

a continental scale down to fine-scale processes such as trophic interactions within ecosystems (e.g. Parmesan, 2006; Alcamo et al., 2007; IPCC, 2007). However, such analyses are often restricted to the phenology of life history stages (e.g. Crick et al., 1997; Sokolov, 2001; Menzel et al., 2006), or to variations in the geographical distri-
5 bution of species (e.g. Grosbois et al., 2006) as response variables. Consequently, ultimate impacts on ecological processes remain largely unclear. Research on climate effects on ecosystem structure and function contributes to explaining biogeographical patterns and processes and their long-term variation (Githaiga-Mwicigi, 2002; Walther, 2002; Parmesan, 2006; Lyon et al., 2008). In particular for climate change related con-
10 servation strategies, investigations of historical records (of both climate and biodiversity) are an important basis for the development of long-term models (e.g. Willis et al., 2007). Recent advances in climate reconstructions into the past open a way to extending the time scale of investigations of climate–ecosystem interactions. Exploring the history of responses of ecological systems to past climate variation may contribute to
15 understand and scale the actual changes (Willis and Bhagwat, 2010; Willis and Mac-Donald, 2011), and to assess reaction norms and system resilience (Summers et al., 2012).

The effects of large-scale, fundamental climatic forcing (through atmospheric circulation patterns) on local habitat and the phenology of species may vary over relatively
20 small areas (Saether et al., 2003; Both et al., 2004), and the effect size may vary substantially amongst populations of a species since both the underlying trophic interactions and the plasticity of systems may differ (Visser et al., 2002; Both et al., 2004; Gordo and Sanz, 2006, 2009; Martin, 2007; Charmantier et al., 2008). Due to the scarceness of data, climate impacts have rarely been tracked down to key param-
25 eters of population dynamics such as reproductive (Saether et al., 2003) or survival rates (Catchpole et al., 2000). Consequently, both the the history and future of climate forcing on ecosystem function remain highly debated (Martin, 2007).

In birds, response to large-scale climate patterns has been reported for various species (Møller et al., 2010; Visser et al., 2002; Both et al., 2004). For tit species in

particular, climate affects the phenology and reproductive traits (Sanz, 2002; Visser et al., 1998, 2002). This suggests that differential phenologies of components of the trophic web may lead to a loss of synchronization or even disruption of major trophic relationships (van Dongen, 1997; Visser et al., 1998; Przbylo et al., 2000; Adahl et al., 2006; Drever and Clark, 2007).

Here, we analyse an exceptionally long population record of great tits (*Parus major Linnaeus*), collected in Switzerland for the entire 20th century. Specifically, our analysis addresses three main issues: First, we aimed at tracking the effects of two large-scale atmospheric processes, the North Atlantic Oscillation (NAO, e.g. Hurrell, 1995; Wanner et al., 2001; review in Hurrell et al., 2003) and the North Sea-Caspian Pattern (NCP, Kutiel and Benaroch, 2002) on late winter/spring climate conditions, the effect of these envelope factors on the vegetation phenology and the tits' timing of reproduction, and ultimately, the impact on annual reproductive output. Second, we used independent phenological and reproductive data series of the habitat, the great tit and the blue tit (*Cyanistes caeruleus*) to validate the resulting hierarchical model quantitatively. Third, we reconstructed climate-related ecological responses back to 1500 AD by applying the structural equation model from the 20th-century analysis to new reconstructions of monthly NAO and NCP indices. This model was verified using independent data on habitat phenology based on historical plant phenological observations for the period 1750–1900.

2 Materials and methods

2.1 Great tit breeding phenology and population observations

The great tit is a small hole-nesting passerine of deciduous and mixed forests. In Switzerland, the largest proportion of the population (∼75 %) occupies altitudes below 800 m a.s.l. (Schmid et al., 1998). The species' reproductive ecology is adapted to the quick seasonal changes in the vegetation and food resources in spring (the

"caterpillar peak", Naef-Daenzer and Keller, 1999; Naef-Daenzer et al., 2004; Charmantier et al., 2008; Lyon et al., 2008), and the peak in predation rates later in the season (Naef-Daenzer et al., 2001). The initiation of clutches is strongly related to ambient temperatures and the phenology of the lower levels of the trophic chain, i.e. the development of tree leaves and phyllophagous invertebrate larvae. These are the main protein supply for egg formation and nestling growth (e.g. Nager and Van Noordwijk, 1992). Thus, climatic conditions in late winter/early spring play a key role in the cascade of mechanisms influencing the annual reproductive performance (Naef-Daenzer and Keller, 1999; Charmantier et al., 2008; Lyon et al., 2008).

The nest record scheme of the Swiss Ornithological Institute recorded breeding data of great tits since 1901 on standardised nest record cards. No great tit data were available in 22 yr (during world wars and economic crisis), and the overwhelming part of the records was collected after 1945. The records were meticulously checked for inconsistencies in the data. We used only records with at least two visits at the nest. The date of first egg (laying date) was calculated by backdating one egg per day from the date of recording clutch size. Records with implausible data were rejected, e.g. if the time between laying date and date of reporting brood size was less than a minimum incubation period of 13 days. Where only brood size or number of fledglings was reported, no estimate of the laying date was made. Out of 7429 records, 6276 originating from 348 sites were included in the analysis, 1153 (16 %) records were eliminated due to one or multiple questionable entries.

