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IMPACT OF CLIMATIC VARIATIONS ON BIRD SPECIES OCCUPANCY RATE IN A SOUTHERN EUROPEAN FOREST

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Abstract

Species that are affected by climatic variations can undergo modification in range and/or abundance. Knowing how individuals or species occupy their habitat is essential to understand how species use their environment, and detecting variations that might affect this use can be determinant in species management.

Hierarchical modeling is regularly used to assess for occupancy rate (i.e. proportion of patches occupied in a region), particularly when it is required to consider detectability-related issues. The present study is the first application of the conditional model presented in Dupuis *et al.* (2010), and which is applied in the case of a heterogeneous area that might be divided into homogeneous sub-areas. Their approach is used to study the impact of three consecutive particularly cold winters on a selected set of bird species in a forest of southern France in the context of available prior information on birds detectability.

We examined a limited range of factors that might influence the response of some bird species to climatic. We considered the case of sedentary, partially migrating and migrating species. We also assessed if the biogeographical origins of the different species affect their occupancy rates. Globally, changes in occupancy rates between 1985 and 1987 indicates for the first time a continentalization of the regional forest fauna, reflected by the expansion of Palearctic and Turkestano-european faunistic type species, with depletion or extinction of European, Turkestano-mediterranean and Mediterranean sedentary species. We have also shown the importance of prior information.

Keywords: Climatic changes, detectability, hierarchical modeling, occupancy rate, prior information.

Introduction

Two of direct effects of climate change that species will likely have to face are an increase in mean temperature) (e.g. Malcom *et al.*, 2006) and an increased in the frequency of extreme temperatures (e.g. Colombo *et al.*, 1999). Species' responses to these climatic changes may include evolution or adaptation, modification in range and abundance, or extinction (Ackerly, 2003 ; Parmesan, 2006).

Most of the examples of rapid adaptation to climate change lie in evolution toward higher frequencies of already existing heat-tolerant genotypes in the interiors of species' ranges (Parmesan, 2006). While adaptation can occur after a significant amount of time, for punctual variation of the climate, migration and extinction are more likely (Huntley, 1991 ; Davis & Zabinski, 1992 ; Coope, 1994). Extinction or increased risk of extinction due to climatic changes have been documented in a wide range of taxa such as amphibians (Pounds *et al.*, 1999, 2005), tropical corals (Hoegh-Guldberg 1999; Wilkinson 2000), mammals (e.g. Arctic polar bears, Derocher ; 2005, Stirling *et al.* 1999) and birds (e.g. Antarctic Adélie Penguins, Ainley *et al.*, 2003 ; Croxall *et al.*, 2002). In fact, if an unusual variation in temperature occurs, such as a significantly colder winter, species that are not adapted to cold temperature and that have not migrated might have to undergo extreme conditions and potentially go locally extinct. Range shifts are expected to occur poleward and upward. Several species of Lepidoptera (butterflies and moths) have undergone an expansion of northern boundaries situated in Finland (Mikkola, 1997), Great Britain (Hill *et al.*, 2002), and across Europe (Parmesan *et al.*, 1999). Some bird species have been shown to have a northern shift of their range boundaries (Thomas & Lennon, 1999). Some species have even shown elevational shifts in response to climate changes (e.g. lowland birds, Pounds *et al.*, 1999, 2005 ; alpine flora, Grabherr *et al.*, 1994, Pauli *et al.*, 1996).

In this context, understanding how individuals or species occupy their habitat and use their environment (Krebs, 1978) will be essential to predict population response to extreme climatic conditions and take suitable management dispositions (Kendall, 2001; Williams *et al.*, 2002 ; Nichols, 2004 ; MacKenzie *et al.*, 2006). Site occupancy modeling has been thoroughly developed during the last decade, leading to powerful methods to estimate site occupancy, which in turn allows estimation of population parameters such as colonization and extinction probabilities. These models have proven to be reliable for common ecological data (i.e. detection-non detection), and when the area of interest is large (such as a country) or relatively small (e.g. a forest), or when the considered area is divided in an important number of quadrat (i.e. sub-unit of the global area that might be sampled) or not.

Site occupancy rate is one of the key variables for determining how species use their environment. While density and abundance carry information on the population state, occupancy rate describes how species use the spatial environment they live in. It is defined as the proportion of patches occupied and is a state variable in various metapopulations models (e.g., Levins, 1969, 1970 ; Lande, 1988 ; Hanski, 1997). Site occupancy rate by definition has to be considered in a 'closed environment', i.e. with a finite number of locations (termed sites or quadrats). While this has been well studied when there is a large number of sites, improvements are still needed when the number of sites is small (MacKenzie *et al.*, 2006).

Estimating occupancy rate using hierarchical modeling allows accommodation of issues related to detectability. We now can account for the fact that when a species is not detected it could correspond to an effective absence or just a failure in detection. Modifications of the original approach of MacKenzie *et al.* (2002) allowed for a more accurate estimation of occupancy rate in the specific case of a small homogeneous area with a small total number of quadrats (e.g. MacKenzie *et al.*, 2006) or when species are particularly hard to detect (Dupuis *et al.*, 2010). This difficulty in detection can emerge from individual's characteristics (e.g.

cryptic abilities) or simply because a species has a low presence probability, which is typical of endangered species.

Here, we apply the conditional model presented in Dupuis *et al.* (2010) to the case of a heterogeneous area that can be divided into homogeneous sub-areas (e.g. edge and inner part of a forest). One of the main characteristics of this model is that it uses a conditional approach for estimating the quantity of interest (here, occupancy rate); conditioning bearing on the presence of target species in the region of study. The unconditional approach (MacKenzie *et al.*, 2006) does not presuppose that the target species is present in the whole region of interest. Conditional approach has been proven to be a necessary approach in the case of undetected species which are known to be present in the area from another source of information (such as net capture) (Dupuis *et al.*, 2010). Moreover, we shall take advantage of that some prior information on detectability is available, since it is expected that this significantly improves the precision of estimates when the target species has been very few or not detected, and is known to be easily detectable (Dupuis *et al.*, 2010). The data used in this study present several such examples. Furthermore, in each instance where a species is not detected in our dataset it is known from external sources that it was in fact present in the study area.

We focus on several factors that might influence the response of bird species to climatic changes (here the succession of three significantly colder winters). First, occupancy rate in the inner forest might be less affected by the decrease in temperature than in the edge of the forest because more protection is available for individuals. Evolution of occupancy rates might be crucially different between the external and the inner parts of a forest. For example, species can have preferences into one or the other part, and if no distinction is made between these regions, one could not see a modification of occupancy. Second, we compare sedentary, partially migrating and migrating species. We expect migratory species occupancy rate to be less impacted by cold winters than that of sedentary species, because they are not directly

affected by local low temperatures at reproduction sites. Specifically, we predict sedentary species' occupancy rate to decrease. Third, we compare species with different bioclimatic affiliations which illustrate tolerance of a species to cold. We predict that species with a more continental bioclimatic affiliation will not experience a dramatic decrease in occupancy rate compared to other species. Finally; in the discussion, each of the conclusions resulting from this local application will be examined in the light of what happened at the continental scale.

