

# Birds' response to climate change: new insights from key demographic factors.

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## *Résumé<sup>1</sup>*

Les changements climatiques en cours affectent la biodiversité à l'échelle mondiale. Les réponses des espèces à FCES perturbations ont été précisément décrite mais les processus sous-jacent restent mal connus. Pourtant, leur compréhension est cruciale pour la conservation. Nous étudions ici les réponses des oiseaux aux changement climatiques à travers trois paramètres démographiques (productivité, phénologie, tendances des populations) en lien avec leur rareté. Grâce aux deux programmes suivant les oiseaux nicheurs de France depuis 1989, nous avons montré que 1) la productivité et la phénologie suivaient finement les anomalies de températures 2) les précipitations apparaissaient également comme facteur clefs de la réponse spécifique 3) les espèces dont la phénologie est la plus sensible étaient généralement les espèces en augmentation. Ajuster sa phénologie pourrait être bénéfique pour les oiseaux face aux changements climatiques. Nous proposons et discutons des scénarios expliquant les réponses des espèces aux changements globaux et les réarrangement des communautés.

Mots clefs: phénologie, productivité, oiseaux communs , changement globaux.

## *Abstract*

Climate changes affect worldwide ecosystems. Species responses to these modifications lead to stark biotic communities rearrangements. Understanding the processes underlying these responses is crucial for conservation of biodiversity. We studied how birds respond to climate change using three demographic indicators (phenology adjustment, productivity and long-term trends) and linked these responses with different aspect of species commonness. We used two long-term and large scale monitoring programs on French breeding birds. We found that 1) productivity and breeding time adjustment closely matched temperature and 2) precipitations also appeared as an important variable in studied processes. 3) species with high phenological sensitivity have more a positive dynamics, suggesting that an ability to adjust phenology allows to be less impacted by climate change. This study provides and discusses some possibilities to understand factors underlying vertebrates' response to climate change and thus leading to rearrangements in communities.

Key-words: phenology, productivity, birds, commonness, global changes.

*1: en vue de valoriser par un article scientifique les cinq mois de stages ayant aboutit à ce rapport, celui-ci à été rédigé en anglais.*

## Introduction

Recent human induced global changes (the combination of land-use and climate changes) are already known to affect biodiversity at a global, worldwide scale (Thomas *et al.*, 2004). Distribution of life on Earth is largely determined by climatic conditions (Sunday *et al.*, 2012; Khaliq *et al.*, 2014), global climate changes, which modify climatic niches, are now considered as one of the main driving forces of species dynamics (Thomas *et al.*, 2004; Pereira *et al.*, 2010). Global change impacts have also been reported at community scale through stark reshuffling of communities compositions (Bertrand *et al.*, 2011; Schaefer *et al.*, 2014; Inger *et al.*, 2014; Godet *et al.*, 2015) by direct (favouring some species over others) and indirect processes (modifying species interactions) (Farrer *et al.*, 2014). These modifications of biodiversity under global change regime lead to an increasing interest from scientific and political perspectives. In this respect, scientists and policy makers are looking forward to the next United Nations Climate Change Conference that will be held in Paris in 2015. The conference's objective is to achieve a legally binding and universal agreement on climate from all nations. **In this context, there is a crucial need for policy makers to understand the factors underlying the response of species to climate change.**

A large body of theoretical and empirical literature has documented impacts of climate change on both species and communities, for different ecosystems and at different spatial/temporal scales (Walther *et al.*, 2002; Parmesan, 2006). These responses include changes in population dynamics (Biro *et al.*, 2007; Inger *et al.*, 2014), spatial distributions (Hickling *et al.*, 2006) and phenologies (Sherry *et al.*, 2007; Gladalski *et al.*, 2013). On the first hand, these studies showed that we were able to describe numerous patterns of responses induced by climate change. On the other hand, only a few have managed to identify finer processes at stake in the species' specific responses (Cahill *et al.*, 2012). In other words, we mainly witness species responses and resulting changes in communities but the ecological drivers responsible for those changes are still obscure. **Overall, despite the increasing interest for climate change impacts, studies identifying most likely general rules (*i.e.* covering different species, life history traits and responses modalities) are still lacking.**

Identifying and understanding which are the most impacted species remains a first order question for biodiversity conservation (Hannah *et al.*, 2007; Foden *et al.*, 2013 ). According to Caughley (1994), conservation has two options: (i) to focus on declining populations before it is too late or (ii) to avoid ultimate extinction of populations of low

numbers. Caughley, however, emphasized that these two paradigms have a major defect. The first attempts is compromised by the multiple and interactive biotic and abiotic factors that are nearly impossible to separate. The second can tackle more obvious causes (whether deterministic or stochastic) but comes often too late to avoid extinction. In short there is a paradox in conservation: either one can do something before it is too late but ignore the causes or one understands the causes but it is often too late.

This tension is indeed shaping the literature on climate change impacts: studies have focused either on fine causal links, but on small and local populations, or on describing trends of many common species, but using descriptive and correlative approaches. A first solution to solve this paradox lies in testing clear predictions on critical stages of the life history. The life history of organisms is composed of parts that interact in ways that have been moulded by natural selection to maximize reproductive success and survival under given environmental conditions (Roff, 2002). Accordingly, changes in climatic conditions affect particular life-history components such as reproductive behaviour and the number of offspring (Parmesan, 2006), which in turn impact species long-term trends (Saether *et al.*, 2013). Moreover, phenology and reproductive success are strongly linked and for instance it was shown that flowering date influences reproductive success of plants (Nemani *et al.*, 2003). These two parameters are so integrated that some theoretical work treats these as properties of the same life-history character (Rowe *et al.*, 1994). A framework for studying these two aspects separately would thus focus on critical components of species' responses regardless of its commonness. Indeed, there is now strong evidence that an inability to adapt in terms of phenology to a seasonality modification is detrimental for a population (Both *et al.*, 2006; Moller *et al.*, 2014). Similarly, impact of climate change on long-term dynamics has also been described. These dynamics are determined by the growth rate, which is traditionally divided into two main variables: reproduction and survival. In birds for example, the relative importance of these two variables (independently from environmental stochastic variability) in the final growth rate is dependent of the studied species' life history traits and generation time (Saether *et al.*, 2013). Considering passerines birds, Saether (2013) showed that contribution of fecundity to growth rate was larger than the contribution of survival. **Overall, by working on two main critical phases, phenology and breeding success, we should be able to test predictions about finer processes at play in species' responses to climate change.**

A complementary solution to the “Caughley's paradox” lies in working on common biodiversity. The study of common species' populations allows to examine the processes

involved in communities rearrangements, to understand them and, if necessary, to carry out preventive conservation actions. To a large extent, conservation priorities are defined by judgements about species extinction. Although all the rare species are not threatened by imminent extinction, all the threatened species are bound to be rare (*i.e.* having small global populations and/or restricted distribution) (Gaston & Fuller, 2008). Thus, at the species level, current conservation is mainly concerned by rare species that receive more attention than common ones, while they should also be of concern (Inger *et al.*, 2014). However, how can we define a rare species ?