The analysis includes yearly averages for laying date, clutch size, brood size and number of fledglings over all nests available per year (average $n = 124$ broods, range 1–365). Since the altitudinal distribution of nest sites was constant over the study period we used uncorrected data on breeding phenology. According to Dunn and Winkler (1999) we analysed whether years with small annual brood samples (<5 broods, $N = 16$ yr) may bias the statistical results. The respective tests are given in the results section.

2.2 Large-scale atmospheric circulation data

The North Atlantic Oscillation Index (NAOI) is widely used as a general indicator for the strength of the westerlies over the Eastern North Atlantic and western Europe and, most importantly, for winter and early spring climate in Europe (Hurrell, 1995; Wanner et al., 2001). For the analyses and the retrospective modelling back to 1500 we used the series of NAO indices by Luterbacher et al. (2002, available at http://www.cru.uea.ac.uk/cru/data/naojurg/). The series gives monthly NAOI back to 1659 and seasonal indices from 1658 back to 1500. Accordingly, we included spring NAOI on the basis of December–February indices for 1500–1658 and average January to April indices from 1659 on.

A second atmospheric teleconnection system between the North Sea and the Caspian Sea (the North Sea – Caspian Pattern NCP, Kutiel and Benaroch, 2002, available at http://www.cru.uea.ac.uk/cru/data/ncp), which is similar to the EU Pattern (Barnston and Livezey, 1987) also affects the airflow over continental Europe. As with NAOI reconstructions, we reconstructed seasonal NCPI estimates for the period before 1948 on the basis of to the pre-1948 station pressure series (Slonoski et al., 1999; Jones et al., 1999; Allan and Ansell, 2006) and other climate proxies back to 1500 (Luterbacher, unpublished data). The reconstruction method and details on underlying data are given in Luterbacher et al. (2002). In its negative stage (i.e. low pressure over the North Sea) the North-Sea-Caspian pattern amplifies the NAO effects, allowing westerly streams to move farther into the continent, with the effect of above normal precipitation in Central Europe (Xoplaki et al., 2004). In the positive state (high pressure over the North Sea) this system counteracts the NAO effects by directing dry and cool continental air towards Central Europe.

2.3 Local temperature, precipitation and habitat phenology

Meteorological data were obtained from the Swiss Federal Office for Meteorology and Climatology MeteoSwiss. We included average January to April temperature and average January to April precipitation from the station Bern, Switzerland.

The date of beech (*Fagus sylvatica*) bud burst is an important trigger for the appearance of invertebrate food for great tits (Naef-Daenzer et al., 2004; Charmantier et al., 2008; Lyon et al., 2008). Since the spring phenologies of the most common deciduous tree species and of their invertebrate fauna are similar (for details see Fischbacher et al., 1998), historical data on beech leafing phenology are an excellent proxy for the phenology of great tit breeding habitats. The Swiss plant phenological observation network SPN (Defila, 1991; Defila and Clot, 2001) supplied data on plant phenology (www.meteoswiss.ch). We included the yearly average date of bud opening of beech ($n = 39$–109 observation sites/year) from the north of the Alps (1951–1999). Additional phenological records for 1901–1950 were extracted from the Euroclimhist database (Pfister and Dietrich, 2006). For years without records of beech phenology ($n = 16$), the bud break date was estimated from historical records of the date of cherry flowering in Liestal, Switzerland (Defila and Clot, 2001; Rutishauser and Studer, 2007; beech bud break = $40.6 + 0.691 \cdot$ date of cherry flowering, $R^2 = 0.77$, $n = 49$ yr).

2.4 Model validation data

We validated the final model against independent data at two levels. First, we compared structural equation model (SEM) predictions with independent data of great tit and blue tit laying dates and reproductive output from Braunschweig, Germany, 1970–2000 (Winkel and Hudde, 1997). We used average laying date and average number of fledglings per pair ($N = 31$ yr). Since the start of reproduction of great tits is generally later in Northern Germany compared to Switzerland, we tested the residual laying date and reproductive success against predicted values as calculated from the NAOI and NCPI according to the equations in the final path model. Regression tests after Kleijnen

et al. (1998) were applied to test differences between observations and predictions in respect to average or variance.

Second, we validated the retrospective model with an independent data series of the onset of spring in Switzerland for the period of 1750–1900 (Rutishauser et al., 2007; available at http://www.ncdc.noaa.gov/paleo/phenology.html). This spring index was calculated on the basis of 23 overlapping phenological records (for methods and detailed results see Schaber and Badeck, 2002; Rutishauser et al., 2007). Unfortunately, results on the reproductive performance of the great tit cannot be verified against independent observations before 1900 due to lack of data.

2.5 Statistical analyses

In summary, the data included biotic (plant phenology: beech bud burst; animal phenology: egg laying date; reproductive performance: clutch size, brood size and number of fledglings) and abiotic variables (NAOI, NCPI, station temperature and precipitation). The final data set included 77 yr (1901–1999) in which all variables were recorded. We excluded four outliers from the analysis (all outside $\pm 2.57 \cdot$s.d. range, $\alpha = 0.02$; 1 extreme in spring precipitation; 1 extreme in clutch size; 2 extremes in number of nestlings). A systematic overview of the data sets used in the analysis and models is given in Table 1.

