Long-term population dynamics of a migrant bird suggests interaction of climate change and competition with resident species

Torben Wittwer, Robert B. O'Hara, Paul Caplat, Thomas Hickler and Henrik G. Smith

T. Wittwer (torben.wittwer@nateko.lu.se) and P. Caplat, Dept of Physical Geography and Ecosystem Sciences, Lund Univ., Sölvegatan 12, SE-223 62 Lund, Sweden. TW, PC and H. G. Smith, Centre for Environmental and Climate Research, Lund Univ., Sölvegatan 37, SE-223 62 Lund, Sweden. HGS also at: Dept of Biology, Lund Univ., Sölvegatan 37, SE-223 62 Lund, Sweden. – R. B. O'Hara and T. Hickler, Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, DE-60325 Frankfurt am Main, Germany. TH also at: Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, DE-60325 Frankfurt am Main, Germany.

The separation of abiotic and biotic factors affecting populations and communities is an important step in understanding how climate change can influence ecological processes, but quantifying their relative contribution to community changes is a challenge. We assessed the effect of temperature and species interactions on the population dynamics of a forest bird community with a hierarchical dynamic population model in a Bayesian framework. We used a long-term time-series (1956–2012) of four secondary cavity-nesting birds with similar food and nesting requirements but different migration habits, to analyse the effects of the four species population size and the local weather fluctuations on each species' population dynamics. We found clear evidence of a negative effect of two resident species (blue tit and great tit) on a long-distance migrant (pied flycatcher). Among the residents we only found a competition effect of the great tit on the marsh tit. The birds showed opposite responses to weather: the pied flycatcher favoured colder springs whereas the blue tit and great tit favoured warmer springs. Although alternative mechanisms cannot be ruled out, our results suggest that the resident species (blue tit and great tit) could adjust to increasing spring temperature while the migrant species (pied flycatcher) could not, leading progressively to the exclusion of the pied flycatcher from the area. These results point out the potential role of competitive interactions by providing insightful clues, call for refined research, and support recent efforts to include population dynamics in species distribution models.

Ongoing climatic changes have already translated into changes in species distribution patterns (Thomas and Lennon 1999, Parmesan and Yohe 2003, Bellard et al. 2012, Lindström et al. 2013, Svenning et al. 2014, Virkkala and Lehikoinen 2014) and population dynamics (Sæther et al. 2000, Both et al. 2006a). However, the important idiosyncrasies in species' responses (Auer and King 2014, Bradshaw et al. 2014) call for a better understanding of the mechanisms driving the dynamics at multiple scales (Sorte 2013). The role of population processes for ecological networks (Wells et al. 2014) and macro-ecological patterns has been increasingly emphasized in climate change studies (Kearney and Porter 2009, Zurell et al. 2009, Franklin 2010, Pagel and Schurr 2012).

The responses of populations to climate change are complex, as a species' life-cycle can be affected, directly or indirectly, by a change in weather patterns. A typical example is the effect of climate on temperate bird phenology. Many bird nestlings' diets consist of caterpillars (Perrins 1991, Wilkin et al. 2009), which respond to increases in spring temperatures by advancing their phenology. Corresponding to the resulting change in caterpillar peak many bird species are forced to adjust their breeding cycles (Lack 1954, Visser et al. 2006, Burger et al. 2012). How exactly these phenological shifts affect whole populations remains an open question (Johansson et al. 2014).

In addition, species are not isolated – distributions reflect current and past interactions between species (Kissling et al. 2012, Lovette and Hochachka 2006, Wisz et al. 2013). In particular, resource competition is a ubiquitous phenomenon in ecological systems (Cody 1974, Connell 1983, Schoener 1983). For example, within a given habitat birds often compete for food and nesting sites (Dhondt 2012) and the competition for a resource can be strong enough to exclude species locally (Alatalo et al. 1985). These interactions can, in turn, translate into large-scale patterns (Wisz et al. 2013, Gotelli et al. 2010), although they might not be easy to detect as interactions may be less strong compared to processes at a larger scale (Araújo and Rozenfeld 2014).

