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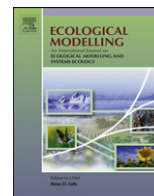
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Are Swiss birds tracking climate change? Detecting elevational shifts using response curve shapes

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ABSTRACT

Climate change is affecting biodiversity worldwide inducing species to either “move, adapt or die”. In this paper we propose a conceptual framework for analysing range shifts, namely a catalogue of the possible patterns of change in the distribution of a species along elevational or other environmental gradients and an improved quantitative methodology to identify and objectively describe these patterns. Patterns are defined in terms of changes occurring at the leading, trailing or both edges of the distribution: (a) leading edge expansion, (b) trailing edge retraction, (c) range expansion, (d) optimum shift, (e) expansion, (f) retraction, and (g) shift. The methodology is based on the modelling of species distributions along a gradient using generalized additive models (GAMs). Separate models are calibrated for two distinct periods of assessment and response curves are compared over five reference points. Changes occurred at these points are formalized into a code that ultimately designates the corresponding change pattern. We tested the proposed methodology using data from the Swiss national common breeding bird survey. The elevational distributions of 95 bird species were modelled for the periods 1999–2002 and 2004–2007 and significant upward shifts (all patterns confounded) were identified for 35% of the species. Over the same period, an increase in mean temperature was registered for Switzerland. In consideration of the short period covered by the case study, assessed change patterns are considered to correspond to intermediate patterns in an ongoing shifting process. However, similar patterns can be determined by habitat barriers, land use/land cover changes, competition with concurrent or invasive species or different warming rates at different elevations.

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1. Introduction

Climate change is affecting biodiversity worldwide (Kappelle et al., 1999; Heller and Zavaleta, 2009). In recent years, evidence has mounted about its impacts on different groups of species and stages of a species lifecycle (Hughes, 2000; Parmesan, 2006). Especially for birds (Crick, 2004; Chambers et al., 2005; Leech and Crick, 2007; Wormworth and Mallon, 2007), climate change has been shown to induce poleward (Hitch and Leberg, 2007) and upward shifts of the distributional ranges (Pounds et al., 1999), to alter the timing of major seasonal events such as migration (Jenni and Kéry, 2003; Jonzen et al., 2006; Gordo, 2007) or egg laying (Crick and Sparks, 1999; Torti and Dunn, 2005; Both and te Marvelde, 2007) and to influence survival and productivity and hence, population dynamics (Sanz et al., 2003).

Organisms can adapt to climate change either via phenotypic plasticity (physiological, behavioural plasticity) and/or evolutionary changes (microevolution or evolutionary genetic changes involving multiple generations) (Visser, 2008; Williams et al., 2008). Adaptation can take place in different dimensions: in geographic space, individuals can adapt by modifying their distribution in order to follow favourable climatic conditions and habitats; in environmental space, individuals can shift their phenotypes according to the new environmental conditions, which can possibly lead to the inheritance of new traits through selection; finally, in the temporal dimension, seasonal events such as reproduction or migration may ultimately occur earlier or be delayed (Fig. 1). Adaptation can occur predominantly in one particular dimension, but generally involves all of them. When populations cannot adapt in one of these dimensions or cannot adapt fast enough (Devictor et al., 2008; Visser, 2008), a species may be driven to extinction, even though today's projections are probably overestimated (Botkin et al., 2007) due to assumptions and limitations of current forecasting methods (refer to Thuiller, 2004, and Thuiller et al., 2008, for the spatial dimension).

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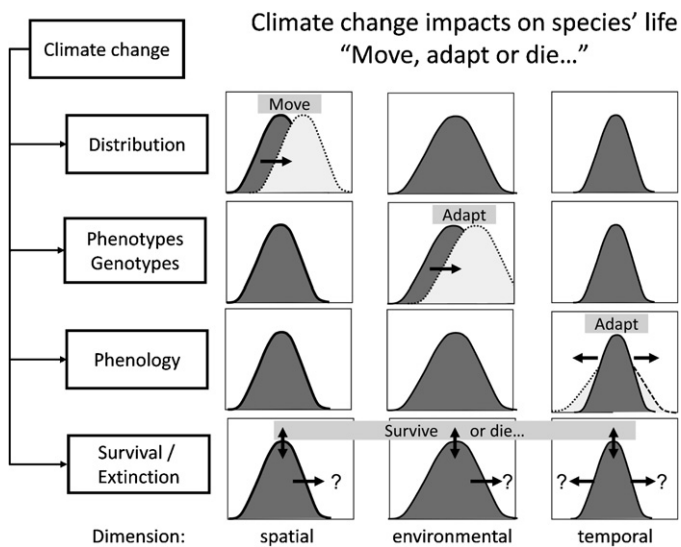