We used structural equation modelling (SEM) with Generalized Least Squares Maximum Likelihood (GLS-ML) estimation for taking the hierarchical structure of the mechanisms into account (StatSoft Inc., 2006). We pre-defined a series of models assuming that all influences act from higher to lower levels of the system (i.e. atmospheric circulation → weather → vegetation/birds), but excluded any feedback upwards in this hierarchy. A set of pre-defined models was based (1) on the preliminary analysis of the effects of the NAOI and NCPI on precipitation and temperature conditions, and (2) on existing empirical and experimental evidence on the phenology of woodland habitats, and on the effects of the timing of breeding and food availability on clutch size and reproductive output (e.g. Naef-Daenzer et al., 2001; Both et al., 2004; Charmantier et al.,

2008). All candidate models assumed that the atmospheric systems had no direct effect on the bird sub-system (e.g. NAOI → Clutch size), because empirical evidence for an underlying mechanism is lacking. We used the Bentler-Bonnett Non-normed index (BBnn-index, Bentler and Yuan, 1999) as measure of model fit. Like other information theoretic criteria (e.g. AIC, Anderson and Burnham, 1994), this index rewards model parsimony. We favoured the model with the highest index excluding non-significant relationships.

2.6 Retrospective model 1500–2000

The equations of the relationships in the favoured path model were implemented in the modelling package ModelMaker 2.0 (Cherwell Inc., 1995) to allow simulation of the long-term effect of the NAO and NCP on variation of great tit breeding parameters back to 1500 AD. We expressed the expected changes in the productivity relative to the average annual fecundity of 5.553 chicks per pair (1500–2000). We modelled the expected population effects (i.e. cumulative effects of variation in productivity) as an index set to 100 points in year 2000. Accordingly, this relative index quantifies the impact of NAOI and NCPI on a theoretical population in which the long-term (500 yr) reproductive success is constant. The model explicitly excludes habitat changes and demographic mechanisms (such as density dependence) that may superimpose, but not conceal, the component effect of NAOI and NCPI because no reliable assumption on the long-term variation of these secondary dynamics can be made.

The model results in respect to variation in timing of breeding, reproductive performance and NAO/NCP component effects on population fluctuations are given as 25-yr moving averages (11-yr averages at ends of time series). Additionally, we applied 10×2 Fourier series polynomial regression to estimate 90 % confidence bands to annual values (TableCurve 2D Ver. 4, AISN Software Inc., Lowell, Oregon, USA).

3   Results

3.1   Structural equation model 1901–1999

The correlation matrix of all variables that were included in structural equation model selection for the period 1901–1999 indicates strong relationships between the atmospheric oscillation indices and spring temperature and precipitation (Table 2, $N = 73$ yr). Particularly strong were the correlation of the NAOI with spring temperatures ($r = 0.57$, $P < 0.001$), and that of the NCPI with spring precipitation ($r = -0.75$, $P < 0.001$). Furthermore the habitat phenology was correlated with abiotic (temperature and precipitation) and with biotic variables (laying date, reproductive performance).

Variables of bird reproduction also showed significant relationships with weather and habitat phenology (Table 2). The average annual laying date was correlated with spring temperature ($r = -0.31$, $P = 0.008$), spring precipitation ($r = 0.26$, $P = 0.025$) and habitat phenology ($r = 0.33$, $P = 0.004$, Fig. 1a). The average clutch size varied in relation to habitat phenology ($r = -0.39$, $P = 0.001$), and the average number of chicks fledged per brood was negatively related to habitat phenology ($r = -0.42$, $P < 0.001$, Fig. 1b) and temperature ($r = 0.26$, $P = 0.025$). At the level of bivariate relationships, including the years with small brood samples increased the variance in most variables, however, caused insignificant changes in regression coefficients (Fig. 1, other correlations not shown).

The model selection process started with interactions of the abiotic and biotic subsystems (models 1–6, Table 3). The purpose of this first step was to clarify the relationships within sub-systems. The results suggest simple relationships between NAOI/NCPI and spring temperature and precipitation. Models assuming laying date as a main determinant of reproductive performance received little support (models 2–3, BBnn index 0.448–0.467). The best-supported model in the first set (model 6, Table 3) indicates that habitat phenology is the central factor for both the timing and success of tit reproduction. This model was used as the "null-model" for the second

set of candidate models evaluating the relationships among the abiotic and the biotic subsystems (models 7–14, Table 3).

The main link between the abiotic and the biotic sub-systems in the favoured structural equation model (model 14, Table 3) was a relationship between spring temperature and habitat phenology and influences of spring precipitation on habitat phenology and laying date. All included relationships were statistically significant. Equations are given in Fig. 2, parameter estimates and statistics are given in Table 4. The favoured model suggests a chain of relationships in which the phenology of the habitat is the crucial link between the abiotic sub-system and great tit reproduction (Table 4): the NAOI explained approximately one third of the variance in late winter/spring temperature ($R^2 = 0.31$, $P < 0.001$), whereas the NCPI accounted for approximately half of the variance in late winter/spring precipitation ($R^2 = 0.55$, $P < 0.001$). Second, late winter/spring temperature and precipitation influenced the date of beech bud burst. Third, the average laying date of great tits was related to habitat phenology, whereas spring temperature had no significant effect on laying dates. In years with warm late winter and spring, beech buds opened significantly earlier, and in turn the average laying dates were advanced. The overall variation in average annual laying dates was large (Average Julian laying date = 119.5 ± 8.7 SD, range 99–149, $N = 73$ yr). Fourth, the analysis revealed a significant impact of the habitat phenology on the number of eggs laid and the number of juveniles that finally fledged. In years with early tree leafing the reproductive output was significantly improved (number of fledglings = $14.58 - 0.076 \cdot$ date of beech bud opening, $R^2 = 0.18$, $P < 0.001$).