Furthermore, different species respond individually to environmental change (Tylianakis et al. 2008), which causes temporal and spatial disassociations of species interacting at different trophic levels (Harrington et al. 1999), and which in turn can affect the strength of interspecific interactions (Ahola et al. 2007) and lead to non-analogous communities (Keith et al. 2009). For instance, different bird species might

vary in their capacity to shift their breeding cycle to match with the peak of caterpillar abundance. Typically, migratory birds might not adjust their phenology as fast as resident species, due to the complexity of their life cycle (Both and Visser 2001). This can thus change timing of a demand for essential resources (such as caterpillars as food, or nest sites) to a period of strong overlap of two species and changing thus the competitive balance between species (Ahola et al. 2007). Consequently interaction between phenology and migration habits can lead to complex and non-linear responses to climate changes (Walther 2010).

Modelling approaches can help to understand how prevailing competition and climate change interact to affect species dynamics (Ives et al. 2003, Mutshinda et al. 2011). Traditionally population modelling studies have focussed on the dynamics of individual species, but technical (such as easy to use Bayesian software) and conceptual advances (such as multivariate population models) have made it possible to test whether the dynamics of one population is affected by inclusion of other species (Mutshinda et al. 2009).

We used a multivariate autoregressive model (Ives et al. 2003, Mutshinda et al. 2011) to explain how competition in concert with temperature changes affects the long term dynamics of an avian community in a temperate forest. So far, evaluations of population models, which analyse competitive relationships in combination with temperature changes in bird communities, are lacking but are necessary to improve for instance the accuracy of predictive modelling at larger scales (Wisz et al. 2013). Those evaluations could be done against prior knowledge about competition, phenology and temperature changes.

To this end, we focussed on a guild consisting of four cavity nesters: the long distance migrant pied flycatcher *Ficedula hypoleuca*, and three resident birds: the blue tit *Cyanistes caeruleus*, great tit *Parus major* and marsh tit *Poecile palustris*, with partly known competitive relationships (Dhondt 1977, Ahola et al. 2007). By focussing on population dynamics, we aimed at getting insights on the mechanism driving long-term community dynamics that cannot be detected in community patterns (Wells et al. 2014). We expected to identify signals that would reflect competitive interactions documented elsewhere, such as between the great and blue tit (Dhondt 1977), whereby which species dominates depends on the resource under competition, or between the great tit and the pied flycatcher (Slagsvold 1978). Especially, competition for nest sites is expected since a previous study from the same area showed that cavities for nesting are strongly limiting the population sizes of cavity nesters and are therefore a resource under competition (Enemar et al. 1972).

Methods

Data

We analysed the dynamics of an avian community consisting of four cavity-nesting species in Fågelsångsdalen surveyed annually between 1952 and 2012 (Fig. 1). The site is a small valley (~ 13 ha) in southern Sweden, 9 km east of the town of Lund, with deciduous forest. This area has been protected since 1963, but is managed to keep it in a condition
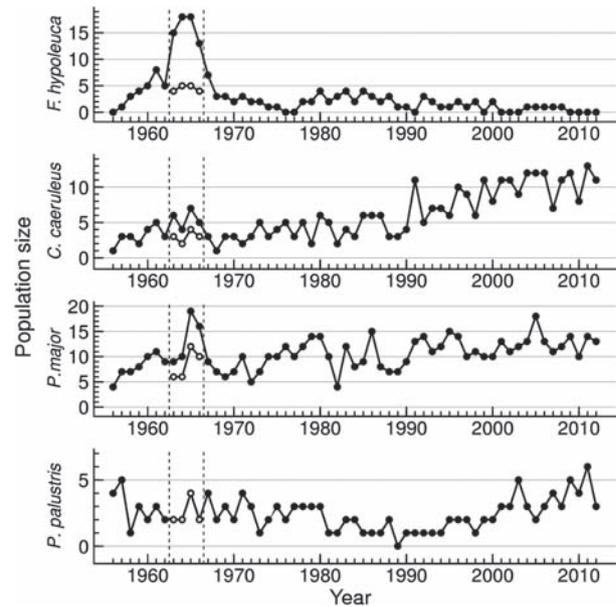
Figure 1. Population sizes of the pied flycatcher *Ficedula hypoleuca*, the blue tit *Cyanistes caeruleus*, the great tit *Parus major* and the marsh tit *Poecile palustris* in the Fågelsångsdalen from 1956 until 2012. Empty circles denote numbers of individuals not nesting in nest-boxes. Vertical lines denote the period with nest-boxes (1963–1966).