In a simplistic way, it is possible to consider as rare, the species with fewer individuals than others of the same taxonomic level. It is also possible to consider as rare, the species having restricted distributions. Another characteristic of being rare could also be defined as the ecological and/or functional specialisation of a species (Rabinowitz, 1981). Limitations of these three approaches taken independently are obvious. Indeed, a species can be common at a given spatial scale and rare at another scale (Hartley & Kunin, 2003). Many examples of worldwide distributed organisms are never abundant locally such as the peregrine falcon *Falco peregrine*. On the other hand, endemic species have a short range but are sometimes very numerous (*Amblyrhynchus cristatus*). Thereby, a recent study, following the Rabinowitz theory (1981), has proposed to disentangle the rarity into three complementary facets in birds: geographical range, local population size and habitat specialization (Godet *et al.*, 2015). On the one hand, species' range is determined by their physiological tolerance to climate variables. One of the most significant response of organisms to anthropogenic climate change is their redistribution on Earth (Walther *et al.*, 2002; Parmesan 2006, Sunday *et al.*, 2012). On the other hand, species may respond to this disturbance according to their range which is, in large part, determined by species thermal optimum (Khaliq *et al.*, 2014). Finally, recent studies have showed a strong link between climate pressure and community composition, including the ratio of generalists versus specialists (Devictor *et al.*, 2008; Barnagaud *et al.*, 2011; Davey *et al.*, 2013; Gaüzere *et al.*, 2015). Generalists are known to be more adaptable to varying thermal conditions and so may be less impacted by climate change (Gilchrist *et al.*, 1995). **Therefore, combining the study of the critical phases of individual responses (reproductive success and phenology) with the definition of different aspects of commonness should be an original and powerful framework to better explain processes of community rearrangements under climate changes.** Building such a framework has been particularly limited by the absence of long-term data-sets providing information on both phenological dates, breeding success and long-term trends concerning species whose biology

is well known.

Birds are one of the most monitored and studied taxa. They therefore provide an excellent model to investigate the impact of global changes on different critical stages according to different facets of species rarity since (i) they vary strongly in abundance, range and specialization level (ii) intensive European monitoring programs provide long-term and robust data-set concerning species dynamics, beginning of the reproductive season, breeding success and survival. Moreover, some European birds are strongly declining while others show very positive dynamics. (Jiguet *et al.*, 2010; Inger *et al.*, 2014) Some of these trends have received straightforward explanations. In particular, the decreases in the population of farmland species is most likely caused by agricultural intensification (Donald *et al.*, 2001). The impact of climate change on these trends, however, is much less understood. Most studies have only shown that species with high temperature preference had more positive dynamics than species with low temperature preference (Devictor *et al.*, 2008; Godet *et al.*, 2011; Kampichler *et al.*, 2012). To our knowledge, however, these trends have not been linked to critical population stages such as reproductive success and phenology and the link between species response to climate change and species commonness is still unclear in birds.

Here, we studied how birds' communities and species respond to climate change using three indicators : phenology adjustment, productivity and long-term trends, based on a 24 year survey. We used two independent citizen science programs: French Constant Effort Sites Program (CES) and French Breeding Bird Survey (BBS). These are long term standardised capture-recapture and count points, monitoring the abundance and demography of a wide range of species since 1989. We linked these two datasets with meteorological data from Météo-France in order to achieve four objectives:

**1) to determine the extent to which breeding success is impacted by anomalies in climatic variables.** To the best of our knowledge, although many studies already addressed this issue, this question had never been tested with a large spatial dataset before. Beyond the effect of climate change on long-term population trends, simple predictions can be derived from the metabolic theory (Porter & Gates, 1969): a positive temperature anomaly (+1-2°C) in a local site compared to the average temperature of that site could be beneficial in terms of productivity by providing more energy in the ecosystem especially in temperate regions where energy seems to be the limiting factor for species (Hawkins *et al.*, 2003). Even if previous studies have shown that avifauna responds to climatic change with a time-lag of 1-3 years (Lindström *et al.*, 2012), **we**

**predict an increase in birds' productivity concomitantly of years for which temperatures are slightly higher than normal.**

2) to test the relation **between shift in breeding time and temperature anomaly** in order to determine species ability to track climate fluctuations. Phenology, could be simply considered as the way for species to track changes in climatic niches (Walther *et al.*, 2002). Hence, phenological plasticity is one of the variables which are susceptible to respond stronger to changes in climatic conditions (Gladalski *et al.*, 2013; Fletcher *et al.*, 2013; Dunn & Moller, 2014). As a consequence, **we expect a fine adjustment of the timing of reproductive behaviour to the changes in climatic variables.**

3) to evaluate species dynamics to explore the link between species long-term trends and both productivity and phenology responses to the current climatic conditions. As mentioned above, for passerines, contribution of stochastic environmental events (like climatic pressure) in fecundity to growth rate is larger than the contribution from survival (Saether *et al.*, 2013). Therefore, assessing **how long-term population trends are linked to the responses in productivity and phenology, will give us some information about the relative importance of stochastic environmental events in fecundity and behavioural plasticity.**

4) to link these three indicators (productivity, phenology and long-term trends) with traits of rarity and commonness to identify species that are likely to suffer from climate change. It will be interesting to study generalists' responses in productivity to examine whether these species are more favoured than specialists by climate warming. In agreement with the biotic homogenization process, **we expect that species with high degrees of commonness (defined from local abundance, range or specialization) might be able to better track their climatic niche by phenological adjustment and thus, have a productivity less sensitive to climate changes.**

We explore these three aspects of birds' populations dynamics (reproductive success, phenology and long-term trend) combined with the definition of three different facets of commonness thanks to long-term and large-scale datasets. Our original approach provides a powerful framework in theoretical and conservation biology to better explain processes of organism's responses under climate changes.

## *Methods*

### 1. Data.

#### 1. 1. Bird data.

We used data from two long-term and large-scale monitoring programs in birds started in France in 1989 on the model of the American Breeding Bird Survey (Sauer *et al.*, 1997) and the British Constant Effort Site (Peach *et al.*, 1998). The aim of the French Breeding Bird Survey (FBBS) is to assess the spatial and temporal variations in the abundance of breeding populations of common birds. The French Constant Effort Site (FCES) intended to study the variations of the two most important demographic parameters (adult survival and reproductive success) by trapping and ringing birds. Both FBBS and FCES are based on volunteer skilled ornithologists following a standardized protocol on the same sites for several years (Julliards *et al.*, 2011 ; Jiguet *et al.*, 2012).

For the FBBS all birds seen or heard are counted during five minutes in 10 points inside a 2km\*2km square (Figure 1.). In this study we worked at the square scale and we summed all the birds find in a squares (*i.e.* in all the points). Squares are randomly placed to ensure a good representation of the habitat diversity. Moreover, points are placed proportionately to different habitats in the square. Each site (square) is sampled twice during the breeding season when birds sing (April/mid-June) within the three weeks around the pivotal date of May 8th to ensure the detection of both early and late breeders. To be validated on the long term, the counts must be repeated on approximately the same date of the year ( $\pm 7$  days), the same time of the day ( $\pm 15$  min within 1-4h after sunrise), by the same observer. The maximum count per point for the two spring sessions is retained as an indication of point-level species abundance. From the beginning of the FBBS in 1989 to 2001, surveyed plots were freely chosen. A new sampling design was started in spring 2001 for which plots were selected randomly, ensuring that the sampled habitats were representative.

FCES is a ringing scheme. Individuals are counted by means of catching with mist-nets during breeding period. The number of mist-nets (three to five) and the date of trapping (between May and mid-July) are fixed for a given site. Captured birds are ringed before being released to avoid double counting. Species and age are determined unambiguously from plumage. As for the BBS, counts must be performed on the same date of the year and by the same volunteer.