The favoured model supports the hypothesis of a cascade of relationships from large-scale atmospheric circulation indices down to great tit breeding phenology and key parameters of reproductive performance. The effect size for the NAO/NCP impact is strikingly strong. Extremes (± 3 s.d.) in NAO and NCP indices result in a differential of 1.1 fledglings per pair or $\pm 8.5\%$ of the long-term average productivity, keeping all other effects constant. This indicates that the stages of the continental atmospheric

circulations may severely shift crucial life-history functions and thus, have a decisive influence of the long-term dynamics and persistence of populations.

To test the robustness of the final model against potential bias from years with small samples of great tit broods, we re-calculated the SEM excluding years with less than 5 broods ($N = 16$). The changes in parameter estimates for each relationship were very small, however, the test statistics for four parameters were insignificant (results not shown). In combination with the bivariate tests for potential biases, we conclude from these tests that potential bias caused by small sample years was neglectable and that the benefit in statistical power from using the data from these years outweighed the increase in (unexplained) variance.

3.2 Independent validation of structural equation model

Comparing annual mean hatching dates and the mean number of fledglings in Braun-schweig (1970–2000) with predictions from the favoured structural equation model, we found that neither the observed average laying date nor the number of fledglings pro-duced differed significantly from the model prediction (Fig. 3, hatching date: $P = 0.64$, number of fledglings: $P = 0.95$). However, the observed annual variance in both hatch-ing date and number of nestlings exceeded the variance of the predictions (Fig. 3, hatching date: $P < 0.001$, number of fledglings: $P < 0.001$). Hence, the structural equa-tion model appropriately predicts the average breeding phenology and reproductive performance. The local annual variation in these variables is larger than predicted, likely due to variables not represented in the model.

3.3 Retrospective model 1500–2000

Given the substantial impact of the NAOI/NCPI on the annual variation in fecundity, the large-scale atmospheric oscillations may strongly contribute to long-term fluctua-tions of the great tit population since their stages prevail for decades (Fig. 4a, b). Thus a surplus or a deficit in population growth rates of several percent may result in marked

population trends. To further explore these long-term effects, we used the seasonal indices of both oscillations back to 1500 AD to estimate the multidecadal effects on breeding phenology and fecundity. The retrospective model (using NAO/NCP indices as the only input) is illustrated in Fig. 4.

5 The modelling results suggest that around 1500 and 1540–1600 laying dates were relatively late, and the average productivity appeared to be below average for the entire period 1500–1650. Thereafter, the model shows marked fluctuations in both laying dates and productivity (Fig. 4c, d). Three periods of early start of breeding and high productivity emerge: around 1740, 1880 and from 1975, respectively. Also, the modelled

10 effect of NAOI/NCPI on the population index indicates episodes of low productivity and population minima (Fig. 4e). The first minimum coincides with the Maunder Minimum (1650–1720), a second one with the Little Ice Age Type Event I (1810–1850, Wanner et al., 2001). After 1850 the modelled reproductive performance and the relative population index increase strongly and more or less steadily, except a third minimum during

15 1950–1975. In parallel with the strong positive trend of the NAOI from the mid 1970s to the mid 1990s, the model suggests a quick trend towards very early laying dates and a dramatic increase in reproductive output, which both exceed the range of variation over the past centuries (Fig. 4a, c, d).

At the annual scale, the model results suggest that laying dates and fecundity de-

20 viated particularly strongly from the long-term average when high or low states of the NAO and NCP coincided. Figure 5 illustrates the effects on tit fecundity of coinciding negative and positive states of the two oscillations separately for the periods from 1500–1974 and 1975–2000. This shows that the forcing of high/high and low/low constellations of the atmospheric oscillations was reinforced in the post-1975 period com-

25 pared to the long-term variation. Thus, the raise in fecundity after 1975 is probably due to the over-proportional frequency of high/high states (Pearson $\chi^2 = 18.34$, d.f. = 4, $P = 0.001$). Coinciding high states of both oscillations signify relatively warm and dry spring weather and thus, favourable breeding conditions.

3.4 Verification of the retrospective model against independent data

No validation data of bird phenology and productivity are available prior to 1900. However, the estimates of habitat phenology from the retrospective model were validated against an independent data series of spring phenology 1750–1900. This period includes the Little Ice Age Event I cooling. At the interannual level, the modelling results are significantly correlated with the Rutishauser et al. (2007) spring index ($R^2 = 0.11$, $n = 151$ yr, $P < 0.001$), however, the relationship is weak. At a multidecadal level (25-yr moving averages), model estimations and validation data agree well ($R^2 = 0.32$, $n = 141$ yr (no moving averages were calculated at series edges), $P < 0.001$, Fig. 6). This suggests that the retrospective model appropriately assessed the variation in bird breeding phenology, including warming and cooling episodes.

Qualitative evidence supports the model results of great tit production for the 19th century where no quantitative data are available. The British and European great tit populations likely decreased markedly in the first half of the 19th century, whereas after 1850 populations increased and expanded continually (Alexander and Lack, 1944; Kalela, 1950). This agrees with our reconstruction of the NAOI/NCPI-related variation of population dynamics from 1800 to present (Fig. 4d), and with the verification series of spring phenology by Rutishauser et al. (2007). We are not aware of any evidence for bird population trends before 1800.