of a mosaic of broad-leaved forest, which is constituted of a mix of mainly beech, oak, maple, ash, hawthorn and black thorn, and nearby grazed meadows. Nevertheless, much of the habitat changes occurring are due to natural ageing of the forest (Enemar et al. 1994). An exception of anthropogenic influence on the bird community was the placement of 60 nest boxes in the valley between 1963 and 1966, which increased the total abundance of the four cavity-nesting bird species (Enemar et al. 1972; cf. Fig. 1). Another mentionable influence on the valley is the Dutch elm disease, which arrived in southern Sweden in the 1970s and killed many of the elm trees leaving snags standing potentially available for cavity-nesting birds in the valley. This could have influenced the cavity-nester population, but we lack quantitative information and have therefore not included it in the following analysis.

All four species are known to nest in cavities, and hence may compete for these nesting sites (Slagsvold 1975, Alatalo 1982, Dhondt 2012). The pied flycatcher is the only species of the four that is a long distance migrant. In the study area, the blue tit is a partial migrant, and the great tit (although it shows occasionally irruptive behaviour) and marsh tit are residents during the winter months (Ulfstrand 1962, Smith and Nilsson 1987, Nilsson and Smith 1988).

These four species are the most common cavity nesters of the local bird community. Other cavity nesters were not included in this study as they were rare; the nuthatch *Sitta europaea* with 22 years of absences, starling *Sturnus vulgaris* with 11 years of absences and tree sparrow *Passer montanus* with 45 years of absences. During the years of presence the nuthatch had a maximal number of territories of 6, the starling of 12, and the tree sparrow of 4.

The data used for the analyses came from territory mapping surveys (Enemar et al. 1994, Svensson et al. 2010,

Thorner 2011). The surveys started in 1952 but we omitted the years 1952–1955 as the surveys in these years were based on too few census visits. For the territory mapping, individuals were tracked by sight and sound, and their territories spatially delimited based on several census visits (up to 16 times per year, and since 1986 consistently ten times per year between April and June). The sampling effort to delineate the territories is very high, leading to very close estimates of the true breeding bird populations in the area reducing the risk of observer effects (Bibby et al. 2000). In addition, the species we considered are predominantly monogamous (Krebs 1971, Lundberg and Alatalo 1992), and while territory mapping relies on the activity of males, this number reflects also the number of females and is thus a good estimate of population size.

We used temperature data from the Swedish Meteorological Institute recorded in Lund, 9 km west of Fågelsångsdalen, to represent weather conditions in the valley. We used the monthly average temperatures to calculate the spring (March, April and May), summer (June, July and August), autumn (September, October and November), and winter (December, January and February) average temperatures for each given year (with January and February measured the following calendar year). We prepared the temperature data for the analysis by centring the data on zero, and standardising the standard deviation to one (Fig. 2) with a mean of 6.8, 16.6, 9.0 and 0.4°C, and a standard deviation of 1.2, 1.0, 0.9 and 2.0°C for spring, summer, autumn and winter temperatures, respectively. Correlations between all pairwise combinations of the seasonal temperatures were tested using Pearson correlation coefficients. All correlations had an absolute value lower than 0.34, so our interpretations should be robust to this covariance (Dormann et al. 2013).

Population dynamic model

Model overview
We constructed a model describing the temporal change in population size for the four cavity nesting birds. In the model the size of populations is driven by seasonal
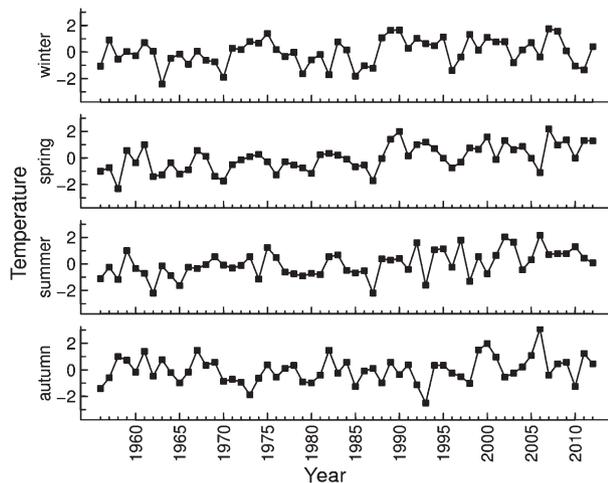
Figure 2. Spring, summer, autumn and winter average temperatures for the period 1956–2012 measured at the Lund weather station. Values are centred around 0 and standardised to unit variance.