Fig. 1. "Move, adapt or die". Individuals can adapt to climate change by either shifting their distribution in the geographic space or adapting in the environmental or temporal space. Populations that are not able to adapt in one of these dimensions or adapt fast enough can drive their species to extinction.

As stressed by Parmesan (2006), in spite of numerous studies indicating local adaptation to climate change, Pleistocene fossil records reveal little evidence for the evolution of new phenotypes despite temperature shifts of a greater magnitude than currently observed. It can therefore be assumed that species are more prone to shift their ranges to track favourable climatic conditions, rather than to remain in place and evolve new forms, especially in view of the speed of projected climatic change. The large majority of recent studies on climate change impacts have therefore focused on the estimation of the shifts in species ranges that are expected according to different climatic and land use scenarios. These studies are mainly based on species distribution modelling and are employed in order to forecast changes in the distribution of single species (Pearson and Dawson, 2003; Araujo et al., 2006; Beaumont et al., 2007; Huntley et al., 2007; McKenney et al., 2007; Lawler et al., 2009), ecosystems (Berry et al., 2003; Thuiller et al., 2006) or biodiversity (Bakkenes et al., 2002; Thuiller et al., 2005; Dormann et al., 2008). These techniques allow forecasting changes and are therefore important tools for current conservation planning in order to mitigate the impacts of climate and land use change on biodiversity (Hannah et al., 2007). However, the question can be posed as to the evidence for the influence of recent climate change on species distribution. Monitoring programs are essential in order to observe biodiversity and detect shifts in species ranges. In recent decades, many schemes have been established, especially after the adoption by many countries of the UN Convention on Biological Diversity at the UNCED summit in Rio de Janeiro in 1992 (Schmeller et al., 2008). Data gathered in these schemes now begin to provide evidence for changes in species' distributions even though the cause–effect relationship with climate change is not always obvious (Thuiller, 2007).

The Swiss national breeding bird survey (MHB; Schmid et al., 2004) was launched in 1999 and is conducted on an annual basis. Although a priori a decade appears a rather short period to relate climate change to possible changes in bird distributions, the highly variable Swiss topography may let one expect distributional changes at least in the third dimension, i.e. along the elevational gradient. Here, we propose a conceptual framework with a catalogue describing the possible patterns of change of a distribution along a gradient such as elevation and a quantitative methodology to identify and objectively describe these patterns. Theoretical

expectations are verified using MHB data. Previous similar studies have expressed elevational changes in terms of changes that have occurred at the optimum of the species distribution (Wilson et al., 2005; Lenoir et al., 2008). This is based on the assumption that the entire distribution shifts as a whole, whereas in reality, and especially over short periods, different patterns in the elevational shift may be expected. Indeed, different processes may be responsible for the changes occurring at the "leading" and "trailing edges" of a distribution when range shifts occur: colonization and migration mostly happening at the leading edge, and speciation, persistence or extinction at the trailing edge (Hampe and Petit, 2005; Thuiller et al., 2008). Our description of range shifts also considers changes that have occurred at the borders of the distribution and is based on the outer and central border defined by Heegaard (2002). These measures allow describing the non-parametric response curve of a species–environmental relationship estimated by generalized additive models (GAMs). While Heegaard used them in order to define the range and tolerance of a species along an environmental gradient, we used these measures in order to position the response curve along the environmental gradient using five reference points and to evaluate the changes that have taken place between two distinct periods of assessment. Changes that occurred at the five reference points are formalized into a code that allows the identification of the corresponding change pattern described in the catalogue.