Material & Methods

Location – We focus on data collected in May 1985 and May 1987 in order to estimate occupancy rates of nesting bird species present in the Montech forest (located near Toulouse, France), and the impact of 3 successive particularly cold winters. Montech forest has an area of 900ha and is part of the French National Forest System (*Office National des Forêts*). While this forest has a mixed management regime of mature and coppiced forest, it is now only managed as a mature forest The forest is dominated by oak species (*Quercus robur*, *Quercus sessiliflora* and *Quercus pubescens*). The undergrowth is composed of hawthorns (*Crataegus)*, blackthorns *(Prunus spinosa)*, brooms *(Fabaceae)*, and heaths *(Erica)*. Some Coast Douglas-firs *(Pseudotsuga menziesii)* and Maritime Pines *(Pinus pinaster)* plots are present in the south part of this forest. The study area is proximate to continental, Mediterranean, alpine and Atlantic ecoprovince (fig.1).

Data are a part of a broad study of bird populations in the Midi-Pyrénées region of southwest France. Data collection began in 1985 (Joachim *et al.*, 1997). Montech forest underwent 3 colder-than-usual winters in 1985, 1986 and 1987. During these winters, mean monthly temperatures dropped up to 5°C below the average monthly temperature of 14

previous years, and 3°C below the coldest temperatures during this reference period (Fig. 2). These three winters correspond to a hinge period. In contrast, from 1965 to 1985, winters were fairly mild. Empirical observations suggest that these mild temperatures led to a colonization of Mediterranean and a retreat of continental bird species. The exceptional 1985-1987 period contrasted strongly and that likely impacted the fauna potentially leading to a strong re-continentalization. While species might easily overcome one colder than usual winter, the succession of 3 cold winters on end can be expected to have consequences for bird species.

Data and species list – We focus on to the estimation of occupancy rate and detection probabilities of 10 bird species of the overall 47 detected species. The list of the species of interest is denoted by $\mathcal{L}$. Here, the list of chosen bird species, liable to be present in the forest of Montech, in spring 1985 and 1987 includes 10 species: whitethroat, chiffchaff, nightingale (which are migratory species), Eurasian nuthatch, green wood pecker, short-toed treecreeper (which are sedentary species), and finally song thrush, common blackbird, European robin, mistle thrush (which are partial migrants). Partial migrant species are species with overlapping reproductive and wintering areas. Migratory status and biogeographical origins are presented in table 2. Moreover, for each species, prior information on detection probability is available (tab. 3).

Montech forest, with a surface area of 900 hectares has been divided into A homogeneous subregions of biological interest, here A=2 with the two sub-regions being the inner forest (a=1) and the edge forest (a=2). A sampling is performed in each sub-region R_a. The sub-region R_a is divided into J_a spatial units, here termed quadrats. They are also called sites in the literature. A subset of T_a quadrats is sampled. Draw is usually performed at random so as

to have a sample representative of the whole region R_a. We assume that these quadrats are of equal area. Twenty-two quadrats are located in the inner forest (J_1=22), while 18 quadrats correspond to forest's edges (J_2=18). In 1985, all quadrats were sampled (T_1=J_1=22 ; T_2=J_2=18), while in 1987 only 14 quadrats were sampled in inner forest (T_1=14) and 6 in edge forest (T_2=6).

Information about the presence of nesting species was provided by acoustic recognition of singing males according to the following procedure. Listener spent a twenty minutes at each station, listening for birds. This time spent on each quadrat was divided into K equal sessions, here K=4, during which detection are recorded. The number of quadrats in region R_a in which species s has been detected is denoted by $V_s(a)$. Total number of sessions in region R_a during which species s has been detected is denoted by $W_s(a)$. These data are given in table 1. All records were made following the listening point method (EPS, Spitz 1974, EFP, Blondel, 1975) over a 500-meters sided grid. Length of the side of a quadrat (that is 500 meters) has been chosen so that the listening range (a disk of 150-meter radius) is strictly included within the quadrat. Consequently, from a station performed in a given quadrat, the observer cannot hear songs of (males) conspecifics that would nest in adjacent quadrats; consequently, if the song of a male of a given species s is detected in the quadrat j, thus the species s is present in this quadrat. Further details of the protocol can be found in Decamps *et al.* (1987).

The dataset of observations is afterwards denoted by y; therefore $y = \{y_s(a); s \in \mathcal{L}, a = 1,..., A\}$, where $y_s(a)$ denotes the observation related to species s in region R_a. A possible record of $y_s(a)$ for a region R_a could be $y_s(a)$=4021003. Here, $V_s(a)$=4, $W_s(a)$=10. Finally, the number of detection of species in the sampled quadrat j is denoted by y_{sj}.

Modeling

Underlying processes and missing data structure – To specify the missing data structure inherent in quadrat sampling data, we view the record y_s as the result of two processes: one is related to the presence-absence process (in quadrats), and the other is related to the detection process. Such a formalism also allows us to formulate rigorously the biological assumptions made and to introduce, in a natural way, the parameters of biological interest.

We denote by z_{sj} the indicator of presence of species s in quadrat j; therefore, $z_{sj} = 1$ if species s is present in quadrat j, and 0 otherwise.

Conditioning on $z_{sj}=1$, x_{sj} is the number of times that species s has been detected in quadrat j during the K sessions. It is clear that $x_{sj} = 0$ and $y_{sj} = 0$ do not have the same meaning. The event $x_{sj} = 0$ means that the species s (present in quadrat j) has not been detect in it; while the event $y_{sj} = 0$ resorts two distinct situations. Missing can occur in different circumstances. First, when a species s has not been detected in quadrat j (that is when $y_{sj} = 0$), it is clear that z_{sj} is missing; the event $y_{sj} = 0$ covers in fact two exclusive situations: either species s is present in quadrat j but has not been detected, or it is not present in quadrat j (and cannot have been detected). Formally, one has the equivalence $(y_{sj} = 0) \Leftrightarrow (z_{sj} = 1 \text{ and } x_{sj} = 0) \text{ or } (z_{sj} = 0)$. Conversely, when $1 \le k \le K$, one has $(y_{sj} = k) \Leftrightarrow (z_{sj} = 1 \text{ and } x_{sj} = k)$. Second, z_{sj} is also missing, when quadrat j is not a part of the sampled quadrats.

Notation – Throughout the paper $p(.)$ denotes a probability mass function. The local occupancy rate of species s in region R_a is denoted by γ_{sa}; therefore, one has:

$$\gamma_{sa} = \frac{1}{J_a} \sum_{j \in R_a} z_{sj}$$

We apply the conditional model of Dupuis *et al.* (2010) to each sub-region R_a for estimating γ_{sa}. Biological assumptions related to the occurence of species in the J_a quadrats are supported by the values of z_{sj}, and those related to detection in the T_a sampled quadrats by the values of x_{sj}.

Modeling detectability – We assume that the probability of detecting species s in quadrat j does not depend on its detection in the other quadrats. Considering the experimental protocol, size and distance between sampled quadrats , this is a realistic assumption.

For any quadrat j of R_a, we assume that conditionally on z_{sj}=1, x_{sj} follows a Binomial (K, q_{sa}). Here q_{sa} represents the probability of detecting species s in quadrat j (located in region R_a) during any session (given that it is present in quadrat j). Detection probability can vary strongly among species, and can also differ depending on the subarea considered. We also can define the parameter $\mu_{sa} = \Pr(x_{sj} \geq 1 \mid z_{sj} = 1) = 1-(1-q_{sa})^K$ which represents the probability of detecting species s in quadrat j (conditionally on its presence) over the K sessions of a visit. This parameter is commonly the parameter on which prior information is available.