These two monitoring schemes are complementary. The first one concerns a large number of sites (2321) and sets up a relatively light protocol providing information about the

majority (393 species detected) of birds breeding in France. The FCES is implement on a smaller number of sites (236) and species (153), but sets up a heavy protocol providing information on the key processes of population dynamic: the reproductive success. Although it represents a valuable source of information, the FCES is largely underused compared to the FBBS. The complementary use of these two monitoring programs gives the opportunity to overcome the intrinsic limits of each method and provides great information on dynamic, phenology and breeding success of a large number of species within various taxonomic and geographic scales.

During the period under study (1989-2012), a total of 2337206 individuals were counted on 2321 sites surveyed over an average of six years. Thanks to the FCES, 304130 birds were caught on 236 sites from 1989 to 2014. For both FBBS and FCES methods, the unit of interest for this study is the number of individuals of a given species at a given site in a given year.

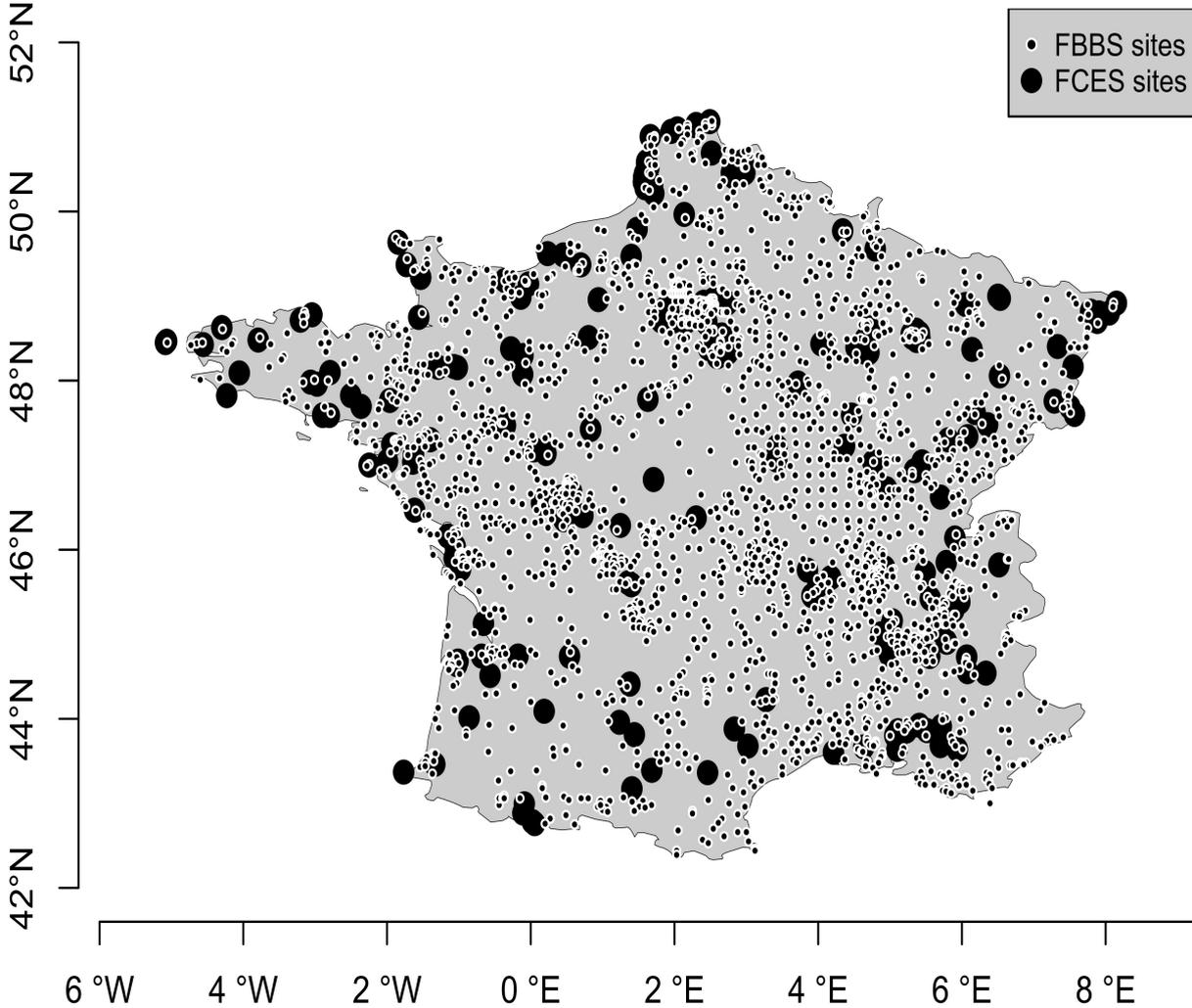


Figure 1: geographical distribution of FBBS and FCES sites.

### 1. 2. Climatic data.

Climatic data (monthly mean temperature and accumulated precipitations) were extracted from the SAFRAN meteorological model (Quintana-Seguí, 2008). The SAFRAN system is an analysis system for surface variables which provides climatic data to cover France including air temperature and rainfall on an 8 km\*8 km grid. SAFRAN does interpolation by taking into account all of the observed data from Metéo-France's observation network and data from some well instrumented stations within and around the area under study (1000 stations in total for temperature and more than 3500 for precipitation). Data are calibrated by the meteorological model which includes an analysis of atmospheric models (ARPEGE or ECMWF from Metéo-France). It has been shown that the temperature and the precipitation analyses were robust and not biased by Quintana-Seguí (2008) who presented a detailed description and assessment of the SAFRAN analysis over France.

We matched each of the FBBS and FCES sites monitored at a given year with the nearest point on the SAFRAN's grid (*i.e.* nearest than 8km) and we calculated mean spring precipitation (April to June, in mm per month) and mean spring temperature (April to June, in °C) for this given year. Climate change is not a constant process in space and time and consists also in an increase in variability (IPCC 2007). On the studied time range, a global increase in temperature is evident but with a strong oscillation pattern. Hence, we decided to analyse spring temperature and precipitation anomalies compared to site-scale average. In order to find the temperature or precipitation anomaly for a given site and a given year, we scaled both variables for each site.

### 1. 3. Birds' traits.

To explore the link between birds response and their commonness, we used three indexes decomposing different forms of commonness in birds (Rabinowitz, 1981; Godet *et al.*, 2015):

**Species abundance index (SAI):** this index represents the local abundance of species. It is high for gregarious species such as common starling (*Sturnus vulgaris*) and low for solitary species such as European robin (*Erithacus rubecula*).

**Species range index (SRI):** this index is an estimator of the total area of the species within the boundaries of the French metropolitan territory.

**Species generalization index (SGI):** this last index represents the degree of generalization for habitat in a given species. Higher SGI corresponds to a higher level of generalization. Higher SRI and SAI correspond to greater commonness with respect to their

range size and their local abundance, respectively.

For more details about calculations, please refer to Barnagaud (2001), Julliard (2006), Devictor (2010), and Godet (2015).

## 2. Data analysis.

In this study, we worked on two different levels:

**For each species**, our objective was to link climate change effects on critical drivers of population dynamics with different forms of commonness. Thus, we defined three variables: productivity as a proxy of breeding-success, breeding time index (BTI) as a proxy of ability to adjust the phenology and long-term trend. In a second time, we defined following variables: in productivity sensitivity (PrS) and productivity response (PrR), and phenological sensitivity (PhS) and phenological response (PhR). sensitivity is here defined as the  $R^2$  of the relation between explanatory variable (productivity or BTI) and climate variable. Response is the slope of the same relation.