fluctuations (i.e. spring, summer, autumn and winter temperatures), and additional unmeasured environmental fluctuations are included as a stochastic variable. The population is regulated by density dependence (i.e. intraspecific competition) and, potentially, the population size of other species (i.e. interspecific competition). It is further bounded by a carrying capacity (e.g. availability of tree cavities to establish nests). The resulting population size is also modulated by demographic stochasticity.

Model formulation

Changes in population size from year t to t + 1 are affected by demographic stochasticity, represented by a Poisson distribution:

$$x_{i,t+1} \sim \text{Pois}(y_{i,t+1}) \tag{1}$$

where $x_{i,t+1}$ is the estimated population size from the territory mapping census of species i at year $t + 1$, while $y_{i,t+1}$ represents the expected population size at $t + 1$ without the demographic stochasticity in the same year.

To account for density-dependence we used the Gompertz model (Dennis et al. 2006, Mutshinda et al. 2011), which is linear on the natural logarithmic scale and is equivalent to a first-order autoregressive model, which accounts for temporal autocorrelation. The model predicts the population size of a species i, a year t, as a function of its population size the previous year, the population size of another species j, a species-specific carrying capacity K, and temperatures T, following:

$$\ln(y_{i,t+1}) = ln.x_{i,t} + r_i \left(1 - \Sigma_j \alpha_{i,j} ln.x_{j,t} / K_{i,b}\right) + \Sigma_k \beta_{i,k} \cdot T_{tk.} + \varepsilon_{i,t} \tag{2}$$

where $ln.x_{i,t} = \ln(x_{i,t} + Imm_i)$ with Imm_i the immigration rate; r_i is the intrinsic population growth rate of species i (growth in absence of environmental and density effects); $\alpha_{i,j}$ is the per capita effect of species j on the per capita growth rate of species i.; β_i describes the effect of each of the k seasonal temperature variables on the per capita growth rate; $\varepsilon_{\cdot,t}$ denotes stochasticity in population growth rate arising from environmental variability.

The priors for the carrying capacity K were drawn for each species from a normal distribution with the hyperparameters (i.e. parameters on a higher hierarchy that constrain the parameters at the species level) $K.m$ and $K.s$ for mean and standard deviation, respectively. For both hyperparameters, we chose uniform positive priors between 0 and 10.

As competition can be defined as the reduction of the growth rate of one species by another (Morin 2011), the α-parameters can be interpreted as competition. A special case is given by $j = 1$, which is intraspecific competition. For this case we set all $\alpha_{i,i}$ to 1. We allowed for asymmetric competition between the species and, as coexistence between species is only possible if intraspecific competition is stronger than interspecific (Chesson 2000), we set the prior for the interspecific competition coefficients $\alpha_{i,j}$ (with $j \neq i$) to be maximally 1. Further, we allowed for facilitation letting $\alpha_{i,j}$ ($j \neq i$) to be minimally -1.

The priors for the intrinsic population growth rate r_i were drawn from an exponential distribution. The priors for the seasonal temperature coefficients were uninformative with N(0,1000) except for the effect of the autumn and winter temperatures on the migratory pied flycatcher, which we set to 0.

The environmental stochasticity was defined by a multivariate normal distribution around the zero vector **0** with covariance matrix Σ_t:

$$\varepsilon \cdot_{,t} = \text{MVN}(\mathbf{0}, \Sigma_t) \tag{3}$$

The diagonal of the covariance matrix Σ_t was the unexplained residual variation for the species, whereas the off diagonal elements were the unexplained correlations with competitors stemming from unexplained environmental variation (Mutshinda et al. 2009).

Parameter estimation and posterior predictive check

We estimated the unknown model parameters from the observed population sizes by using Bayesian inference (Ellison 2004, Clark 2005, Kéry 2010) with the Gibbs sampler implemented in 'JAGS' ver. 3.4.0, which we ran within 'R' ver. 3.0.2 using the packages 'R2jags' ver. 0.03-11 and 'rjags' ver. 3-11. We ran three chains each with a length of 215 000 iterations. We omitted the first 15000 iterations as burn-in, and thinned to every 20th value to give us a total of 30 000 draws from the joint posterior.