Modeling occupancy – Let s be a species present in the study area R_a, we set $z_s(a) = \{z_{sj};\ j \in R_a\}$. Since we adopt a conditional approach, $z_s(a)$ is distinct from the null vector. The p.m.f. (probability mass function) of $z_s(a)$ is:

$$p(z_s(a) \mid \varphi_{sa}) = \frac{\varphi_{sa}^{N_s(a)}(1-\varphi_{sa})^{J_a - N_s(a)}}{1-(1-\varphi_{sa})^{J_a}} \tag{3.3}$$

where $N_s(a)$ is the number of quadrats (of R_a) where species s is present. φ_{sa} is the probability that species s is present in quadrat j of R_a, given that it is present in at least one other quadrat

of R_a. Note that φ_{sa} is a conditional occurrence parameter (contrary to what appear in MacKenzie *et al.*, 2006). Also γ_{sa} is not a parameter of the model, in contrast to φ_{sa}; but they are linked, since $E[\gamma_{sa} \mid \varphi_{sa}] = \varphi_{sa}/[1-(1-\varphi_{sa})^{J_a}]$. Due to the conditioning, the random variables z_{sj} are not independent. However, a certain form of conditional independence between the z_{sj}'s holds. Let i, j be any two quadrats of R_a, z_{si} and z_{sj} are independent, if species s is present in at least one other quadrat of R_a (distinct from i and j).

Therefore, from a biological point of view, we assume that the presence of species s in quadrat i is not affected by the presence of that species in quadrat j (given that it is present elsewhere in R_a); this assumption is standard (disregarding the conditioning).

Prior information on species detectability – These data are part of a large study in the Midi-Pyrénées (i.e. South-West of France), therefore we have access to prior information on the probability of detecting species during the entire visit. Information on this detectability is also available from the literature. It should be noted that, astonishingly, in the literature Bayesian studies using informative priors are not as common as it could be expected. Here, since this information is available and can bring substantial improvements to estimates, we have logically used it in the process of occupancy rate assessing.

Typically, litterature provides information on species detectability and these species can be define for example as highly detectable or hardly detectable (Blotzheim & Bauer, 1985, 1988, 1993, 1997). Dupuis & Joachim (2006) have defined categories of detectability in order to classify bird species depending on this information for 1985. Using information provided by external data, they have found the Beta prior distribution for detection probability μ_{sa} corresponding to each of these categories.

Here we use 4 categories: low, intermediate low, intermediate high and high detectability. The mean and 95%$_{CI}$ of the prior distributions for each category, respectively, are 0.2 [0 – 0.4], 0.4 [0 – 0.65], 0.6 [0.3 – 0.8] and 0.8 [0.65 – 1]. These specific priors for each species are presented in Table 3. We have used the prior means and CI$_{95\%}$ intervals on μ_{sa} to determine coefficients of the corresponding Beta distribution by the use of a binary search algorithm (see MatLab code in appendix 1). Then, these coefficients are used to estimate coefficients of the prior Beta distribution on q_{sa} (the probability that a species is detected during each session of a visit) through the use of classical Monte Carlo methods (see MatLab code in appendix 2). Finally, the prior information on q_{sa} is used to estimate γ_{sa}.

Prior information on detectability for some species varies between 1985 and 1987 and/or between areas (see Table 3). Modification of detectability classification for some species in 1987 is due to regional specificities or changes in the abundance of individuals. For example, the song thrush is less inclined to sing as the number of conspecifics in the neighborhood decreases. In the case of the whitethroat in the forest interior, no estimation has been done because it is known that this species does not live in this type of environment (therefore, no prior has been specified in table 3).

Likelihood – The parameter of the model is $\theta = \{\varphi_{sa}, q_{sa}; s \in \mathcal{L}, a = 1,.., A\}$. The likelihood of θ based on $y = \{y_s(a); s \in \mathcal{L}, a = 1,.., A\}$ is:

$$L(\theta; y) = \prod_{s \in \mathcal{L}, a=1,\ldots,A} p(y_s(a) \mid \varphi_{sa}, q_{sa})$$

Note that we implicitly assume that species behave independently with respect to occupancy. For any species s such that $y_s(a)$ is different from the null vector:

$$p(y_s(a) \mid \varphi_{sa}, q_{sa}) = \frac{\rho_{sa} \varphi_{sa}^{V_s(a)} q_{sa}^{W_s(a)} [1 - q_{sa}]^{U_s(a)} [(1 - q_{sa})^K \varphi_{sa} + 1 - \varphi_{sa}]^{T_a - V_s(a)}}{1 - (1 - \varphi_{sa})^{J_a}} \qquad (1.1)$$

where $U_s(a) = KV_s(a) - W_s(a)$, and $\rho_{sa} = \prod_{j \in R_a} \binom{K}{y_{sj}}$; moreover, if $y_s(a)$ is a null vector, we have:

$$p(y_s(a) \mid \varphi_{sa}, q_{sa}) = \frac{((1-q_{sa})^K \varphi_{sa} + 1 - \varphi_{sa})^{T_a} - (1-\varphi_{sa})^{J_a}}{1-(1-\varphi_{sa})^{J_a}} \quad . \tag{1.2}$$

Computational details are available from the authors on request. The formulae (1.1) and (1.2) allow computation of the probability (in function of J_a, T_a, K, φ_{sa} and q_{sa}) that a species s present in R_a has not been detected (or rarely detected). This occurs with relatively high probability when species s is spatially rare and/or hard to detect (Dupuis *et al.*, 2010).

Estimating the occupancy rate – We use Monte Carlo Markov Chain methods (MCMC) in order to obtain the bayesian estimations of γ_{sa}. Here, we are especialy interested is the estimation of the occupancy rate but in some cases it could be required to also estimate the parameters q_{sa} and φ_{sa}. The MCMC algorithm, taking advantage of the missing data structure, is implemented on (θ,z_m) where $z_m = \{z_s^{mis}(a); s \in \mathcal{L}, a = 1,.., A\}$ and $z_s^{mis}(a)$ is the set of the missing z_{sj}'s related to s (where j is in R_a). The bayesian estimate of γ_{sa} is easily obtained by applying the ergodic theorem (details are omitted). For further details, refer to Dupuis *et al.* (2010). The MatLab code for estimating γ_{sa}, φ_{sa} *and* q_{sa} is provided in Appendix 3.

We also compare differences between estimates obtained under both MacKenzie *et al.*, (2006) unconditional and Dupuis *et al.* (2010) conditional approaches in the case of not detected species that are known to be present and easily detectable. This comparison is done with non informative and informative priors on the detection probability.

Results

Globally, occupancy rates variations between 1985 and 1987 do not seem to be mainly directed by the migratory status (Tab. 4). For example, while some sedentary species' occupancy rates decreases (e.g. the short-toed treecreeper), others have increased (e.g. the Eurasian nuthatch). The same result exists for migrating species and partial migrants (e.g. mistle thrush occupancy rates increased contrary to the song thrush).