To explore how French avifauna responds in term of breeding-success and breeding date adjustment to climate variations, **for all species together**, productivity and breeding-time index (BTI) were aggregated.

### 2. 1. Defining descriptors of birds' populations dynamics.

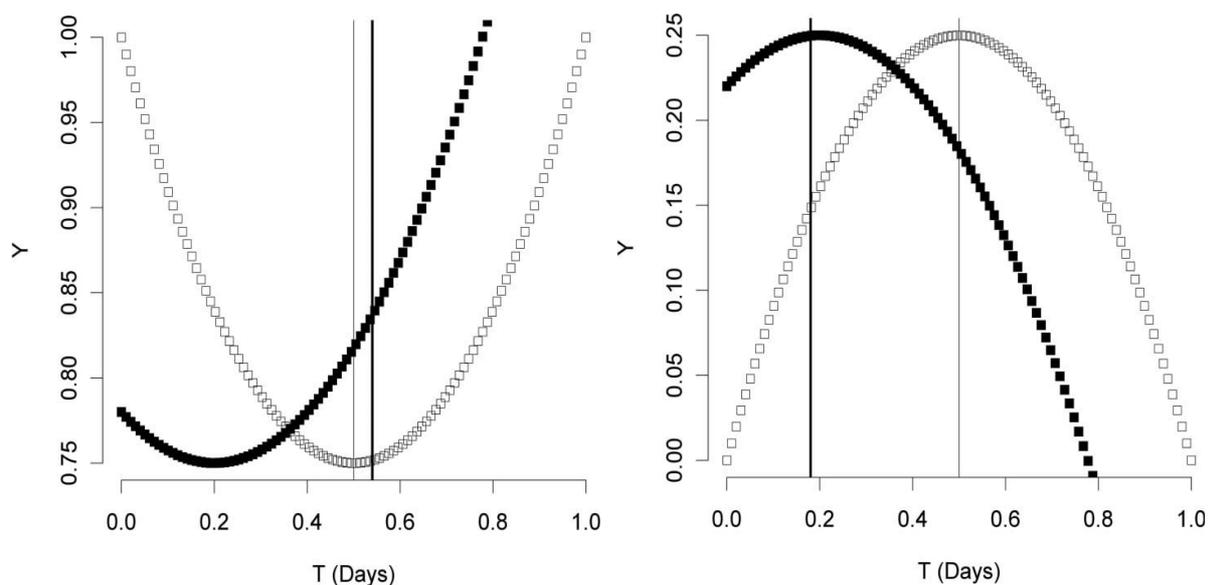
#### 2. 1. 1. Productivity.

Productivity estimates are calculated thanks to the French Constant Effort Site program as the proportion of juveniles among samples of all individuals caught during spring for a given species. All species with at least 150 individuals on 15 sites captured were retained. We excluded five reed bed specialist for which local factors such as drought are likely to override global change effect (Julliard *et al.*, 2004). The final dataset contains 41 species caught on 235 sites which are monitored with an average of 6 years.

#### 2. 1. 2. Phenology.

The FBBS provides information about birds' phenology by analysis of the occurrence date for each species. Birds are detected from the moment they sing which is indicative of the beginning of the reproductive behaviour. Some simple methods have been created to infer phenological shifts between two years by using mean or median count dates weighted by abundance (Sparks *et al.*, 2005; Jonzen *et al.*, 2006, Knudsen *et al.*, 2007). Unfortunately, it is impossible to compare the shifts of different species with different life history traits with these

techniques (the sign of the shifts depends to the shape of the count distribution, Figure 2). According to the Moussus (2009) method, we estimated a breeding time index (BTI) as the difference in phenological timing of a species between two years. This temporal shift is calculated by making all couple of years' seasonal trends (*i.e.* the variations of abundance through Julian date) match using an iterative algorithm and a generalized additive mixed effects model (GAMM) to the count data of both years. To achieve this, numbers of bird counted were summed over all FBBS sites per species, per year and per day (in days after 1 April). For each couple of years, data of one year are temporally shifted until they match the data of the other year by fitting a generalized additive mixed effects model (GAMM) to the count data of both years. The fit of each model corresponding to each value of shift is monitored by its Akaike information criterion (AIC) (Akaike, 1981). Finally, the BTI of a given species represents the optimal shift in days of the reproductive behaviour between two years. For more information about these techniques please refer to Moussus (2009).



**Figure 2:** Mean shifts reflecting the same effective phenological shift, depend on the shape of the seasonal count distribution (From Moussus *et al.*, 2009)

### 2. 1. 3. Long-term dynamic.

Here, we qualify the long-term dynamic of a population as its tendency to increase or decrease over years (Julliard *et al.* 2004). To explore the link between long-term trends and both productivity and phenology responses, species' annual growth rates were estimated by fitting a generalized linear mixed effects models (GLMM, Bates, 2005 ; Zuur *et al.*, 2009) of numbers of birds counted (quantitative explanatory variable assuming a Poisson's distribution) by year as a quantitative response variable. Considering that variability between plots

(observers, habitat, regional species pool, and bioclimatic region) adds uncontrolled variations to this analysis, the random variation of the intercept on each plot was allowed by adding site as a random intercept term. Thus, the long term temporal trend of a species was summarized by a single estimate, the instantaneous growth rate (Figure 3). We calculated this estimate for 112 species over 24 years of the FBBS surveys (2321 sites). New sampling design was started in 2001. Before this date, surveyed plots were freely chosen and volunteer's choice to site with more birds is susceptible to create a bias in long-term trends estimates. We argue that, even if it is not a perfect solution, this effect is attenuate by adding site as a random intercept (as most of sites were changed after 2001). Another solution could be for instance to add a factor “old protocol” (before 2001) and “new protocol” as a fixed effect in the model.

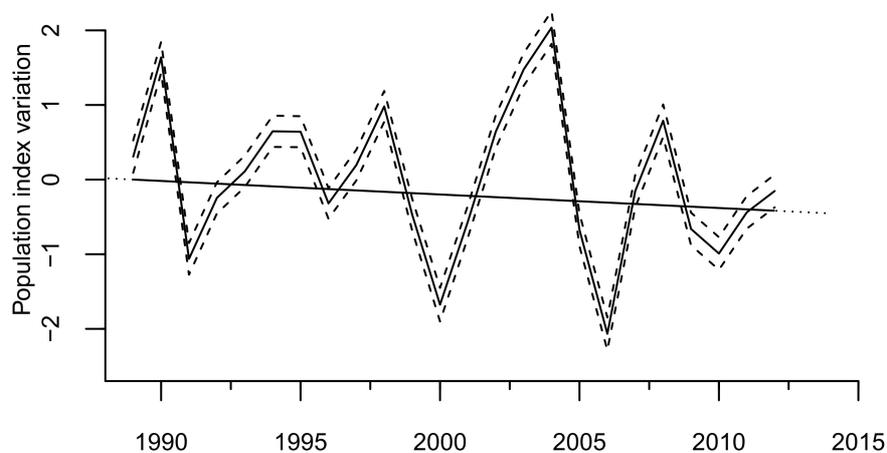


Figure 3: Population long-term trend : an example of a negative trend for the chiffchaff (*Phylloscopus collybita*) with population variations ( $\pm$  standard error).