We used a posterior predictive check to evaluate model adequacy by simulating a new dataset of population counts given the estimated model parameters and model assumptions, and compared this replicated dataset with the observed population counts. Based on the sum of squared residuals of the replicated and original dataset as discrepancy measure, we calculated a Bayesian p-value for each species. A Bayesian p-value of 0.5 indicates a perfect fit and has a reasonable range from 0.05 to 0.95 (Gelman et al. 2014).

All estimated parameters are reported with its uncertainties as the highest posterior density interval (HPDI), calculated with the R package 'boa' ver. 1.1.7-2.

Analysis of species interactions

To test for the existence of competition or facilitation interactions between any pair of species, we used a Bayesian variable selection method called 'stochastic search variable selection' (SSVS; O'Hara and Sillanpää 2009, Mutshinda et al. 2011). In the SSVS, we defined the priors for the competition coefficients as mixtures of two normal distributions, with one being very close to zero (spike) and the other being uninformative (slab), so that any non-zero value would be selected given that the competition differed sufficiently from zero if there is enough evidence for competition in the observation data. Hence, the ratio of the spike to the slab part is an indicator of either presence or absence of competition. Formally, whether the competitive effect should be included in the model is decided on basis of the Bayes Factor, which describes the change of the prior odds of including the variable in the model to the posterior odds given the observed data. A variable was included if the Bayes Factor was larger than 1, and the Jeffreys' scale (Jeffreys 1983) divided the Bayes Factor in 5 additional classes: between 1 and 3 there

is 'barely worth mentioning' evidence, between 3 and 10 'substantial' evidence, between 10 and 30 'strong evidence', between 30 and 100 'very strong' evidence, and above 100 'decisive' evidence of including the variable.

Results

Runtime, convergence and posterior predictive check

The running time of estimating the unknown parameters in the model took about six hours on a notebook equipped with an i7 M620 CPU running at 2.66 GHz and 4 GB RAM. All three chains for each parameter had converged to a stationary distribution, which we assessed using the Gelman–Rubin statistics with a threshold of 1.1 (Gelman and Hill 2006).

For the pied flycatcher, the blue tit, the great tit and the marsh tit the Bayesian p-value was 0.61, 0.81, 0.87 and 0.94, respectively.

Population growth rates

The population growth rate was highest for the great tit with the mode at 1.09, and the 95% HPDI between 0.00 and 1.92 (Fig. 3). The next highest intrinsic growth rates described, in declining order, the blue tit with a mode at 0.55 (95 % HPDI: 0.01–1.06), the marsh tit with a mode at 0.35 (95% HPDI: 0.00–1.09), and the pied flycatcher with a mode at 0.30 (95% HPDI: 0.00–1.27).

Competition coefficients

We found 'substantial' evidence for competition of the blue and great tit on the pied flycatcher (Table 1). There was 'barely worth mentioning' support for competitive effects of the great tit on the marsh tit. We could not find any evidence of interaction between the other species combinations.

For the three pairwise interaction, for which we found evidence of competition, the posterior modes of the non-zero competition effect were 0.91 (95% HPDI: 0.10–1.00) for the effect of the blue tit on the pied flycatcher, 0.88 (95%
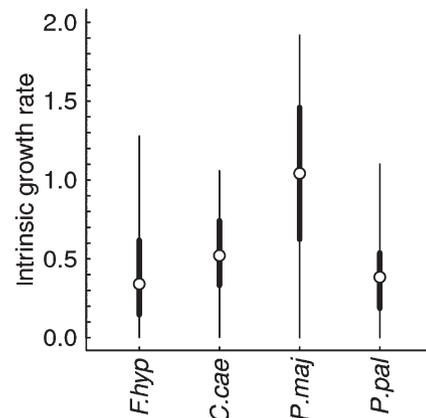
Figure 3. Posterior densities for the intrinsic growth rates. Circles denote the mode, and the thick and thin denote the 50% and 95% highest posterior density interval (HDPI).