Overall, occupancy rates in interior and edge forests presented the same type of changes (i.e. increase or decrease), but the extent of these variations can differ between these two sub-areas. For example, while the song thrush and the nightingale greatly retreat between 1985 and 1987 in the edge forest, this variation is less important in the inner forest. On the other side, increase in mistle thrush population was more important in the inner forest than in the edge forest, apparently revealing a protecting role of the inner forest.

In the end, variations of occupancy rates seem to be mainly driven by biogeographical origins with an occupancy rate increase of European and continental species (e.g. mistle thrush, Eurasian nuthatch, European robin) and a decrease of Mediterranean and Atlantic species (e.g. nightingale, song thrush).

We observe that the bayesian non informative estimates of the occupancy rates are precise when the number of detections is high. Moreover, in 1987 and in edge, most of species have been few detected (except the common blackbird, the chiffchaff, and the mistle trush), and, not surprisingly, we observe that most of non informative estimates are imprecise.

We also observe that taking into account the prior information available on detectability significantly improves the precision of estimates when the target species has been very few detected ($W_s(a)$=1) or has not been detected ($W_s(a)$=0): the green woodpecker, the nightingale

and the whitethroat are concerned by this remark (tab. 4 and 5). In Dupuis *et al* (2010), this observation has already been mentioned, and indicated that this improvement is particularly significant when the target is highly detectable.

Finally, we observe that taking into account the prior can make decrease the precision of the bayesian estimate. For the mistle trush (in 1987 and in inner forest), the range of the 95 % posterior credible interval is 0.37 in non informative situation, and 0.46 in informative situation. This unusual phenomenon typically occurs when the two following conditions are fullfilled: the weights of the data and the prior are similar, and the (informative) prior mean of the parameter of interest and its (non informative) posterior mean are very different, which indicates a `conflict' between the prior and the data. In our case, the prior variance of q_{sa} in informative situation (namely 0.075^2) is effectively relatively close to the posterior variance of q_{sa} in non informative situation (namely 0.084^2), while the (informative) prior mean of q_{sa} (namely 0.21) is effectively very far from the non informative posterior mean of q_{sa} (namely 0.66).

Use of priors here can be essential to obtain a better estimation of occupancy rates. For example, raw data in edge forest are identical for the whitethroat (1985) and for the green woodpecker (1987). With $V_s(a)$=2 and $W_s(a)$=2 for these 4 species, we would have failed to detect variation in occupancy rate without prior information (e.g. for the whitethroat), or we could have underestimated the extent of the species occupancy rate variation (e.g. for the green woodpecker). We can highlight the importance of including prior information on detectability when available in the case of low detection data and easily detectable species.

For a species not detected by the quadrat sampling, but for which it is known that it was in fact present in the region of study R_a (e.g. the Green Woodpecker in 1985 or the Nightingale in 1987 in edge forest), tables 6a and 6b show that ignoring such an additional information (by using the unconditional MacKenzie *et al.*, 2006, approach) will underestimate γ_{sa}. In non

informative situation, distances between both estimates are very important when the region of study has been entirely sampled ($J=T=18$) (tab. 6a), and less important (though not negligible) in the opposite case ($J=18$, $T=6$) (tab. 6b). In informative situation, distances in absolute values are definitely less important (though not negligible), regardless the region of study is totally or partially sampled. Nevertheless, we note that when $J=T=18$ the ratio between both estimates is particularly high (namely >3.5). To be complete, let us add that when the target species has been well detected estimates obtained under conditional and unconditional approaches are quite similar.

Discussion

Globally, occupancy rates variations between 1985 and 1987 do not seem to be mainly directed by the migratory status and no important differences between interior forest and edge forest has been shown. The main factor responsible for species' response to climate changes appeared to be their biogeographical region of origin.

Migratory status - Contrary to what we expected, the species migratory status did not seem to be an important cause of differences in changes of occupancy rates under climate changes. Evolution of occupancy rates as a response to climate changes could have been affected because of direct effects on bird species of these changes, or secondary consequences. For example, decrease may be due to the direct impact of rigorous winters on populations (especially for sedentary species) or indirect impacts such as a decrease in available resources (particularly for migratory species that should not be affected by the direct consequences of cold in the region). An increase of occupancy rates or a less important impact of the specific regional climatic events might be expected because other species might be negatively

impacted by cold winters and therefore leave unused resources and part of ecological niche. Variation in population is the result of trades-offs between these negative and indirect positive consequences and the influence of other external factors (e.g. a population already in a decrease phase).

The impact of climatic extremes on bird densities is well-known (Wiens, 1981, Grzybowsky 1983, Balda *et al.*, 1983 ; Hejl & Beedy, 1986). According to these authors, rigorous winters affect sedentary but not migratory bird species. In our study area, Palearctic and Turkestano-european faunistic type species expanded, while European, Turkestano-mediterranean and Mediterranean sedentary species experience population reductions or extinction. This signifies a continentalization of the local avifauna. However, not all of the sedentary birds were negatively affected by cold winters. Woodpeckers, Eurasian Nuthatch and tits population increased. Fauna continentalization can also be seen with migrants. Whitethroat, Tree Pipit, Spotted Flycatcher, but also Yellow Wagtail, Red-backed Shrike and Garden Warbler have increasing occurrence frequencies.

The absence of clear impact of the migratory status can be due to the specific characteristics of some of the species' local populations. For example, the Chiffchaff, which has an important over-wintering population in Midi-Pyrenees, is found in winter near to stagnant and running waters in the plain, where birds are sedentary. It is therefore strongly affected by rigorous winters, leading to a drop in numbers in riparian forest, observed between 1985 and 1987 (Lauga & Joachim, 1992). However, local populations, which are mainly migratory outside of riparian forests, are not greatly affected (Affre, 1975*b* ; Joachim *et al.*, 1997). Another example implies the European Robin. It was a common bird in this region before the cold January of 1985. Rarer in 1985 spring, it almost disappeared from the study area by spring 1987. It was only present in the largest terrace forest where its frequency was greatly reduced (F = 30% instead of 80% in 1985). This local extinction happened in

plains and hills of the piemont Garonne. However, in mountainous areas such as Haute-Garonne Pyrenees and Ariège, no significant frequency variation occurred between 1985 and 1987: F=100% for Cagire beech groves (Haute-Garonne, 1000 m) and beech and birch groves in the Beille plateau (Ariège, 800-1400m) for both years (Joachim *et al.*, 1997). Therefore, it can be hypothesized that the European Robin from the Garonne plains was sedentary and did not survive the rigorous winters while the one from Central Pyrenees are migratory and avoided these winters. Génard & Lescourtet (1985) found insular type adaptative characters in European Robin of the Pyrenees. However, this species general range skirts Mediterranean areas and shows no interruption between Pyrenees and the rest of France. Therefore, the authors could not explain this phenomenon. Recent events suggest a distinction between East and Central Pyrenees populations and more northern populations. First, during cold winters, the Garonne population disappears and there is a real separation between areas. Second, during mild winters, a sedentary Garonne population of European Robin develops but because it is sedentary, it stays isolated from migratory Pyrenees' European Robins which have then developed specific insular peninsular characteristics.

Interior vs. edge forest - We have not detected significant differences between interior and edge forest, and globally species occupancy rates seemed to vary the same way in these two sub-area. No changes of habitat preferences has been detected, but response to climate changes might be less important in some cases in the interior forest than in the edge forest indicating that actually, the interior forest might have provided a better protection. The extent of this phenomenon may even be more important that what we could see here. In fact, because of the poor sampling rate in the edge forest, the credible intervals of estimates are large leading to a possible underestimation of the protection role played by the inner forest. It is

interesting to note that without the use of prior information, the detection of this effect would have been compromised.