The main aims of this study are first, to conceptually define the possible patterns of change in the distribution of a species along an elevational or other environmental gradient and to propose a methodology in order to identify them. Second, to apply this methodology to the data of the Swiss national breeding bird survey to investigate whether elevational shifts occurred during the period 1999–2007 and, finally, to evaluate if temperatures significantly changed in Switzerland during the same period.

2. Theoretical patterns of shift

2.1. A catalogue of shift patterns along a gradient

Especially when considering short periods, upward shifts observed along an elevational gradient – or shifts along any other gradient – are rarely complete shifts. Instead, intermediate patterns are observable. Fig. 2 illustrates conceptually what are the possible patterns in an upward-shifting process. Curves represent the distribution of the abundance or the occurrence probability of a given species along an elevational gradient at two different periods. Solid lines represent the initial distribution (time t_0) whereas dotted lines represent the distribution at the second period of assessment (time t_1). When capturing the entire distribution, this is represented by a bell-shaped curve (central column). However, when considering geographically limited areas, it is possible that only part of the entire elevational distribution of the species is captured and the curve is therefore truncated either at its lower (left column) or at its upper end (right column). Working at a regional scale can therefore prevent the detection of changes occurring at the truncated end of the distribution or prevent the unequivocal identification of the pattern of change (cases 1–5, which show similar truncated curves).

Changes can either occur at the leading or the trailing edge of the distribution with expansion towards higher elevations or retraction from lower elevations. Also, expansions of the leading edge and retractions of the trailing edge can occur with (types E–F) or without (types A–B) a follow up of the core of the distribution. Special cases are represented by pattern D, where only the optimum moves upward, the remainder remaining constant, or pattern C that corresponds to a range expansion in both directions, i.e. up- and

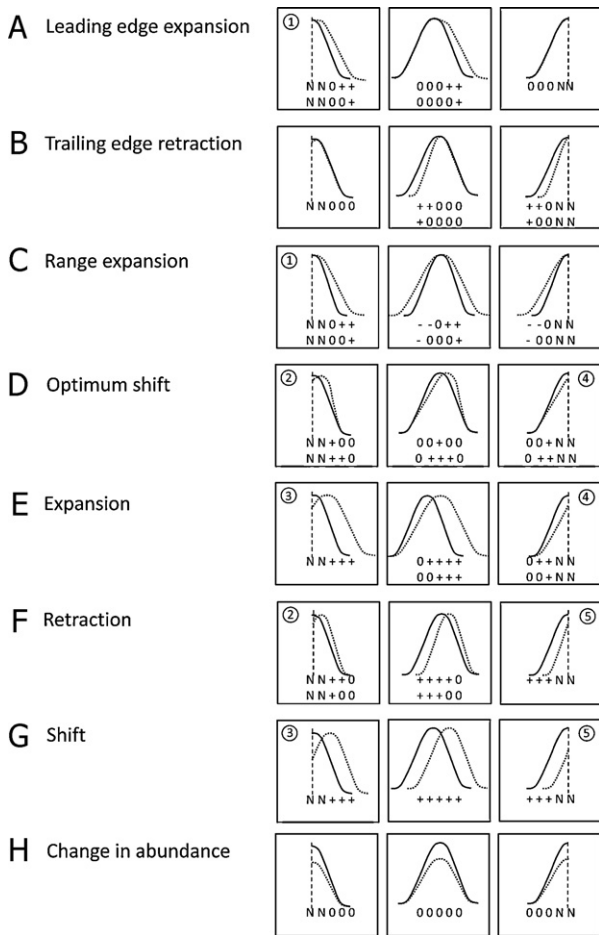


Fig. 2. A catalogue of the possible shift patterns along a gradient. Solid lines represent the initial distribution (time t_0) and dotted lines represent the distribution at the second period of assessment (time t_1). The code under each curve expresses the significance and direction of the change that occurred at each of the five reference points (OBL, CBL, OPT, CBR, OBR, defined in Section 2.2) with the following symbols: +, significant upward shift; -, significant downward shift; 0, non-significant shift; N, truncated curve with no information for the point. Response curves in the central column represent main shapes. Response curves in the left and right columns are curves that are truncated at the OPT point. Patterns with the same number are patterns corresponding to truncated curves that cannot be distinguished unequivocally from one another.