Table 1. Bayes factor for evaluation of inclusion of coefficient for species interactions. '**' denote 'substantial' and '*' denotes 'barely worth mentioning' evidence for competition. The sign denotes the direction of the competition effect. A '+' is for a competitive effect of the species in the column on the species in the row; a '−' vice versa.

	Ficedula hypoleuca	Cyanistes caeruleus	Parus major	Poecile palustris
Ficedula hypoleuca	–	+ 3.54**	+ 3.11**	+ 0.71
Cyanistes caeruleus	+ 0.45	–	+ 0.63	+ 0.56
Parus major	− 0.29	− 0.49	–	+ 0.39
Poecile palustris	− 0.96	+ 0.85	+ 1.53*	–

HPDI: 0.08–1.00) for the effect of the great tit on the pied flycatcher, and 0.51 (95% HPDI: –0.07–1.00) for the effect of the great it on the marsh tit. As these estimates come from mixtures of zero and non-zero centred Gaussians, some part of the non-zero part could spuriously be assigned to the zero part, which would consequently lead to an overestimation of the above reported competition effect. We, therefore, need to report here the posterior probability of being non-zero. The posterior probability for being non-zero is for the effect of the blue tit on the pied flycatcher is 47%, for the effect of the great tit on the pied flycatcher 44%, and for the effect of the great tit on the marsh tit 28%.

Covariate effect sizes

We modelled the effects of environmental covariates, i.e. average spring, summer, autumn and winter temperatures, on the population growth (Fig. 4). We found strong reciprocal effects of spring temperatures on the pied flycatcher (mode: –0.19; 95% HPDI: –0.46–0.04) and the blue tit (mode: 0.19; 95% HPDI: 0.03–0.36), whereas the probabilities of a true non-zero spring temperature effect were very high with 95% and 99%, respectively. The summer
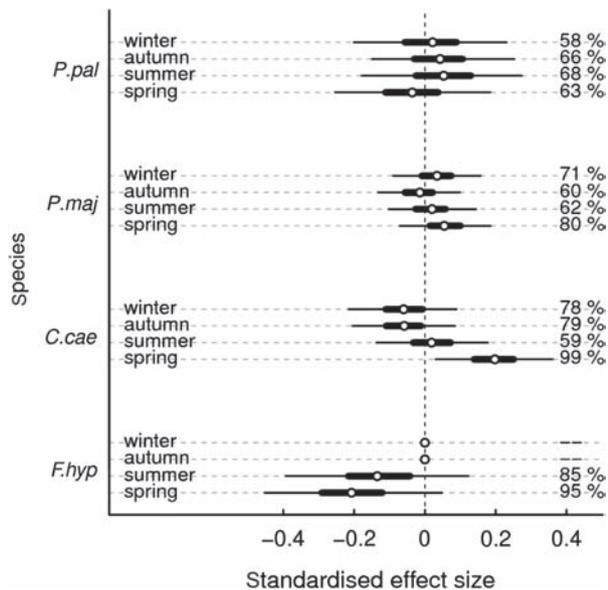
Figure 4. Standardised covariate (spring, summer, autumn and winter temperature) effect sizes on the per capita growth rate on the bird species. Circle denotes mode, thick bars 50% HPDI and thin bars 95% HPDI.

temperature was also found to have an effect on the pied flycatcher (with 85 % probability), with colder summers being favoured (mode: –0.20; 95% HPDI: –0.45–0.05). For the great tit warmer springs had with 80% probability a positive effect (mode: 0.06; 95% HPDI: –0.07–0.19). The probabilities of the other covariates to have an effect on the growth rate were all below 80%.

Discussion

We applied a multi-species model that accounts for direct and indirect effects of interacting species and weather fluctuations on the population dynamics of four cavity nesting birds. This revealed seemingly an asymmetric competition network in which two resident species (blue and great tit) had the strongest competitive effect on the migratory pied flycatcher, but surprisingly little competition between the residents. Here we discuss possible processes that could explain the result found for climatic and competitive effects on the population dynamics but also limitations of the modelling approach pointing out future research directions.

Climate effects, migrant and residents

Territory-mapping data for our study area showed a long-term increase (since the 1960s) for two resident species, the blue tit and great tit, while the only migratory cavity-nesting species, the pied flycatcher, decreased until extirpation from the area. This observation of the pied flycatcher is in line with the general decline of long-distance migrants in Europe (Berthold et al. 1998). In Sweden a long term survey confirms the decline (Green and Lindström 2014). Both et al. (2006b) argued that climate driven mistiming of migrants with their food source is a widespread phenomenon leading to European wide population declines.