On a larger scale, detected variations in frequency are generally associated to colonization or retreat from areas that do not correspond to preferred habitat (defined by sampling from 1985; Joachim, 1986). Largely wide-spread in woods located in this area, the Chiffchaff has partially retreated from riparian forests while wren populations decreased in terraces. Birds that are mainly forest birds have colonized small groves (e.g. Mistle Thrush, Lesser Spotted Woodpecker), and open-field birds have penetrated into forest edges (e.g. Tree Pipit, Whitethroat). These clues suggest that bird species with continental affinities, even if progressing for various reasons, have difficulties in finding their optimal habitat. The local frequency increase with occupation of unusual environments might reflect healthy neighboring continental populations (e.g. in northern France, the Massif Central, or the Pyrenees) with individuals that would settle in environments marginal to our region. Such phenomena have been demonstrated by Askins & Philbrick (1987), and Askins *et al.* (1987) for forest fauna in Connecticut (USA), by Van Dorp & Opdam (1987) in Dutch groves, and by Helle & Järvinen (1986) in northern Finland.

In open-fields of near the study area, ornithologists have pointed out the disappearance of some species (*Cisticola juncidis*, Indo-african faunistic type, *Sylvia undata*, Mediterranean faunistic type), but no disappearance has been noticed in woody areas. *Cettia cetti* has undergone a drastic regression in riparian forests without disappearing, and so has *Erithacus rubecula* in all forests. Globally, species from forest areas seems to cope better with climatic variations (even if affected) than sedentary open-field species. Some forest species have even profited of new climatic conditions.

Role of the species' biogeographical origins - Continentalization of the regional forest fauna has not been yet reflected by loss or gain of species, but instead by population reduction or expansion by locally common species. However, some species have been more affected and show a general reduction (or even extinction) or global colonization in the studied area. Some extant monitoring programs such as the European Bird Census Council (http://www.ebcc.info/) are interested in the expansion or regression of occupied areas of several species, but no particular attention is drawn to the biogeographical origins of species, which, as shown here, can be crucial.

In a broader context, during the 1970's, a different situation occurred with the settlement or expansion of Mediterranean species (e.g. Dartford Warbler, Subalpine Warbler, Woodchat Shrike), Turkestano-Mediterranean species (e.g. : Cetti's Warbler, Bee-eater) or Indo-African species (Zitting Cisticola) in our study area during a succession of mild winters (Affre 1975*a* and *b*, Yeatman 1974). This expansion often extended to the French Atlantic coast which provided a mild winter climate (Yeatman, 1976). Highly contrasting seasons from 1985, 1986 and 1987 have been correlated with regression and even local extinction of sedentary populations to the benefit of these colonizing species, leaving small populations on the Atlantic coast (e.g. Warblers). Depending on annual climatic variations, the Val de Garonne area is alternatively colonized by Mediterranean thermophilic species using early stages of plant successions, or continental species (especially forest species) uncomfortable in isolated wood patches present in the agricultural plains (Blondel, 1984). These temporary colonizations still permit the exchange of individuals between populations that are intermittently isolated from each other (e.g. populations from the Pyrenees' continental fauna and mid-Europe reservoir, and Mediterranean populations from the Atlantic coast and Mediterranean reservoir). European partial migratory species with a sedentary edge area that encompass the South-West of France hardly succeed to sustaining populations.

Various biogeographical influences acting on this region, usually thought to be an enriching factor to natural environment, here, are paradoxically related to a noticeable faunistic deficit (Balent *et al.*, 1988). Climatic variations and advanced deforestation only allow commonly wide-spread species and pioneer species. Riparian Garonne forest seems to be important, because regardless of climatic conditions, it contains a fauna of diverse biogeographical regions, such as the Turkestano-Mediterranean Cetti's Warbler , the European Garden Warbler (Affre, 1980) and the palearctic Marsh Tit (Joachim, 1987). Avifauna responses to climatic variations are slower here than in the open-fields of neighboring agricultural plains. While the Garonne riparian forest, with a small area, can not be a local fauna local reservoir and populations therein are not as unchanging as in large forest areas (Glowacinski, 1981). It constitutes a moderating element in Garonne landscape because of its slow response to climatic variations,. It also provides a more or less hospitable link between remote patches of biogeographically different faunas and their source areas.

Taking into account some prior on the detectability of the target species can significantly improve the estimation of its occupancy rates when it has been very few detected (or not detected) and is known to be easily detectable (as already pointed out by Dupuis et al., 2010). As a matter of fact, ignoring such an available prior may have led to different conclusions such as detection of a variation in occupancy rate while not true (e.g. Green Woodpecker or Whitethroat in edge forest), a wrong estimation of the impact of rigorous winters (e.g. Nightingale or European Robin in edge forest), or worse, it would have failed to detect a diminution of the occupancy (e.g. Nightingale in the inner forest). Moreover, in our dataset, we have undetected species which were known to be present in the study area; we have thus adopted the conditional approach of Dupuis *et al.* (2010) for estimating their occupancy rates.

As shown in the comparison between unconditional and conditional approaches, not accounting for the known presence of an undetected species can lead to significant underestimation of its occupancy rate.

Appendices

Appendix 1. MatLab code for the binary search algorithm to determine the coefficients of the Beta distribution placed on detection probability over the whole visit μ_{sa} from a prior mean and 95% credible interval. *Output: Beta distribution parameters a and b.*

```
function [ParamBetaMu] = BinarySearchAlgorithm()

mu=input('Prior mean of Mu(sa): ')
CIinf=input('Lower bound of prior CI95%: ')
CIsup=input('Upper bound of prior CI95%:')
prec=input('Required interval precision: ')

CI=[CIinf CIsup]  ;


% Initialization
margin=prec+1 ;
lambda1=0    ;
lambda2=10000 ;

% Binary search algorithm

while (margin>prec)
      lambda=(lambda1+lambda2)/2     ;
      a=lambda*mu                ;
      b=lambda*(1-mu)          ;
      prob=betainc(CIsup,a,b)-betainc(CIinf,a,b)     ;
      margin=abs(proba-0.95)                ;

      if (prob<0.95)
         lambda1=lambda             ;
   end

   if (prob>0.95)
      lambda2=lambda        ;
   end
end

a=lambda*mu           ;
b=lambda*(1-mu)       ;
ParamBetaMu=[a b]           ;
```

Appendix 2. MatLab code to obtain the Beta distribution parameters on q_{sa} (detection probability during each session of a visit) from the Beta distribution on μ_{sa}. *Input: Beta distribution parameters on μ_{sa} provided by function BinarySearchAlgorithm(). Output: Beta distribution parameters for q_{sa}.*

```
function [ParamBetaQ]=MuGlobal_QLocal(ParamBetaMu)

a= ParamBetaMu (1);
b= ParamBetaMu (2);

K=input('enter the number of sessions K during a visit:');
L=input('enter the number of iterations for the MCMC algorithm:');

%Initialization
sumq=0;
sum2q=0;

%Beginning of MCMC algorithm

for l=1:L
   X=betarnd(a,b);
   k=1/K;
   q=1-(1-X)^k;
   Y(l)=q;
   sumq=sumq+q;
   sum2q=sum2q+q*q;
   espq(l)=sumq/l;
end;

%End of MCMC algorithm

meanq=sumq/L;
varq=sqrt(sum2q/L-meanq^2);
lambq=((meanq*(1-meanq))/varq^2)-1;

alpha=lambq*meanq;
beta=lambq*(1-meanq);

Force=alpha+beta;
APrioriMean=alpha/(alpha+beta) ;

ParamBetaQ =[APrioriMean  Force];
```