## 2. 2. Describing climate impact on populations dynamics.

### 2. 2. 1. Productivity.

**For all species aggregated**, we used linear mixed effects models (Bates, 2005 ; Zuur *et al.*, 2009) to determine the relation between productivity (*i.e.* the proportion of juveniles among the captured individuals) and climatic variables over the 25 years of survey. In order to study how French avifauna responds in term of breeding-success, we first aggregated productivity values of all species by arithmetic means of years productivity. The response variable was this site-level productivity (n=236), including all 41 species, and was analyzed using standard logistic regression (binomial error). To find which climatic variables best describe productivity variations, we fitted all possible combinations of explanatory variables and selected the best one on the basis of AIC weights (Akaike, 1981; Zuur *et al.*, 2009). To take into account inter-site variability (volunteers, habitat, bioclimatic region and species), all

models fit a random effect of site with a nested species effect.

To determine how productivity and temperature anomalies were associated in time, we performed time series analysis. We used a cross-correlation function to find the best shift in the auto-correlation of both time series. In this function, the variance of the cross-correlation function is dependent on the autocorrelation present in the individual series (Venables and Ripley, 2002).

As climate change is not the same throughout the studied area (Gäüzere *et al.*, 2015), we explored possible spatial pattern in the relation between climatic variables and productivity thanks to a model including latitude or longitude.

**For each species** (n=41), we fitted a linear mixed model of the relation between productivity and temperature anomaly. Considering the variability between plots, we also added site as a random intercept term for these models. We calculated the productivity response (PrR) and productivity sensitivity (PrS) to climate respectively as the fixed effect coefficient (slope) and the marginal pseudo- $R^2$  of the temperature anomaly effect on productivity. Productivity values were not determined with the same accuracy and we used the inverse squared standard estimation errors of the productivity to weight the model. We are aware that calculation of  $R^2$  on mixed models is not yet fully developed and we provide these results as a relative indication which should be considered carefully (Nakagawa & Schielzeth, 2012).

### 2. 2. 2. Phenological adjustment.

**For all species aggregated**, we explored variations of the BTI according to both climatic variables at community level by fitting a linear model. This model linked the average of observed shifts in reproduction season between two years for community of a given site with the difference in temperature between these two years. Model validation was assessed by “residuals repartition” and “deviation from normality” (normal Q-Q) interpretation plots. The model was heteroscedastic and unbiased.

**For each species** (n=112), we calculated the phenological response (PhR) and phenological sensitivity (PhS) to climate as the slope and the  $R^2$  of the temperature anomaly in the following linear model: BTI~temperature anomaly. Phenological shifts were not determined all with the same accuracy. As a consequence, we used the inverse squared standard estimation errors of the BTI to weight the model. We calculated PhR and PhS for 112 species with data from 2321 FBBS sites.

2. 2. 3. Linking species' response and sensitivity with commonness facets and long-term trends.

To address our third objective and test the relationships between species response and sensitivity and their traits (SAI, SGI and SRI), we considered all traits as continuous quantitative variable. We explored relation of response (PrR and PhR) and sensitivity (PrS and PhS) from each of the linear model fitting explanatory variable variations at the species level. Despite these two aspects of variation are well-known in statistic, variance explained is often over-looked (especially for GLMM which are usually analysed with AIC).

We explore relationships between response (PrR and PhR) and sensitivity (PrS and PhS) and species long-term trends by fitting linear model. Model validation was assessed by “residuals repartition” and “deviation from normality” (normal Q-Q) interpretation plots. The model was heteroscedastic and unbiased.

## Results

### 1. Productivity.

When considering all species pooled together, our analysis showed that variations in productivity were best described by a model including temperature anomalies and precipitation anomalies (Table 1). The relative productivity of all species for one site and one year was significantly associated with variations in temperature (linear mixed model; n=41; slope= 0.1123; standard error= 0.005; z value = 19.512;  $\Pr(>| Z |) < 0.0001^{***}$ ) and precipitation anomalies (linear mixed model; n=41; slope= 0.1198; standard error= 0.005; z value = 21.42;  $\Pr(>| Z |) < 0.0001^{***}$ ). In this model, both explanatory variables were scaled and it appeared that temperature effect was stronger (about fivefold). Moreover, temperature effect is highly significant when tested alone (linear mixed model; n=41; slope= -0.0298; standard error= 0.005; z value = -5.451;  $\Pr(>| Z |) < 0.0001^{***}$ ). Thus the productivity increased with warmer (Figure 4a.) and in a lesser extent drier climatic condition. At this scale the result of the time-analysis by cross-correlation function showed that a lag of 0 year support the best autocorellation between variations in productivity and temperature anomalies describing an undelayed response of birds productivity to climate change (Figure 4b.).

Table 1: Results of linear mixed models relating productivity to climatic variables.

Explanatory Variables	Estimate	Std. Error	z value	Pr(>  Z  )	AIC	BIC	LogLik
Temperature anomalies	0.119763	0.005591	21.42	< 0.0001***	26122	26152	-13057
Precipitation anomalies	-0.05522	0.00531	-10.40	< 0.0001***	26472	26502	-13232
<b>Temperature anomalies +precipitation anomalies</b>	<b>0.112292</b> <b>-0.029833</b>	<b>0.005455</b> <b>0.005473</b>	<b>19.512</b> <b>-5.451</b>	<b>&lt; 0.0001***</b> <b>&lt; 0.0001***</b>	<b>26095</b>	<b>26132</b>	<b>-13042</b>

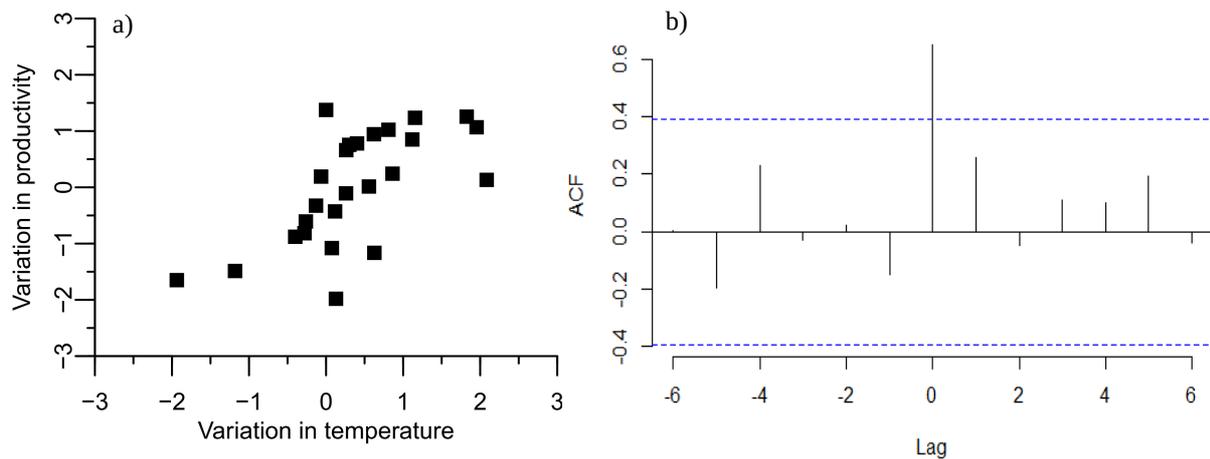


Figure 4: Relation between productivity and temperature anomaly a) was highly significant and productivity increased with warmer b) showed that a lag of 0 year support the best autocorellation between the two variables.