downwards. Patterns A–F may be considered as intermediate steps towards a final pattern, pattern G, which is a complete shift of the distribution. Patterns A, B and D would correspond to early stages, whereas patterns E and F to more advanced stages in such a process. The patterns for a downward shift would simply be symmetrical to those described here for the upward shift. All these patterns are most of the time combined with pattern H that represents a change in the abundance or occurrence probability for an identical range of elevations.

Patterns presented in Fig. 2 can either correspond to intermediate steps in a process of upward shifting or be determined by other factors acting either at the leading or trailing edge of the distribution. These could be for example the encountering of barriers or unsuitable habitats along the gradient, biotic interactions or different warming rates at different elevations. In these cases, theoretically intermediate patterns could also become permanent. Patterns B or F, as an example, are characterized by an upper limit that remains constant and by a retraction of the lower limit towards higher elevations. An upward shift is probably initiated but some kind of barrier is preventing the shift at the leading edge of the distribution. This could be a physical barrier, especially in the case of

animal species with reduced dispersal ability, or a change in habitat type or quality. The barrier could in this case correspond to the transition from open land to forest, to the treeline, to the transition from alpine grasslands to bare rocks, or ultimately to the top of the mountain. The movement could also be prevented by competition with a species persisting and dominating the upper elevations or by a symbiotic species that moves at a different rate. However, the same patterns could also be determined by factors acting at the trailing edge. The upward shift is possibly determined by a change in land use, with consequent habitat degradation or loss occurring at the lower elevations. As an example, this was observed for farmland specialist birds in the French Alps. Archaux (2007) found that farmland specialists decreased from the late 1970s onwards and that the decline was much more important below 1000 m (–70%) than above (–20%). This pattern was not found in farmland generalists or woodland species and may thus be more likely linked to changes in agricultural practices or type of land use than to climate change. This raises the problem of disentangling the effects of climate and land use (Lemoine et al., 2007). Indeed, especially at lower elevations, the effects of these two phenomena can hardly be distinguished because they are often acting in a synergistic manner. Another explanation for the upward shift of the trailing edge could be the competition and unseat by an invading species coming from lower latitudes/elevations. With climate warming, conditions will indeed become more similar to those of the native range of many invasive species and thus facilitate colonization. Moreover, climate change is expected to displace native species out of the conditions to which they are adapted and competitive resistance from native species may therefore become weaker (Hellmann et al., 2008). Shifts in suitable climatic zones will thus tend to benefit invasive species that have traits that favour them in a changing environment, like broad environmental tolerances, short juvenile periods, and long-distance dispersal (Hellmann et al., 2008). In particular for birds, favourable traits for invasive species would include good dispersal ability, high rate of population increase resulting from large clutch size and several clutches per season, ability to compete for resources and habitat with native species (O'Connor, 1986; Sakai et al., 2001).

Patterns A or E are characterized by an expanding leading edge and a persistent trailing edge. This could result from temperature warming at different rates at different elevations. This phenomenon has been reported by Pepin and Lundquist (2008) in their global assessment of extra-tropical regions that shows that 20th century temperatures increased more rapidly near the annual 0°C isotherm due to snow-ice feedbacks. Milder conditions at higher elevations allow the species to expand upwards, while conditions at lower elevations are still favourable and do not prompt the species to retract. Alternatively, populations at the trailing edge may have adapted to the new conditions and maintained their ability to compete with invading species.

Range expansion (pattern C) is a particular case. Dispersal-driven expansion that is normally contained by exogenous factors is here released. New favourable conditions created at higher elevations as a consequence of climate warming prompt the species to move upwards. Competition release or habitat restoration allows the species to reappropriate the lower fringe of its niche.