Appendix 3. MatLab code for estimating γ_{sa} (and φ_{sa} and q_{sa} if required) using the Data Augmentation scheme: φ_{sa} is updated via a Hasting-Metropolis step, q_{sa} and missing data via a Gibbs step. *Input: Total number Vobs of quadrats where the species of interest has been detected, total number W of detection of targeted species, total number J of quadrats in region R_a, number T of sampled quadrats, number K of sessions per visit, number L of iterations for the MCMC algorithm. Output: Estimates of posterior mean and 95% credible interval for occupancy rate γ_{sa}.*

```
function
[estimgamma,ICgamma1,ICgamma2,ICgamma3]=DBJDataAugV1V2(Vobs,W,J,T,K,L)

delta=input('enter value of tuning parameter on phi (by default, take 0.3)
for Hasting-Metropolis algorithm:');

% Computation of Beta distribution parameter of a priori on Qsa
[parammu]= BinarySearchAlgorithm () ;
[paramq]= MuGlobal_QLocal(parammu)  ;
priorq=paramq(1);
lambdaq =paramq(2);

%DATA
dataVW=[Vobs,W];
dataVW;

%Non-informative a priori on phi
priorphi=0.5;
lambdaphi=2;

%Initialization
phi=0.1;
phi_init=phi;
phi_init;

q=0.3;
q_init=q;
q_init;

accept=0;
sumq=0;
sum2q=0;
sumphi=0;
sum2phi=0;
sumgamma=0;





%Beginning of MCMC algorithm

for l=1:L


 % 1) DATA AUGMENTATION
 omega=(phi*(1-q)^K)/(phi*(1-q)^K+(1-phi));

 if (Vobs==0);
   Vsim=0;
   while(Vsim==0)
     Vsim1=binornd(T,omega);
```

```
      if (J>T)
        Vsim2=binornd(J-T,phi);
      else
        Vsim2=0;
      end;
      Vsim=Vsim1+Vsim2;
    end;
  else
    if (T>Vobs)
        Vsim1=binornd(T-Vobs,omega);
    else
        Vsim1=0;
    end;
    if (J>T)
       Vsim2=binornd(J-T,phi);
    else
       Vsim2=0;
    end;
    Vsim=Vsim1+Vsim2;
  end;
   V=Vobs+Vsim;

  gamma=V/J;
  grafgamma(l)=gamma;

  % 2) UPDATE $q$ via Gibbs
q=betarnd(lambdaq*priorq+W,lambdaq*(1-priorq)+(K*Vobs-W)+K*Vsim1);

  % 3) UPDATE $phi$ via Hast. Metro.
e=max(0,phi-delta);
f=min(1,phi+delta);
phihm=(f-e)*rand(1)+e;
ehm=max(0,phihm-delta);
fhm=min(1,phihm+delta);
logratiog=log(fhm-ehm)-log(f-e);

piphihm=betapdf(phihm,priorphi*lambdaphi,(1-priorphi)*lambdaphi);
piphi=betapdf(phi,priorphi*lambdaphi,(1-priorphi)*lambdaphi);
logratioprior=log(piphihm)-log(piphi);

logPrc=V*(log(phihm)-log(phi));
logPrd=(J-V)*(log(1-phihm)-log(1-phi));
logPre=log(1-(1-phi)^J)-log(1-(1-phihm)^J);
logratiolike=logPrc+logPrd+logPre;

logrho=logratiolike+logratioprior-logratiog;
rho=exp(logrho);


if (rho>=1)
    phi=phihm;
    accept=accept+1;
else
    U=binornd(1,rho);
    if(U==1)
      phi=phihm;
      accept=accept+1;
    end;
  end;

sumgamma=sumgamma+gamma;
```

```
sumphi=sumphi+phi;
sum2phi=sum2phi+phi*phi;
sumq=sumq+q;
sum2q=sum2q+q*q;

espgamma(l)=sumgamma/l ;

end;
%End of MCMC algorithm

rate=accept/L;
rate;

estimgamma=sumgamma/L;

estimq=sumq/L;
errorq=sqrt(sum2q/L-estimq^2);

estimphi=sumphi/L;
errorphi=sqrt(sum2phi/L-estimphi^2);

estimationqphi=[estimq,errorq,estimphi,errorphi];

cigamma=sort(grafgamma);

CIgamma1=[cigamma(0.025*L),cigamma(0.975*L)];
CIgamma1;

CIgamma2=[cigamma(0.05*L),cigamma(L)];
CIgamma2;

CIgamma3=[cigamma(1),cigamma(0.95*L)];
CIgamma3;

% Take the shortest CI

estimgamma ;
plot(1:L,espgamma)
```

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Tables and Figures

Figure 1. European map of biogeographical region and location of Montech Forest. (using data provided by the European Environmental Agency: www.eea.eu.int*). (Black point: Montech Forest, Cross hatch: Alpine, Diagonal simple hatch: Atlantic, Ordered stipple: Continental, Horizontal simple hatch: Mediterranean).*

Figure 2. Mean monthly temperatures in 1985, 1986 and 1987 *(Spotted line: 1985, Hachted line: 1986, solid line: 1987)* compared to 1970-1984 period (maximum and minimum values from this 14 year period bounded in gray).. (from Joachim & Lauga, 1992)

Figure 1.