In addition, our model revealed that blue and great tit populations increased more in years with warmer springs, while the pied flycatcher population increased more in years with colder springs. This strongly points towards an effect of climate on the cavity-nesting community, particularly as these findings are consistent with the hypothesis that resident and migrant species differ in their ability to match breeding dates to vegetation and caterpillar phenology (Both et al. 2009). Indeed, long-distance migrants must time the departure from their wintering grounds, and subsequent stopovers, to reach the breeding ground without on-site information on resource availability. It is therefore not surprising that they do not match their arrival to the shifted conditions at the breeding grounds (Jonzén et al. 2006, Charmantier et al. 2008). In contrast, residents can match the onset of their breeding cycle much more to the prevailing conditions and increase their population fitness during spring warming (Charmantier et al. 2008, Vedder et al. 2013). Local observations show that the egg laying for the great tit advanced in the last 40 years by about 10 days (from early/mid May to late April), while the flycatcher's laying date remained during late May (Hans Källander unpubl.), which reinforces the hypothesis of a shift in phenology.

In terms of competition our results indicate that the pied flycatcher is subordinate to the blue and great tit. Is this

result reasonable? There are two well established competition mechanisms that could explain the observed pattern: 1) competition for food with differences in foraging habits, and 2) competition for nesting sites with direct interference of the competitors.

When competing for food early in the season the blue tit has an advantage over the other species as it forages on smaller insect instars (Slagsvold 1975, Dhondt 1977, Török and Tóth 1999). In addition, warmer springs should have, as we found, a positive effect on the blue tit's fitness, since it feeds on the insects before these reach the development stage (cf. Slagsvold 1976).

Nest site competition often leads to direct confrontations with the competitor causing casualties on all sides (von Haartman 1957, Slagsvold 1975, 1978, Lundberg and Alatalo 1992, Källander 1994, Merilä and Wiggins 1995). Especially with an advance of the breeding cycle of the great tit due to warmer spring temperatures, the pied flycatcher is disadvantaged by an increasing frequency of fatal encounters with the great tit (Ahola et al. 2007), which can explain the positive effect of colder springs we found for the pied flycatcher.

Despite the two suggested mechanism being well established elsewhere, we lack the necessary links that connect the suggested mechanism of spring temperature affecting the bird phenology via a chain of effects from vegetation phenology to caterpillar phenology (Both et al. 2009) in our study area. Future field work determining the caterpillar emergence and linking it to local spring temperature could deliver the necessary evidence for the proposed mechanism.

Any observational study, as this one, cannot rule out alternative explanations perfectly. For example, even if the habitat has been protected from human-induced influences there could have been subtle changes in the habitat composition affecting the populations. The pied flycatcher, for instance, can usually breed in any forest habitat, as long as nest sites are provided (Lundberg and Alatalo 1992). Nevertheless, there are differences in population size between deciduous and coniferous habitats, and lower population size in coniferous habitats has been related to lower abundance of food sources (Lundberg and Alatalo 1992). The observed decline of the pied flycatcher could therefore also be explained by a decrease in food supply caused by (undetected) habitat change.

It is also possible that habitat effects in the wintering grounds could carry over to the observed breeding populations (Ockendon et al. 2013). However, this does not contradict our results (competition exerted by the blue tit on the pied flycatcher during breeding), and habitat changes in themselves would not explain the negative effect of warm springs on the pied flycatcher, which points to a climatic effect mediated by biotic interactions.

Coexistence between the resident species

Intraspecific and interspecific competition of great and blue tit have been intensively studied (Dhondt 2012), and these two species compete strongly for nest sites (Minot and Perrins 1986) and for food (Minot 1981). It is therefore surprising that we could not find any evidence for these two species competing. Did our analysis miss an existing competition pattern?