We found no pattern between species' PrR and long-term trends relation (linear model;  $n=41$ ; slope= -1.2424; standard error=0.8058; t value =-1.542;  $\Pr(>|t|) = 0.131$ ) and species' PrS and long-term trends (linear model;  $n=41$ ; slope= 0.4951; standard error=0.4123; t value =1.201;  $\Pr(>|t|) = 0.237$ ).

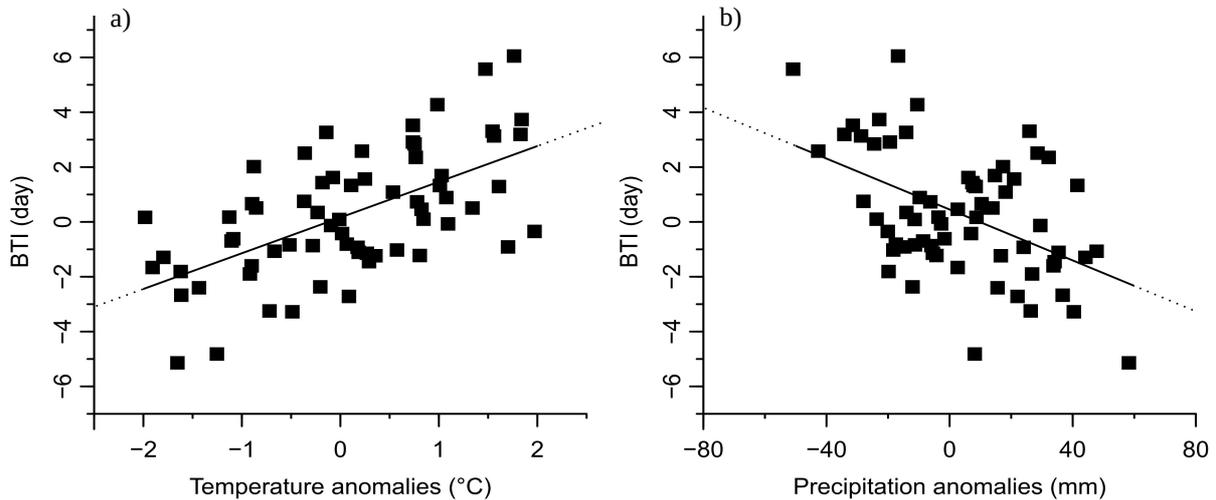
We found no significant relation between productivity and longitude/latitude suggesting that no strong linear pattern exist in the response of birds productivity to climatic variables.

## 2. Phenology

When considering all species pooled together, variations in BTI were best described by a model including spring temperature anomalies (linear model;  $n=112$ ; slope= 1.0405; standard error= 0.229; t value = 4.544;  $\Pr(>|t|) < 0.0001^{***}$ ) and spring precipitation anomalies (linear model;  $n=112$ ; slope= -0.02686; standard error= 0.01; t value = -2.675;  $\Pr(>|t|) = 0.00951^{**}$ ) (Table 2). In this model, both explanatory variables were scaled and it appear that temperature effect was much stronger (about fiftyfold). Moreover, temperature effect is highly significant when tested alone (linear model;  $n=112$ ; slope= 1.3031; standard error= 0.2166; t value = 6.017;  $\Pr(>|t|) < 0.0001^{***}$ ) and AIC of this model is only 5 units (four units discriminate two models) more than the model including both climatic variables. Thus, the beginning of the reproductive behaviour is early during warmer and in a much lesser extent drier year (Figure 5a.b.).

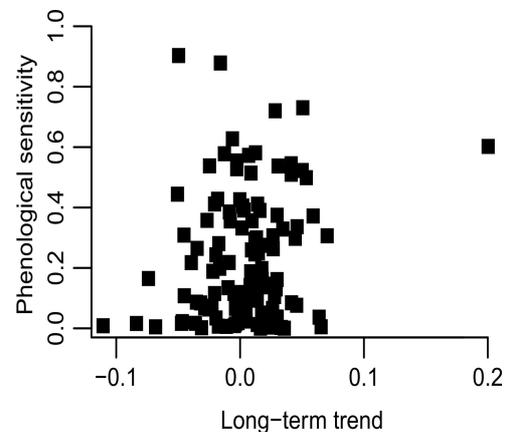
**Table 2** : Results of linear models relating BTI to climatic variables.

Explanatory Variables	Estimate	Std. Error	t value	Pr(>  t  )	df	AIC	R <sup>2</sup>
Temperature anomalies	1.3031	0.2166	6.017	< 0.0001***	64	270.5617	0.3513
Precipitation anomalies	-0.04642	0.01037	-4.476	< 0.0001***	64	282.1733	0.2265
<b>Temperature anomalies +precipitation anomalies</b>	<b>1.04053 -0.02686</b>	<b>0.22897 0.01004</b>	<b>4.544 -2.675</b>	<b>&lt; 0.0001*** 0.00951**</b>	<b>63</b>	<b>265.4608</b>	<b>0.45</b>



**Figure 5** : Strong correlation between BTI values for one year (considering all species pooled together) and a) temperature b) precipitation anomalies in the same year.

At the species scale, species' PhS was significantly but slightly linked (linear model; n=112; slope= 1.0691; standard error= 0.5376; t value =1.989; Pr(>| t |)= 0.0492\*) to their long-term dynamic (growth rate). Increasing species seems to have higher phenological adjustment capacities (Figure 6). No pattern was found for PhR and long-term trend relation (linear model; n=112; slope= 1.394; standard error=12.439; t value =0.112; Pr(>| t |)= 0.911).



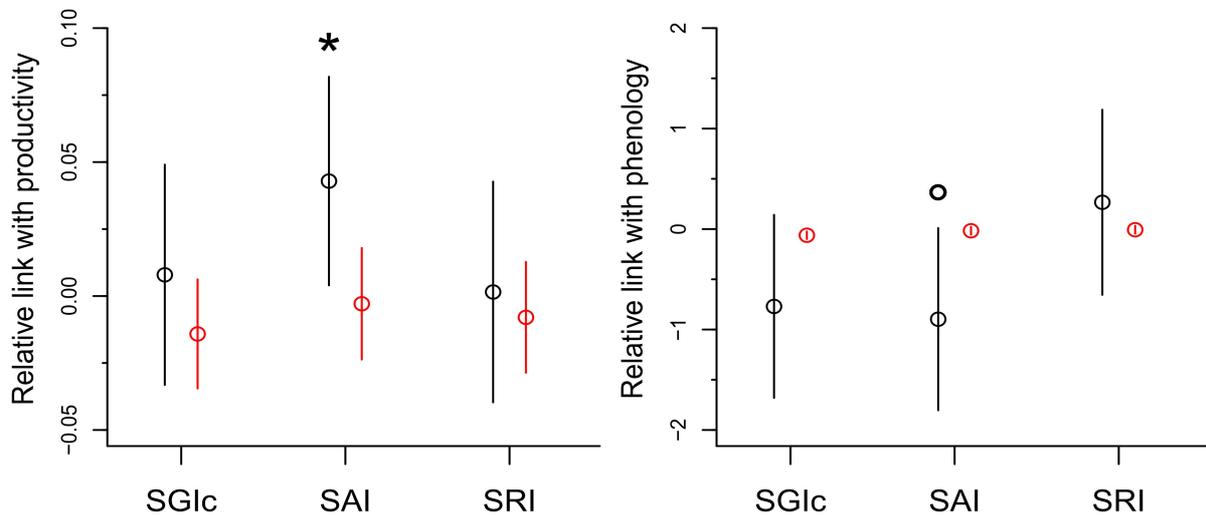
**Figure 6** : Species' PhS was slightly correlated to long-term trend.