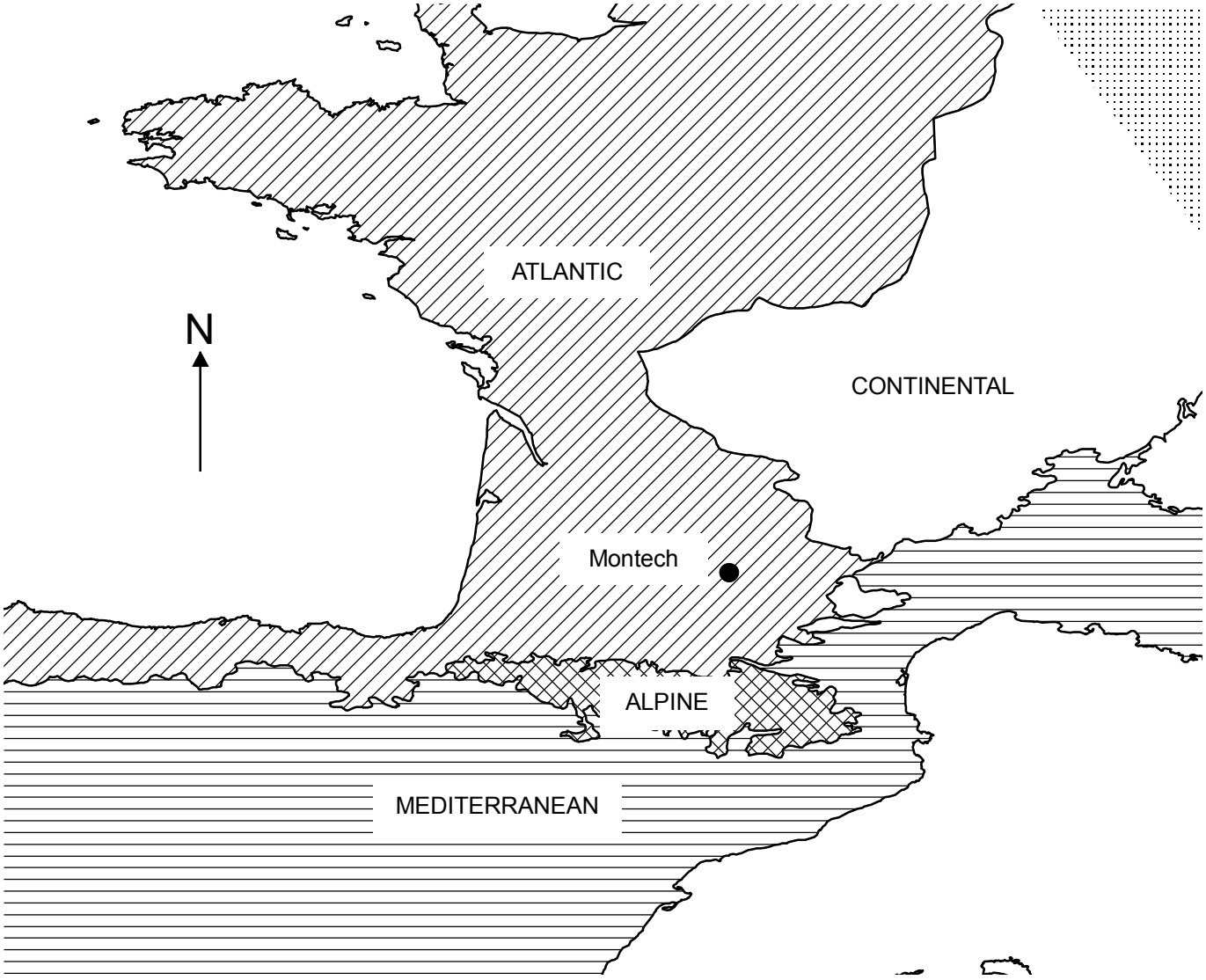

Figure 2.

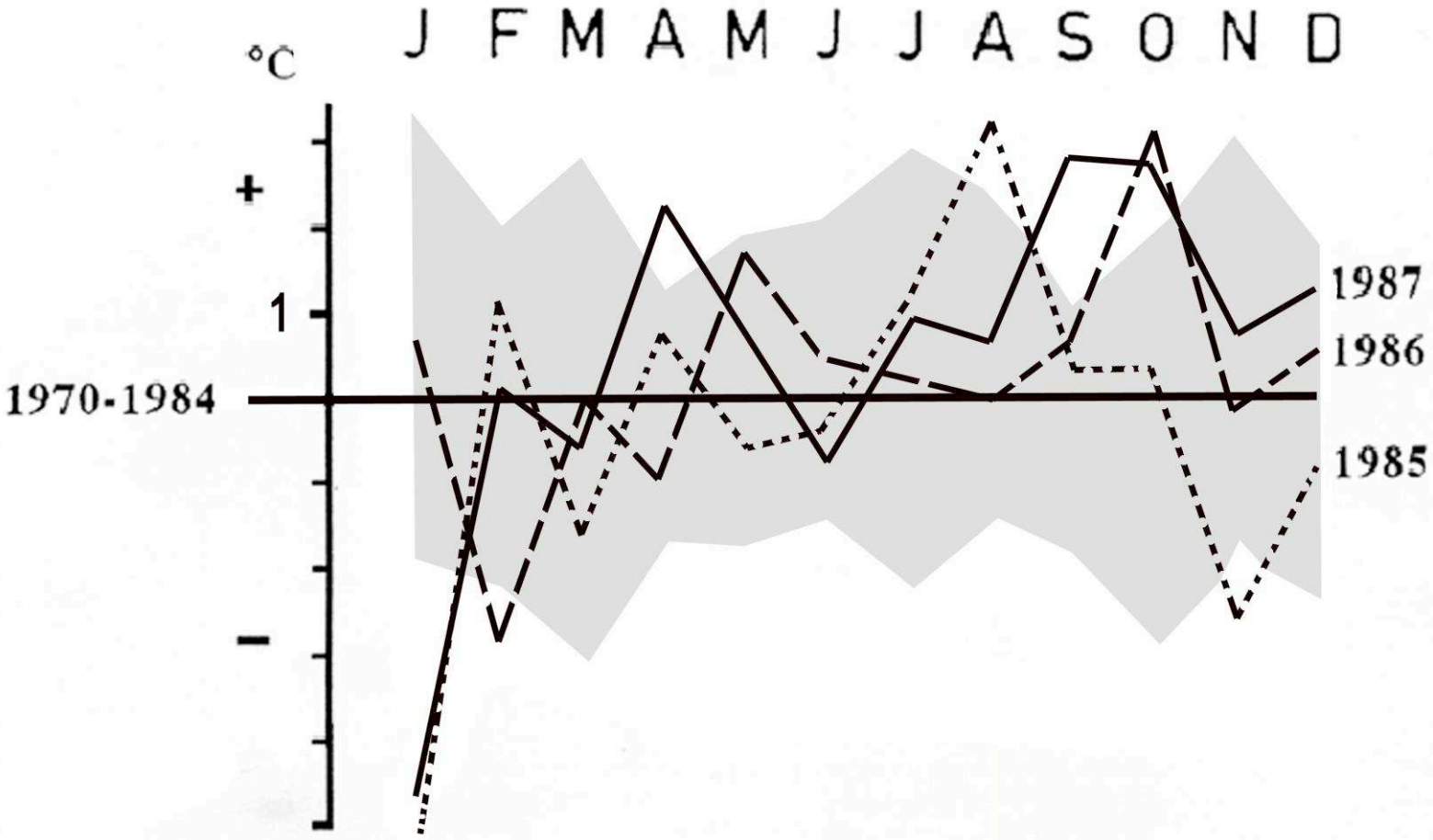

Table 1.

Table 1. Data ($V_s(a)$;$W_s(a)$) for 1985 and 1987 in Montech forest.

Species		Inner forest		Edge forest	
		1985	1987	1985	1987
Song Thrush	*Turdus philomelos*	(20 ; 53)	(10 ; 20)	(16 ; 43)	(1 ; 2)
Common Blackbird	*Turdus merula*	(17 ; 32)	(12 ; 25)	(14 ; 35)	(4 ; 6)
Whitethroat	*Sylvia communis*	-	-	(2 ; 2)	(1 ; 1)
Chiffchaff	*Phylloscopus collybita*	(15 ; 30)	(5 ; 13)	(10 ; 24)	(4 ; 8)
Eurasian Nuthatch	*Sitta europea*	(7 ; 17)	(9 ; 26)	(4 ; 8)	(2 ; 2)
Green Woodpecker	*Picus viridis*	(1 ; 1)	(3 ; 3)	(0 ; 0)	(2:2)
Short-toed Treecreeper	*Certhia brachydactyla*	(15 ; 22)	(10 ; 17)	(11 ; 28)	(2 ; 2)
European Robin	*Erithacus rubecula*	(9 ; 17)	(5 ; 8)	(7 ; 12)	(2 ; 6)
Nightingale	*Luscinia megarhynchos*	(4 ; 9)	(1 ; 1)	(5 ; 7)	(0 ; 0)
Mistle Thrush	*Turdus viscivorus*	(6 ; 13)	(8 ; 22)	(4 ; 5)	(3 ; 4)

Table 2.