4 Discussion and conclusions

4.1 Structural equation model 1901–1999

The favoured structural equation model detected a substantial signal of the NAO and NCP at various levels of the ecosystem. The leafing phenology of the forest habitat was mainly determined by spring temperature and precipitation. Moreover, extremes (± 3 SD) in the NAO and NCP indices resulted in a deviation of 1.1 fledglings per pair, or

±8.5 % from the long-term average fecundity, keeping all other effects constant. Thus, the NAO/NCP-related variation in productivity may cause strong long-term population trends because the NAO/NCP stages prevail for many tit generations (see Fig. 4a, b). For example, a differential in annual productivity of +2 % over 25 yr will result in a 64 % population increase, an anomaly of −2 % over the same period will result in a decline by 40 % (Fig. 4a, b). An effect of similar magnitude of the El Niño Southern Oscillation (ENSO) on the fecundity of black-throated blue warblers (*Dendroica caerulescens*) has been demonstrated by Sillett et al. (2000). Also, Nott et al. (2002) show impacts of the ENSO and the NAO on demographic parameters of several bird species within the late 20th century. Thus, the atmospheric oscillations may act similarly on many species in that they determine fundamental conditions at the scale of decades and operate at the top of cascades that include large-scale weather conditions, local trophic webs and in turn, energetic conditions for reproduction. Huntley et al. (2008) calculated predictions for changing species distribution ranges on the basis of climatic envelopes for a large proportion of European breeding birds.

The data of habitat and bird phenological data available in Switzerland during the 20th century allowed structural modelling of past climate-ecosystem relationships over an exceptionally long period, including decades before the onset of the recent warming phase. Our results provide insight into the network of causal mechanisms linking atmospheric circulation patterns and indicate that the habitat phenology plays a key role in the phenology of the entire trophic chain, and ultimately the final reproductive output of great tits. Furthermore, our results suggest a large plasticity of the great tit breeding system. For example, the average laying date varied by 19.5 days (10 % to 90 % range). The relationship between beech bud burst and great tit start of laying was linear over this entire range, indicating no apparent limitation of the plasticity of the system within the range of variation of climate factors included in the analysis.

The structural equation model including variables ranging from large-scale atmospheric circulation patterns to individual-scale life history processes can neither proof the causal mechanisms linking the parts of the path model, nor can it include all steps of

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the trophic cascade. However, in the case of the great tit, a large record of experimental and observational evidence supports the findings at different levels of this system. Laying dates and reproductive success of the birds are particularly strongly related to the lower levels of the trophic chain (Nilsson and Källander, 2006). Experimental ma-
5 nipulation of ambient temperatures did not affect laying dates, but influenced the egg formation process and clutch sizes (Nager and Van Noordwijk, 1992). This supports the notion that habitat phenology and the related phenology of protein food resources (the "caterpillar peak", Naef-Daenzer and Keller, 1999; Charmantier et al., 2008; Lyon et al., 2008) are key ecological processes linking climate and great tit life histories. The
10 validation of the structural model with independent data also corroborates the results of our analysis.

4.2 Retrospective model 1500–2000

Given the significant effect on average annual habitat phenology and tit reproductive performance, the NAOI and NCPI likely drive substantial long-term ecological fluctua-
15 tions, since their stages prevail for long periods (Fig. 4). The retrospective model further extends the view by including multiple cycles of positive and negative stages of both atmospheric oscillations. Thus, reconstructions of past climate conditions, here monthly data for NAOI and NCPI, allowed to estimate ecological climate effects for the past half millennium. This emphasizes that the the marked changes from 1975 on exceed the
20 range of variation under past climate conditions.

In particular, the minima in tit productivity (and negative population growth rates) were correlated with periods with a late average begin of laying, and coincided with well-documented episodes of harsh weather conditions in Europe, such as the Maunder Minimum (1650–1720) and the Little Ice Age Type Event I (1810–1850). The model
25 indicates multiple periods during which the annual breeding performance deviated by up to 0.5 standard deviations from the long-term average (note that Fig. 3 gives 25-yr moving averages). A striking result is that the model, using seasonal NAOI and NCPI indices as the only input, also appropriately returned the shift towards an early

onset of breeding and high productivity from 1975 on. For the post-1975 period, the NAO/NCP indices predict that laying dates have advanced by 0.6 standard deviations, and reproductive rates increased by 1.2 standard deviations compared to the 500-yr average. As illustrated in Fig. 5, the reinforcing effect of the stages of the two oscilla-
5   tions was markedly increased for the post-1975 period. The causes of this are unclear. We conclude that over the past half millennium the NAOI and the NCPI accounted for substantial variation in ecosystem structure and function, in particular the phenology of the habitat and important life-history traits of its inhabitants.

The retrospective model estimates one key variance component of ecological fluctu-
10 ations on the basis of newly reconstructed data for the NAO/NCP indices covering the entire 500 yr. However, additional factors, for example changes of the woodland habitat (whether climate related or not), density dependent variation in reproductive parameters, or variation in predation rates, likely have superimposed, but not concealed, the effect of the large-scale atmospheric circulation (see also Saether et al., 2007). We
15 conclude that the causal chain linking large-scale atmospheric oscillations to individual life-history traits as given in the analysis part provides an explanation for the fundamental importance of climate factors for the continent-wide spatio-temporal dynamics of the great tit (Saether et al., 2003, 2007). Combining ecological and palaeoclimatological data improves insight in how global atmospheric oscillations and related climate
20 variations determine crucial components of variance in ecosystem structure and functionality from the largest spatio-temporal scale down to the individual level. On one hand, the large variation in the phenological response of the tits (Fig. 4c) indicates high plasticity of the phenology of reproduction. This accords with empirical and experimental evidence from other populations (Charmantier et al., 2008). On the other hand, the
25 marked variation in fecundity (Fig. 4d) and demographic parameters (Fig. 4e) indicates that this plasticity cannot fully mitigate climate forcing on reproductive performance and thus, population persistence in various species (see also Nott et al., 2002; Both et al., 2004). The analysis of climate-ecology relationships over the past half millennium suggests that the recent changes in European woodland habitats and related trends in bird

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populations exceed the range of variation in the past. Future increase in anthropogenic greenhouse gas concentrations is likely to induce a positive trend in the winter NAOI (Alcamo et al. 2007), and thus, amplification of the trend since 1975.