2.2. Assessing elevational shifts

In the previous section we proposed a catalogue of the possible steps in a process leading to a complete upward shift of the distribution. But, how can we detect these patterns in real data? The proposed flow of analysis is illustrated in Fig. 3. As a first step, the presence or the abundance of a species is modelled as a function of elevation using generalized additive models (GAMs; Hastie and Tibshirani, 1990). GAMs are a generalization of GLMs (generalized

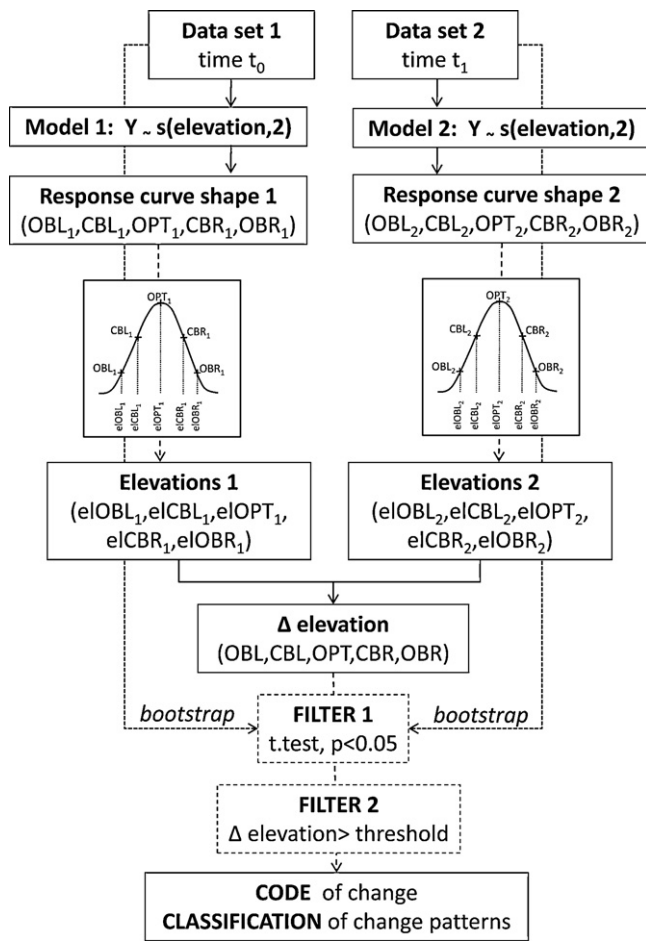


Fig. 3. Analysis flow chart. Data are separated in two datasets relative to a first and a second period of assessment (t_0 and t_1 , respectively). For each dataset the presence or the abundance of the species is modelled as a function of elevation using GAMs. The resulting response curve shape is described by five fixed points along the curve: OBL = outer border left; CBL = central border left; OPT = optimum; CBR = central border right; OBR = outer border right. The significance of the shift at each point between the two periods is tested by a t-test on bootstrapped values (100 times). The shift is considered significant if the t-test between the bootstrapped values is significant at the threshold $p < 0.05$. A supplementary filter can be applied in order to avoid dealing with shifts inferior to a certain threshold. According to the change occurred at the five reference points a code of change is defined and the different patterns grouped in main types.

linear models; McCullagh and Nelder, 1989) that estimate response curves with local smoothing functions. GAMs are therefore data-driven and flexibly explore the shape of complex relationships with much fewer restrictions and assumptions than GLMs (Yee and Mitchell, 1991). This is especially useful to fit response curves that are asymmetrical or that present a plateau or a multimodal distribution.

Separate models are calibrated for two distinct periods of assessment (t_0 and t_1). The position of the response curve along the elevational gradient is described using five reference points (see Fig. 4a). Three main measures determine their position along the response axis: (a) the optimum (OPT), which represents the maximum modelled abundance or maximum occurrence probability; (b) the central border (CB) and (c) the outer border (OB). The central and the outer borders are defined according to Heegaard (2002), i.e. as the response value that is equal to a specified fraction of the maximum response: $\text{maximum response} \times \exp(-2)$ for the outer border and $\text{maximum response} \times \exp(-0.5)$ for the central border. On a bell-shaped distribution there are two points on the curve that correspond to each response value, one on the left and the other on