### 3. Birds' traits.

At species scale, our linear model reveals no associations between the three forms of commonness (SAI, SRI, SGI) and the species' productivity sensitivity. Concerning the species' productivity response, only species abundance index (SAI) was significantly and positively

(linear model;  $n=41$ , slope= 0.0429; standard error= 0.0199;  $t$  value = 2.159;  $\Pr(>|t|)= 0.037^*$ ) related to the response (Figure 7a.).

Concerning the phenology, we found a slight and nearly significant (linear model;  $n=112$ , slope= -0.8971; standard error= 0.4628;  $t$  value = -1.938;  $\Pr(>|t|)= 0.0552$ ) negative relation between species' PhS and SAI (Figure 7b.).



**Figure 7**: Estimates and standard deviation of linear models fitting a) productivity response (black) and sensitivity (red) and b) phenological response (black) sensitivity (red) with traits of commonness. Symbols represent significance of the relation (\* < 0.05, ° < 0.1).

## Discussion

The aim of this work was to go a step further in the understanding of the processes underlying community rearrangements under climate changes. To do so, we first assessed how critical phases driving population dynamics were affected by climate change. Secondly, we investigated whether 3 aspects of commonness were predicting these species specific responses. Accordingly to these objectives, we found that:

- 1) considering all species together productivity and breeding time adjustment were significantly linked to changes in temperature (positive relation) and in a lesser extent to precipitations (negative relation) during spring.
- 2) no clear pattern emerged from the link between productivity and phenological response/sensitivity and long-term trends among species. However, it seemed that species which were more sensitive concerning their phenologies were, on average, those with more positive dynamics.
- 3) most abundant species showed stronger productivity response and (to a lesser extent) lesser phenological response.

## 1. Birds dynamics indicators reveal strongly pattern under climate change.

Relatively few studies have integrated climate effect into demographic study to understand the mechanisms underlying how climate change and its variability influence population dynamics (Jenouvrier, 2013). Our study showed that, local increase in temperature and dryness were clearly promoting productivity for the 41 breeding bird studied. Our analyses were based on a correlative approach, we therefore must consider that this result could reflect a spurious correlation between increasing variables in time. However, the size of our dataset and the fine spatial scale at which the bird and climate data were collected greatly reduced the likelihood of spurious correlations arising. Studies dealing with bird's productivity generally conclude towards a decrease of breeding success (Jenouvrier, 2013). Instead, our results were more consistent with the metabolic theory (Porter & Gates, 1969), according to which a temperature increase (+1-2°C) compared to the average of a given site could be beneficial in terms of productivity. Such climatic events provide more energy in the ecosystem, and a global scale climate change indeed drives an increase in terrestrial net primary production (Nemani *et al.*, 2003). These modifications of thermal conditions have enhanced plant growth, especially in northern mid latitudes and high latitudes (Nemani *et al.*, 2003). To the best of our knowledge, there is no reasons to think that this increase is not transmitted to higher trophic level including birds. This is particularly consistent regarding common birds' juveniles which are in a large part feeding by insects or seeds and limited to temperate zone where energy seems to be the limiting factor for species dynamics (Hawkins *et al.*, 2003). Moreover, this benefit in productivity should probably lead to a tipping point when temperature rise is too important. Climate variability will increase during the next century. Hence the frequency of hot springs is going to increase as well as the frequency of cold episodes (IPCC, 2007). Thereby, we need to study the response of productivity during extreme climatic events.

Moreover, our estimation of birds' productivity includes a lot of demographic parameters: breeding probability, number of clutches, clutch size, hatching success, fledging success and fledglings survival during the dependent phase. As a consequence, it was impossible to determine exactly which one of these parameters is under influence of climatic variables. We found no relation between species' response or sensitivity in productivity and their long-terms trends. This suggest that breeding success is not necessary the main factor in the final growth rate but post-dispersal survival should be also a very important component. Long-terms studies on Emperor Penguins *Aptenodytes forsteri* in Terre Adélie also indicate that climatic anomalies appear to influence survival (Barbraud & Weimerskirch, 2001). In

contrast with work by Saether (2013), according to our result, contribution from stochastic environmental events (like climatic pressure) in passerines' fecundity to growth rate seems not larger than the contribution from survival. A complementary possibility to explain this absence of relation is obviously the fact that: "all is not climate". As we mentioned before European birds are declining and this decline has been attributed to decreases in the number of farmland species (mostly specialist species) caused by agricultural intensification (Donald *et al.*, 2001; Devictor *et al.*, 2008a; Filippi-Codaccioni *et al.*, 2010; Le Viol *et al.*, 2012). It is therefore likely that habitat disturbance and land-use change explain a large part of the current species' dynamics.

A large part of observations of climate change responses have involved modifications of species' phenologies (Walther *et al.*, 2002; Parmesan *et al.*, 2006; Jenouvrier *et al.*, 2013). Here, we showed that considering overall species, birds start their reproductive behaviour earlier during warmer and drier years. Considering how fine the link between the act of singing and beginning of the reproductive season is, our results can't be only due to detectability issues. In line with many studies having documented earlier spring activities since the 1960s for numerous taxa such as birds, butterflies and wild plants (Walther *et al.*, 2002, Parmesan *et al.*, 2006), we think that our result is one more evidence that changes in phenology is one of the major responses of biodiversity to climate change.

While most studies have emphasised on the predominant effect of temperature on phenological adjustment, only a few studies have tackled the potential impact of precipitation changes (Illan *et al.*, 2014). Despite a stronger effect of temperature, our results suggested that rainfall also drove a part of changes in phenology of species. Precipitation was correlated with a decrease in productivity. We assume that rainfall impacts the breeding-success especially by decreasing hatching success according to a lot of experimental and empirical studies (Arlettaz *et al.* 2010; Anctill *et al.*, 2013). We found that birds start their reproductive behaviour earlier during drier years. Indeed, changes in precipitation can affect plant growth, soil moisture, water storage and insect abundance and distributions (Hamlet *et al.*, 2007) and this is susceptible to induce shift in phenological adjustment (Illan *et al.*, 2014). Thus, by impacting both species' productivity and phenology, future shifts in precipitation would also have implications for the composition of communities (Gaüzère *et al.*, 2015). For instance, Lemoine & Böhning-Gaese (2003) found that changes in rainfall had different impacts on long- and short-distance migrants which could lead to rearrangements in bird communities.

**Temperature anomalies, in a range of few degree, seem to increase birds' productivity by providing more energy in the ecosystem. French avifauna is likely to finely track climatic changes in time by adjusting its phenology. Our study showed that rainfall, as well as temperature, is an important variable in climate change pressure on birds and should be considered more thoroughly in future study.**

## 2. Exploring species responses by traits and long-term trend.

The productivity response (PrR) was stronger for the most abundant species whereas the phenological response (PhR) was, to a fewer extent, stronger for the less abundant species. As mentioned in the introduction, population dynamics were determined by the growth rate which could be traditionally divided into two main variables: reproduction and survival. Common bird growth rates are known to be more impacted by stochastic environmental pressure than climate change regarding to their fecundity than to their survival (Legendre *et al.*, 1999; Saether *et al.*, 2013). Therefore, it is possible that most abundant species' productivities respond stronger to climate change because, for these birds, fecundity is the main factor to explain the final growth rate. Negative relation between phenology response and species abundance index should be considered cautiously regarding to the lesser significant level. However, our results describe negative relation between SAI and PrR and SAI and PhR. Indeed, inverse relation between a trait and both explanatory variables should be caused by negative correlation between the two variables.