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Table 1. Overview of data series used in the analysis and models.

Parameter,	Period					
Application	1500	1600	1700	1800	1900	2000
Date of beech bud opening, 1951–2000 **Structural Equation Model 1901–1999**	ı	ı	ı	ı	ı	▬ ı
Date of beech bud opening 1900–1950 **Structural Equation Model 1901–1999**					▬	
NAO index, reconstruction, 1500–2000 **Input to retrospective model**	▬▬▬▬▬▬▬▬▬▬▬▬▬▬▬▬▬▬					
NCP index, reconstruction, 1750–2000 **Input to retrospective model**	▬▬▬▬▬▬▬▬▬▬▬▬▬					
Great and blue tit demographic data, Braunschweig, 1970–2000 **Independent validation data**						▬
Index of spring phenology 1750–1900 **Independent validation data**				▬▬▬▬▬		

Black bars indicate time series that were used for structural equation model (SEM) analysis. Dark grey bars indicate the two time series that were used as input to the retrospective modelling. Light grey bars indicate the two time series used for model verification.

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Table 2. Matrix of bivariate correlations (Pearson's *r*) of the variables included in the structural equation model (SEM).

		Clutch size	Brood size	*N* fledg-lings	Tempe-rature Jan–Apr	Precipi-tation Jan–Apr	NCPI Jan–Apr	NAOI Jan–Apr	Date of beech bud burst
Laying date	*r* =	−0.19	−0.03	−0.12	**−0.31**	**0.26**	**−0.32**	0.05	**0.33**
	P =	0.102	0.792	0.321	0.008	0.025	0.005	0.653	0.004
Clutch size	*r* =		**0.55**	**0.24**	0.18	−0.13	0.11	−0.05	**−0.39**
	P =		<0.001	0.042	0.126	0.274	0.373	0.705	0.001
Brood size	*r* =			**0.45**	−0.03	0.08	0.07	−0.10	**−0.25**
	P =			<0.001	0.809	0.517	0.562	0.417	0.035
N fledglings	*r* =				**0.26**	−0.02	0.12	0.15	**−0.42**
	P =				0.025	0.872	0.318	0.214	<0.001
Temperature Jan–Apr	*r* =					−0.07	0.06	**0.57**	**−0.69**
	P =					0.535	0.613	0.000	<0.001
Precipitation Jan–Apr	*r* =						**−0.75**	−.06	**0.25**
	P =						<0.001	0.612	0.036
NCPI Jan–Apr	*r* =							0.08	**−0.24**
	P =							0.482	0.044
NAOI Jan–Apr	*r* =								**−0.28**
	P =								0.017

N = 73 yr. Bold print indicates coefficients with *P* < 0.05.

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Table 3. Model selection results for structural equation models (SEM, Generalized least squares maximum likelihood estimation). First, models 2–6 evaluate the structure within the biotic (habitat-bird) sub-system, excluding climate forcing. Second, the structure of the biotic sub-system of model 6 was kept constant to evaluate the effects of atmospheric circulation indices (NAOI/NCPI), climate (temperature/precipitation) and habitat phenology on the breeding phenology and performance. The favoured model 14 is the most parsimonious model without statistically insignificant relations. It indicates that the interface between abiotic and biotic components is via ambient temperature and precipitation, both acting on habitat phenology. Factor loadings of Model 14 are given in Table 4, the path diagram and equations in Fig. 2. NAO = North Atlantic Oscillation index, NCP = North Sea – Caspian Pattern index, T = temperature, PR = precipitations, PH = habitat phenology (date of beech bud burst), LD = laying date, CL = clutch size, BR = brood size, FL = number of fledglings.

Model		Bentler-Bonett non-normed index	d.f.	Remarks
1	Independence model	0.0	33	
2		0.448	27	
3		0.467	25	
4		0.536	28	
5		0.570	25	
6		0.579	26	"Null" model for unrelated sub-systems
7		0.913	22	"Full" model, several relations insignificant
8		0.533	24	
9		0.578	24	Precipitation relates the sub-systems
10		0.734		Temperature relates the sub-systems. No effect of phenology on laying date
11		0.853	24	Temperature relates the sub-systems. Multiple effects of phenology on breeding performance
12		0.878	23	
13		0.886	24	
14		**0.908**	23	Final model. Parameter estimates given in Table 4

Table 4. Parameter estimates for the favoured model 14 as in Table 3. $N = 73$ yr.