Table 2. Migratory status and biogeographical origins of the selected species. *Migratory status: Sedentary (S), Migrant (M) or Partial migrant (P).*

Species	Migratory status	Global faunistic class	European biogeographical origin
Song Thrush	P	European	Atlantico-continental
Common Blackbird	P	Palearctic	European
Whitethroat	M	Turkestano-european	Atlantico-mediterranean
Chiffchaff	M	Palearctic	Atlantico-continental
Eurasian Nuthatch	S	Palearctic	European
Green Woodpecker	S	European	European
Short-toed Treecreeper	S	European	European
European Robin	P	European	Atlantico-continental
Nightingale	M	European	Atlantico-mediterranean
Mistle Thrush	P	European	Continental

Table 3.

Table 3. Prior mean and CI $_{95\%}$ of detection probability μ_{sa} during 1985 and 1987 in Montech forest.

Species	Inner forest		Edge forest	
	1985	1987	1985	1987
Song Thrush	0.8 [0.65 – 1]	0.6 [0.3 – 0.8]	0.8 [0.65 – 1]	0.4 [0 – 0.65]
Common Blackbird	0.8 [0.65 – 1]	0.6 [0.3 – 0.8]	0.8 [0.65 – 1]	0.8 [0.65 – 1]
Whitethroat	-	-	0.8 [0.65 – 1]	0.8 [0.65 – 1]
Chiffchaff	0.8 [0.65 – 1]	0.8 [0.65 – 1]	0.8 [0.65 – 1]	0.8 [0.65 – 1]
Eurasian Nuthatch	0.8 [0.65 – 1]	0.8 [0.65 – 1]	0.6 [0.3 – 0.8]	0.6 [0.3 – 0.8]
Green Woodpecker	0.6 [0.3 – 0.8]	0.6 [0.3 – 0.8]	0.8 [0.65 – 1]	0.8 [0.65 – 1]
Short-toed Treecreeper	0.8 [0.65 – 1]	0.8 [0.65 – 1]	0.6 [0.3 – 0.8]	0.6 [0.3 – 0.8]
European Robin	0.8 [0.65 – 1]	0.6 [0.3 – 0.8]	0.8 [0.65 – 1]	0.2 [0 – 0.4]
Nightingale	0.6 [0.3 – 0.8]	0.6 [0.3 – 0.8]	0.8 [0.65 – 1]	0.8 [0.65 – 1]
Mistle Thrush	0.6 [0.3 – 0.8]	0.6 [0.3 – 0.8]	0.4 [0 – 0.65]	0.4 [0 – 0.65]

Table 4.

Table 4. Posterior mean and CI $_{95\%}$ of γ_{sa} for inner and edge regions of Montech forest in 1985 and 1987. Estimates were computed using informative prior on q_{sa}.

	Inner forest				Edge forest			
Species	1985		1987		1985		1987	
Song Thrush	0.95	[0.91 ; 1]	0.85	[0.68 ; 1]	0.93	[0.89 ; 1]	0.47	[0.06 ; 0.94]
Common Blackbird	0.89	[0.77 ; 1]	0.93	[0.77 ; 1]	0.84	[0.78 ; 0.94]	0.76	[0.44 ; 1]
Whitethroat	-		-		0.16	[0.11 ; 0.28]	0.08	[0.06 ; 0.17]
Chiffchaff	0.79	[0.68 ; 0.96]	0.42	[0.23 ; 0.59]	0.63	[0.56 ; 0.78]	0.74	[0.44 ; 1]
Eurasian Nuthatch	0.37	[0.32 ; 0.45]	0.68	[0.50 ; 0.86]	0.36	[0.22 ; 0.61]	0.59	[0.22 ; 1]
Green Woodpecker	0.11	[0.05 ; 0.32]	0.46	[0.14 ; 0.86]	0.07	[0.05 ; 0.14]	0.49	[0.11 ; 0.83]
Short-toed Treecreeper	0.87	[0.73 ; 1]	0.84	[0.64 ; 1]	0.72	[0.61 ; 0.89]	0.59	[0.11 ; 0.94]
European Robin	0.51	[0.41 ; 0.68]	0.60	[0.32 ; 0.96]	0.50	[0.39 ; 0.72]	0.57	[0.11 ; 0.94]
Nightingale	0.28	[0.18 ; 0.45]	0.19	[0.05 ; 0.50]	0.39	[0.28 ; 0.61]	0.15	[0.06 ; 0.39]
Mistle Thrush	0.39	[0.27 ; 0.59]	0.67	[0.45 ; 0.91]	0.59	[0.28 ; 1]	0.75	[0.39 ; 1]

Table 5.

Table 5. Posterior mean of γ_{sa} and CI $_{95\%}$ for inner and edge regions of Montech forest in 1985 and 1987. Estimates were computed using a non informative prior on q_{sa}. *Only results differing from the informative approach are presented here.*

	Inner forest				Edge forest			
Species	1985		1987		1985		1987	
Song Thrush	-		-		-		0.29	[0.06 ; 0.72]
Common Blackbird	-		-		-		-	
Whitethroat	-		-		0.41	[0.11 ; 0.94]	0.42	[0.06 ; 0.94]
Chiffchaff	-		-		-		-	
Eurasian Nuthatch	-		-		-		-	
Green Woodpecker	0.24	[0.05 ; 0.82]	0.56	[0.23 ; 1]	0.25	[0.05 ; 0.82]	0.59	[0.22 ; 1]
Short-toed Treecreeper	-		-		-		-	
European Robin	-		0.52	[0.23 ; 0.86]	-		0.37	[0.11 ; 0.61]
Nightingale	-		0.42	[0.06 ; 0.94]	-		0.24	[0.05 ; 0.78]
Mistle Thrush	-		0.58	[0.36 ; 0.73]	-		0.67	[0.33 ; 1]

Table 6a. Comparison between γ_{sa} estimates under unconditional (MacKenzie *et al.*, 2006) and conditional (Dupuis *et al.*, 2010) approaches when a species is not detected, for a non informative and an informative prior on q_{sa}: case of the Green Woodpecker in edge region of Montech forest in 1985. $J=T=18$.

	Unconditional approach		Conditional approach	
Non informative prior	0.13	[0 ; 0.68]	0.25	[0.05 ; 0.82]
Informative prior	0.02	[0 ; 0.11]	0.07	[0.05 ; 0.14]

Table 6b. Comparison between γ_{sa} estimates under unconditional (MacKenzie *et al.*, 2006) and conditional (Dupuis *et al.*, 2010) approaches when a species is not detected, for a non informative and an informative prior on q_{sa}: case of the Nightingale in edge region of Montech forest in 1987. $J=18$, $T=6$.

	Unconditional approach		Conditional approach	
Non informative prior	0.20	[0 ; 0.78]	0.24	[0.05 ; 0.78]
Informative prior	0.12	[0 ; 0.39]	0.15	[0.05 ; 0.39]