In contrast to our predictions, no pattern was found between productivity and phenology and SGI. Nonetheless, generalist species may be assumed to be more tolerant than specialists to environmental conditions and that has been showed for a lot of taxa including insects (Kotze & O'Hara, 2003), fish (Munday, 2004), mammals (Fisher *et al.*, 2003) and birds (Julliard *et al.*, 2004 ; Moussus *et al.*, 2011). To be adaptable in regard of phenology suggest for instance to gather information concerning the timing of the breeding environment and this should require important cognitive abilities (Dall and Cuthill 1997; Moussus *et al.*, 2011). Generalist species tend to have more developed tracking systems given the variety of resources they can exploit. A stronger sensitivity as well as a higher plasticity allowing a good phenological adjustment capacity is expected for these species. For several ecologist, communities biotic homogenization described by literature should be due in part to the higher sensitivity of generalists to climate change (Devictor *et al.*, 2008; Barnagaud *et al.*, 2011; Davey *et al.*, 2012; Gaüzere *et al.*, 2015; Godet *et al.*, 2015).

No pattern was found between productivity and phenology and species range index. However, it is known that species with wide thermal ranges are able to face extreme climatic events such as heat waves (Jiguet *et al.*, 2006). As a part of our results is built on non-pattern finding, we have to discuss the possibility that the lack of relation between different variables was caused by an insufficient sample. For example, our final dataset did not contain species considered as rare in Europe (concerning their abundances < 1500 breeding pairs; Holling, 2011). Generalists are over-represented in our data-set and this could explain the unexpected non-relation between SGI and phenology and productivity. In the FBBS and FCES, only the most common species are sampled within a single country. Therefore, the distinction of different kinds of commonness seems to be only relevant for a subset of the most common species among the whole national breeding avifauna.

There was an absence of correlation between species' phenological and productivity responses. It has been recorded in other species as Red Grouse, *Lagopus lagopus*, that a higher PhR could enhance breeding success (Fletcher *et al.*, 2013). Indeed, an ability to adapt their phenology by advancing breeding-time when temperature increases could allow species to have more clutches in the same reproductive season (Dunn and Moller, 2014). We can also expect the most phenologically flexible species to be less impacted by a temperature anomaly increasing productivity. Finally, one can expect these birds to be less impacted on the long term by climate changes. We found a positive correlation between phenological sensitivity and long-term trends. Several studies show relations (Visser *et al.*, 2005; Fletcher *et al.*, 2013) or no relation (Dunn & Moller, 2014; Both & Visser, 2001) between these two variables and this question is highly discussed for birds. For example, migrants birds experience a stronger warming climate in their breeding grounds compared to their wintering area, and, despite a phenological adjustment, are likely to be impacted by these modifications because their migration will occur later and they may miss the early stages of the breeding season. (Jones & Cresswell, 2010). Concerning insectivorous sedentary birds, it has been shown that a capacity to adjust laying date with shift in caterpillar biomass phenology could decrease the impact of climate change (Visser *et al.*, 2005; Gladalski *et al.*, 2014). Our results suggest that an increasing number of populations of French common breeding birds are more likely to adjust their phenology to climatic variations, allowing them to be less impacted by climate change.

**Linking species productivity and phenological response and sensitivity with traits of commonness didn't give us the expected results. Nevertheless, these approaches have appeared to be powerful in other studies (Godet *et al.*, 2015) and further analyses may be useful to overcome some limits of our work.**

## Conclusion and limits.

Two critical phases of common birds life, breeding success and beginning of reproductive behaviour, showed strong responses to changes in climatic conditions over 24 years. All species considered, French avifauna seemed to be more productive during warmer years. Timing of reproductive behaviour closely matched temperature anomalies. Bridging the gap between these communities' responses and impact of climate changes on species was still difficult and links with long-term trends are unclear. However, our approach managed to link three different components of populations dynamics (phenology, productivity and trends) with fine scale changes in local climatic conditions. It was successful in unveiling the population scale processes driving species responses to climate changes. Our study suggested that increasing populations of common breeding birds are more likely to adjust their phenology to climatic variations, allowing them to be less impacted by climate change.

It is not just the magnitude of change of global average temperature but the inherent asymmetry in change processes that complicate predictions of ecological responses. We must point out that if we looked at the average temperature anomaly over a month, how long is this anomaly is also a strong factor to explain phenological adjustment and especially productivity which seems to be closely related to physiological. Unfortunately this kind of data is hardly available for the moment. We hope that in the future the accessibility to weather data will be better. It should be interesting to compare our results with those from comparable survey program in Europe such as UK or Dutch programs (despite lack of standardization of sampling procedures). Julliard (2004) performed this kind of analysis for the long dynamic and found similar trends between Western and Central European countries. This suggests that common large-scale causes drive the long-term dynamic of bird populations.

This study suggest possible mechanisms by which functional biotic homogenization is currently leading to alter plant and animal communities (Devictor *et al.*, 2008; Barnagaud *et al.*, 2011; Davey *et al.*, 2012; Gaüzere *et al.*, 2015; Godet *et al.*, 2015). Climate has an important role in the homogenization process but a number of others factors such as land-use change have also been associated with profound changes in European bird populations (Chamberlain *et al.*, 2000, Barnagaud *et al.*, 2013). It has been shown that specialist bird

species are more susceptible to farming intensification than generalists in France (Filippi-Codaccioni *et al.*, 2010). According to habitat and local climatic conditions, particular spatial patterns in climate changes have been described in the studied country. For example, in the Mediterranean region the pattern is not leading to an increase in temperature but more to a local decrease (Gaüzère *et al.*, 2015). However, habitat changes and climate are intrinsically linked and a lot of studies highlighted that habitat affect distribution in response to climate change (Warren *et al.*, 2001; Menéndez *et al.*, 2007; Pöyry *et al.*, 2009, Barnagaud *et al.*, 2012). Therefore, separating cause and effect between climate- and habitat induced changes in communities remains complex and require long-term, high definition and reliable monitoring of habitat over large-areas. In order to increase our understanding of species response to climate change and communities rearrangement ensuing, we need to study independent and joint effects of changes in climate and habitat in global changes.

This study sheds new lights on the factors underlying birds responses to climate change. Showing that temperature increase enhance birds' productivity, we suggest an interesting process contrasting with mostly of literature to explain a part of populations dynamics. We confirm the importance of physiological factor and indirect process as modifications of energy transfers among species in the understanding of climate change impacts. Temperature is the most studied climatic variable. Despite, we claim that precipitation should be considered as well in order to increase our ability to predict vertebrates response under climate change. As predict by Caughley (1994), interactive factors such as habitat and climate changes are difficult to separate in order to study why populations are declining. Despite of this, we think that future studies will provide more and more keys to understand modification of biodiversity under global change. Indeed, since 1989 and the beginning of FBBS and FCES, monitoring programs of citizens science are greatly improved. We could expect that, in future, all these citizens programs could give to scientist data to bridge the gap between different process underlying species response to climate change in order to provide information to policy makers.

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