| Influence	Parameter estimate	Standard error	t	p
NAOI → Temperature	0.708	0.099	7.122	<0.001
NCPI → Precipitation	−0.798	0.055	−14.451	<0.001
Temperature → Date of beech bud opening	−0.686	0.061	−11.12	<0.001
Precipitation → Date of beech bud opening	0.269	0.108	2.490	0.013
Date of beech bud opening → Laying date	0.266	0.118	2.254	0.024
Precipitations → Laying date	0.332	0.142	2.344	0.019
Clutch size → Brood size	0.673	0.250	2.551	0.011
Brood size → Number of fledglings	0.372	0.097	3.850	<0.001
Date of beech bud opening → Clutch size	−0.385	0.120	−3.203	0.001
Date of beech bud opening → Number of fledglings	−0.329	0.114	−2.884	0.004
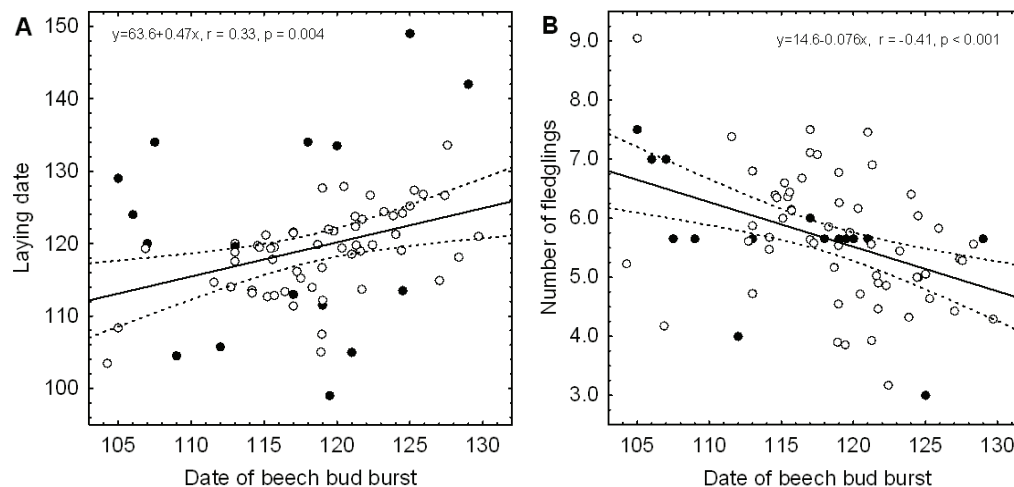
Fig. 1. (A): average annual laying date; **(B)** average annual number of fledglings per great tit brood in relation to the date of beech bud burst 1901–1999. Circles: years with 5 and more broods included. Dots: years with brood sample size below 5.
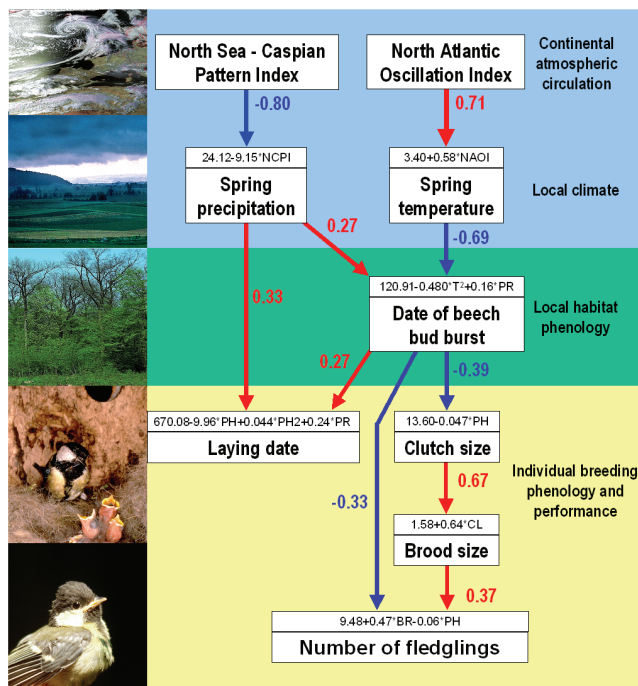
Fig. 2. Path diagram and partial equations for the chain of relationships from large-scale atmospheric circulation to great tit reproductive output. For each relationship the equation (in frames) and path coefficients (bold numbers) are given. NAOI indicates North Atlantic Oscillation index; NCPI, North Sea-Caspian Pattern index; T, Average annual late winter/spring temperature (January–April); PR, average annual late winter/spring precipitation (January–April); PH, habitat phenology, average date of beech bud burst; LD, average annual laying date; CL, average annual clutch size; BR, average annual brood size. Arrow colour indicates positive (black) and negative (grey) relationships. For clarity, disturbances to the variables are not shown. Background colours indicate different stages of the cascade (see also Figs. 3, 4 and 6).
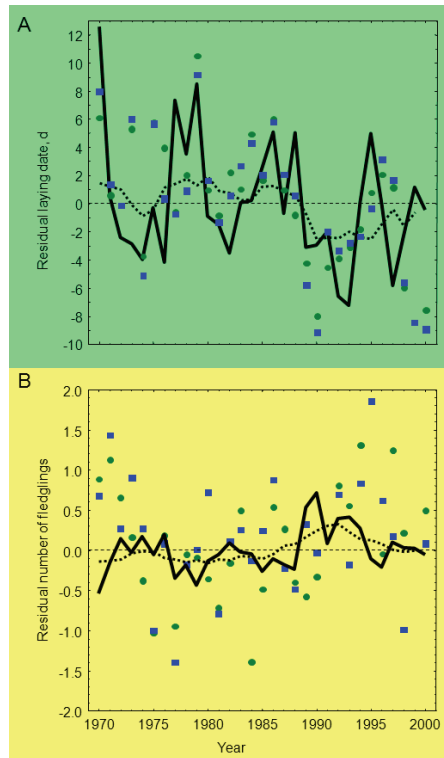
Fig. 3. Validation of structural equation model results against independent observational data. **(A)** Breeding phenology and **(B)** reproductive output in Braunschweig (Germany) 1970–2000, given as the residual from the overall average for the great tit (circles, 31 yr) and the blue tit (squares). Solid lines give predicted values as calculated from NAOI/NCPI data according to equations in Fig. 1. Dotted lines give 11-yr moving averages of predicted values (declining to 3-yr at end points).
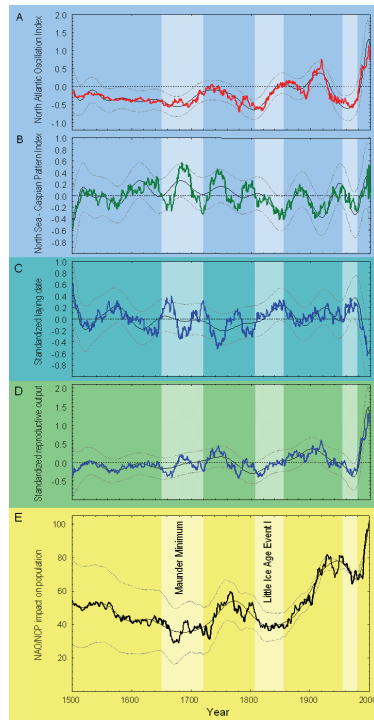
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Fig. 4. The decadal fluctuation in the North Atlantic Oscillation Index NAOI and the North Sea–Caspian Pattern Index NCPI and their effect on key parameters of the great tit population in Switzerland since 1500 AD. Bold lines give 25-yr moving averages (windows declining to 11 yr at end points). Fine solid lines and dotted lines give the fit and 90 % confidence bands to annual values by 10 × 2 Fourier series polynomial regression. **(A)** NAOI reconstruction (blue, Luterbacher et al., 2002). **(B)** NCPI reconstruction (Kutiel and Benaroch, 2002, own data). Note the different scale in the y-axes in **(A)** and **(B)**. **(C)** Residual laying date (in standard deviation units) as modelled from NAOI/NCPI reconstructions. **(D)** Residual number of fledglings as modelled from NAOI/NCPI reconstructions. **(E)** component effect of reconstructed NAOI and NCPI on the population fluctuations, expressed as an index set to 100 points in year 2000. The three minima in the population index coincide with periods in which climatic conditions in Central Europe were harsh: the Maunder Minimum (1650–1720), the Little Ice Age Type Event I (1810–1850), and 1950–1975. Dotted lines give ±2 s.e. bands of relative population index (double smoothing applied).