the right of the optimum. Along the elevational gradient, the position of the response curve is thus described by the outer border left (OBL), central border left (CBL), optimum (OPT), central border right (CBR) and outer border right (OBR). The response curves corresponding to the two periods of assessment are compared on the basis of the elevation corresponding to these five reference points. The methodology is also applicable when a response curve is truncated, in this case the shift can only be assessed on a subsample of reference points. As an example, Fig. 4b represents a bell-shaped distribution truncated on the right – this is the typical distribution for alpine species – for which only the position of the OBL, CBL and OPT can be assessed. Similarly, for the truncated distribution in Fig. 4c – which mainly represents the distribution of lowland species – only the OPT, CBR, OBR can be assessed. The methodology has the advantage of being sensitive also to changes in the response curve shape. As an example, the response curve at time t_1 represented in Fig. 4a is skewed on the right. This will be recognized when determining the elevations corresponding to the CBR and the OBR.

To test whether the difference in elevation between the two periods is significant at each reference point, a bootstrapped t-test is performed with 100 replications per period. A supplementary filter may be applied to avoid dealing with shifts inferior to a certain threshold that may not be considered as ecologically significant. The changes at the five reference points are coded as follows: +, for a significant upward shift; –, for a significant downward shift; 0, for a non-significant shift; N, meaning “no data”, for truncated curves at the lower or upper end of the elevational gradient. The resulting code allows identifying the pattern of change as defined in the catalogue of Fig. 2. Note that a simple change in abundance (pattern H) does not induce a shift at any reference point (see Fig. 4d); any detected change will therefore directly indicate a shift along the gradient.

3. Case study

3.1. Materials and methods

3.1.1. Study region

Switzerland is situated at the boundary between Central and Western Europe and is influenced by contrasting Atlantic, Mediterranean and continental regimes that result in highly variable conditions across the country. The Swiss territory is classically subdivided into six main biogeographical regions (Gonseth et al., 2001): the Jura Mountains, the flat and intensively cultivated area of the Plateau and four regions in the Alps, respectively the Western and Eastern Alps and the Northern and Southern slopes. The Jura Mountains are a limestone range of mountains characterized by an average elevation of 810 m above sea level (asl). The Plateau covers about 30% of the Swiss territory and is characterized by an average elevation of 540 m asl. The Alps, mainly crystalline rocks, occupy nearly two thirds of the Swiss territory. The mean range of elevations for the Alps is 3800 m and the highest point is the Dufourspitze in Canton Valais at 4634 m asl.

3.1.2. Data

We assessed our methodology and the relevance of the theoretical change patterns using the data from the Swiss national common breeding bird survey (MHB, Schmid et al., 2004). This monitoring program has been conducted on an annual basis by the Swiss Ornithological Institute since 1999. For the present study we used data sampled until 2007. The survey encompasses 267 squares of 1 km² that are distributed across Switzerland as a grid and thus are representative of different biogeographical zones, elevation bands and habitats. The elevation (median over the 1-km² square) of sam-