In fact, the competition dominance of the blue and the great tit is shifting during different times of the year (Dhondt 1989) with the blue tit being dominant during the breeding period (Dhondt 1977, Török and Tóth 1999), while the great tit is dominant during winter roosting (Dhondt and Eyckerman 1980, Kempenaers and Dhondt 1991). Species coexistence may therefore be governed by multiple season-specific limiting factors, which may be common in temperate and boreal ecosystems (Chesson 2000). To identify this kind of mechanism, our approach is clearly limited because the annual observation data, which we had used, is the product of the two intra-annual periods with reciprocal dominance, which seemingly negate the effect of competition. If that is true, the predictive performance of approaches, like ours, intending to model species patterns at a macro-scale, will suffer from this effect. The ability to project population changes will be reduced when the coexistence mechanisms are no longer in place and competition might suddenly exclude a competitor. To include this mechanism in any analysis the study design should consider the variations of population sizes and competitive relationships during different times of the year. Conceptually it would only be slightly necessary to modify the model to accommodate the intra-annual population dynamics.

However, it is also plausible that competition between blue tit and great tit is truly relaxed, due to non-overlapping niches or spatial segregation (Lack 1971, Cody 1974, Chesson 2000). Highly structured habitat allows species to spatially segregate and use different parts of the habitat and therefore decrease interspecific competition (Boeye et al. 2014). Since our study uses data aggregated to the whole plot we cannot discern any small scale habitat segregation. In fact the territory mapping data mapped territories per species and year and could be used in a follow-up study to evaluate the small scale habitat associations.

Data and model limitations

The modelling approach we chose seemed the best adapted to include competitive interactions while analysing the long-term population dynamics of bird species. Here we evaluate the limitations of our approach, by discussing the role of 1) scale of the study (number of species, and extent), 2) the model to measure truly competition, 3) ignored habitat changes.

Reliable, long-term time-series of species abundances at a scale where we know they interact, are rare, and as a consequence our study site was relatively small. By working on cavity nesters, we were able to adopt a modelling technique that would have been otherwise limiting, as its computation times increase exponentially with the number of interacting species. We thus ignored a number of potential biotic interactions, both with avian and non-avian competitors and predators, respectively. We, however, think these effects to be minor due to low abundances of competitors and predation prone birds such as open nesters (Martin 1993) fare well in the area.

Could the competition patterns we identified simply reflect unrelated long-term population trends of the species considered where the population trends are driven by an unmeasured environmental factor? In southern Sweden,

the pied flycatcher has indeed been decreasing in abundance, while the blue tit population has been stable (Green and Lindström 2014). As our models correlates the population size of one species with the population change of another, we could expect an erroneously implied competition. But to be identified as competition, these correlations would need to be consistent over time. This seems unlikely as the effect is lagged but possible purely by chance or if both the environmental factor and population size are affected by a third factor.

In addition, there is no reason why the climate-abundance relationships we found would be driven by the regional trends. As a matter of fact, our model might provide some mechanistic explanations for the large-scale population trends of these species, while there is no clear reason why these trends happen. Whether this is truly the case, and how these mechanisms exactly translate at larger scales remains to be determined. This calls for further effort in understanding how population dynamics link with macro-ecological patterns, which has been found to be difficult to analyse due to increased environmental heterogeneity at large scales (Araújo and Rozenfeld 2014).

Our interpretation on competition relied on the assumption that cavities are a limiting resource for the populations. We do not have information on how many potential cavities suitable for nesting exist in the valley, but the data strongly suggests that cavities are indeed an important limiting factor: when nest boxes were added to the area in the 1960s, the abundance of the cavity nesters increased and, hence, the populations were limited by the availability of nest sites. The Dutch elm disease as a another possible factor of change, which killed many trees in the 1970s and left their snags standing in the valley, can be ruled out as a factor affecting the nest site competition. This is mainly because, for instance, the marsh tit population should have increased afterwards as it is able to exploit small cavities caused by the disease early (Ludescher 1973).

Conclusion

Incorporating interspecific interactions in a population model allowed us to point out possible non-linear effects of climate on bird abundance. This was possible by working with a limited number of competing species, and cavity-nesters provide an ideal system to study such interactions. Our results point towards two complementary approaches to understand better the effects of climate change on ecological communities: 1) combining detailed information on species life-cycles, habitat change, and biotic interactions, and 2) incorporate these details in large-scale species distribution models. The structure of our model makes it a good candidate to help achieving the latter, as the mathematical formulation is directly transferable into distribution models by including distributed localities with population time-series, and can accommodate longer time-series.

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