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Fig. 5. Effects of high and low states of the NAOI and NCPI on the predicted annual fecundity of great tits 1500–1974 and 1975–2000, respectively. Coinciding high states (indices > 0) of both oscillations favoured markedly increased predicted annual fecundity. When both states were low (indices < 0) predicted fecundity was particularly low (left panel). After 1975, the effect was reinforced compared to the period 1500–1974. Coinciding high/high states indicate relatively warm and dry springs (see also Fig. 2 and Table 4). No significance tests were performed on predicted values. Bars give annual averages, whiskers denote 95 % confidence intervals for means.

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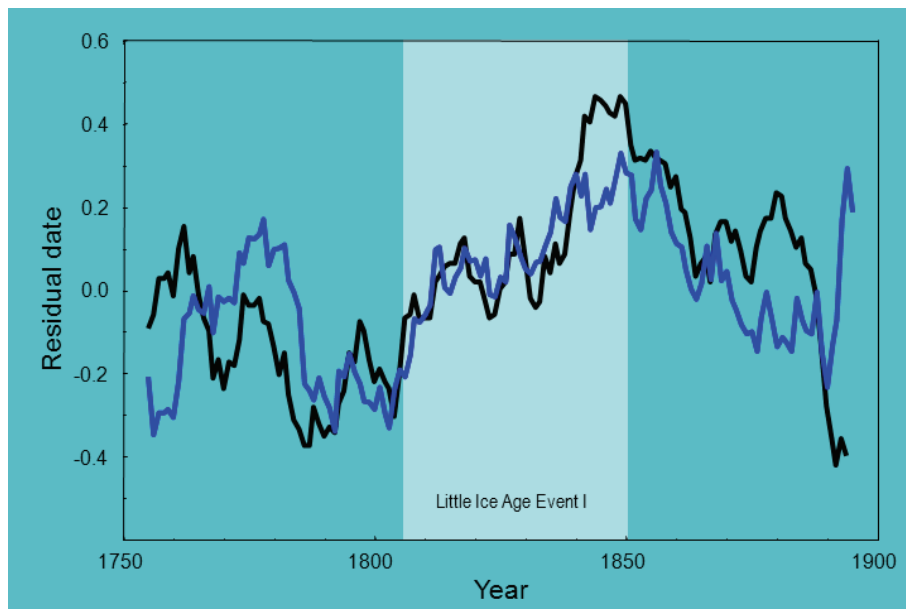
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Fig. 6. Verification of the habitat phenology in the retrospective model against independent data on spring phenology 1750–1900. Grey line: modelled average laying date of great tits. Black line: Index of spring phenology according to Rutishauser et al. (2007). Both indices are given as the standardized residual deviation from the long-term (1750–1900) average laying date and spring index, respectively.