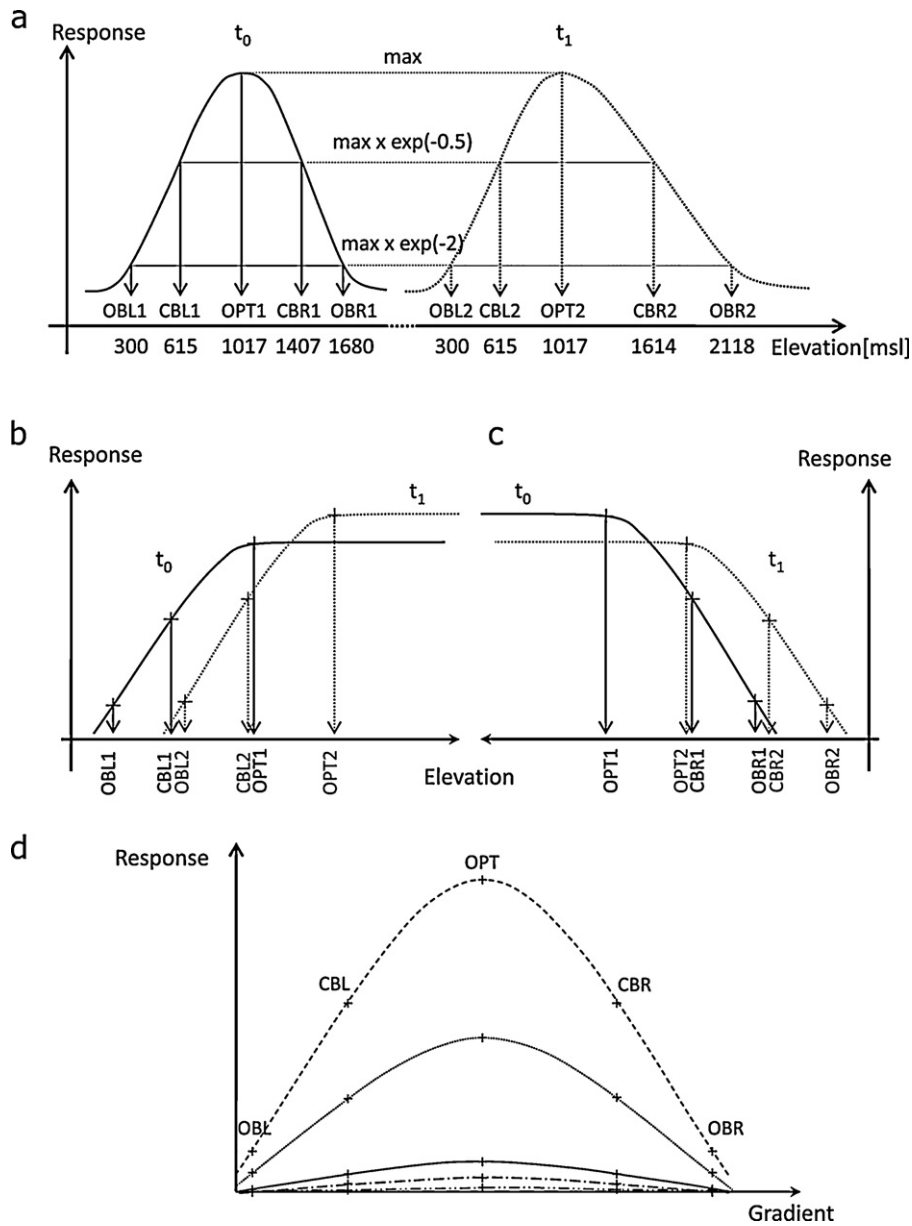


Fig. 4. a) Response curves at time t_0 (solid line) and time t_1 (dotted line). The position of each curve along the elevation gradient is described using five reference points: OBL, CBL, OPT, CBR, OBR (see the text for detailed description). Response curve for time t_1 is skewed, as a consequence CBR₂ and OBR₂ are more distant from the optimum than at t_0 . This is automatically taken into account when searching for the corresponding altitude using the relationship established by the model; b) example of a response curve truncated on the right. As a consequence shifts can only be assessed on a subsample of reference points, i.e. OBL, CBL and OPT. This is a typical distribution of an alpine species; c) example of a response curve truncated on the left. As a consequence shifts can only be assessed at OPT, CBR, OBR. This distribution is typical of a lowland species; d) an initial dataset is randomly generated according to a normal distribution. Supplementary datasets are obtained by multiplying the initial values by 10, 50, 100, 500 and 1000. These values are modelled as a function of the gradient and the responses curves shown in the figure. Crosses indicate the position of the reference points (OBL, CBL, OPT, CBR, OBR). This figure shows that a simple change in abundance does not induce a shift at the reference points.

pling units ranges from 210 to 2710 m asl. Each square is surveyed three times – twice for squares above the treeline – per breeding season (15 April–15 July) by skilled volunteers who map all birds seen or heard along a square-specific route. At the end of the season, territories are identified from the mapped points (see Schmid et al., 2004, for a detailed description of the survey protocol).

Data used for the analysis consist in the observed number of territories per km². These are an index of the true population size related to the latter quantity by detection probability. As is customary in many ecological studies, by drawing our inferences about abundance based on this index, we make the assumption that detection probability is not related to any of the factors studied (Kéry and Schmidt, 2008).

3.1.3. Application of the general methodology in order to detect elevational shifts

The observed number of territories per km² was modelled as a function of the median elevation of each sampling square according to the analysis flow chart presented in Fig. 3. Separate models were calibrated for the periods 1999–2002 and 2004–2007. Using data sampled over several years avoid the comparison of the first and last year that might be exceptional and not representative for the particular period. In particular, the chosen design avoids the year 2003, which was characterized by an exceptionally hot summer in Switzerland (Beniston and Diaz, 2004). Assessing elevational shifts from data sampled in 1-km² squares is not ideal because the elevation range within a square in mountainous areas may be fairly

important and could therefore hide an elevational shift that may have occurred due to climate change. For this purpose, data sampled on transect or point counts would be more appropriate, as suggested by Archaux (2004), especially for detecting early stages of distributional shifts. However, the fact that changes can be identified in spite of the coarse resolution of sampling units indicates that the distributional shift is sufficiently important to pass from one sampling square to a square with a higher median elevation. Only species observed in at least 10 squares were considered for analysis. This is the minimum number of data to be used when calibrating a model with one predictor. A second filter was applied to these data to avoid dealing with shifts of less than 50 m, which were not considered as significant. Despite a few exceptions, the difference between the median altitudes of the sampling squares was, respectively, less than 50 and 14.55 m on average. A filter of 50 m therefore ensured that a species had shifted at least from one square to a higher one. All the analyses were performed with S-Plus ver. 8.0 (Insightful Corp. 2007, Seattle, WA, USA).

3.1.4. Spatial predictions

For each assessment period, the potential distribution of species abundance (i.e. expected number of detected territories per km²) across the Swiss territory was calculated directly within S-Plus and the predictions exported as ASCII grids to be displayed in a geographic information system (GIS; ArcMap ver. 9.2, ESRI 2006). In order to perform the predictions directly within S-Plus, a dataset was prepared by sampling within the GIS the mean elevation of the 41,300 1-km² squares that compose the Swiss territory. The abundance of each species was then predicted for each square as a function of elevation.

3.1.5. Population trends

Population trends were calculated using a GLM with a Poisson distribution within the program TRIM (Pannekoek and van Strien, 1998). Trends were calculated for populations at the trailing and leading edge of the elevational distribution. These populations were arbitrarily defined as the ensemble of individuals having defined their territory below the elevation corresponding to the central border left (CBL) and above the central border right (CBR) respectively.

3.1.6. Temperature trends

Temperatures for the period 1999–2007 were obtained from the weather stations of the automatic meteorological network of Switzerland (SwissMetNet). Daily minimum, mean and maximum temperatures were considered for 67 weather stations distributed throughout Switzerland that were selected for the completeness of their series. The weather stations are distributed between 203 and 3315 m asl. In order to identify trends, temperatures were analysed as a function of elevation and time using generalized linear mixed models (GLMMs; Breslow and Clayton, 1993). Within S-Plus, GLMMs were calibrated by penalized quasi-likelihood using the function *glmmPQL* contained in library MASS. Fixed effects were the elevational bands (lowland: <700 m; montane: 700–1500 m; subalpine 1500–2300 m; alpine-nival: >2300 m asl) and years (1999–2007) whereas weather stations were set as a random effect. Mean changes in minimum, mean and maximum daily temperatures between the beginning (1999) and the end (2007) of the study period are given for the elevational bands presenting a significant increase over the period. Mean daily temperature averaged over a year was also modelled as a function of elevation with a linear regression model using the ensemble of the 67 weather stations and the 9 years of the study period. This allowed defining a general rate of change in mean temperature with elevation for Switzerland. A similar model was also calibrated for the beginning of the study period (year 1999) and the end (year 2007); the difference in the

intercept of the two linear regressions providing information on the general increase in mean temperature between the 2 years at a given elevation.

3.2. Results of the case study

3.2.1. Shifting patterns identified for breeding birds in Switzerland

The analysis was performed for 95 species that were observed in at least 10 out of the 267 squares covered by the monitoring program. For 33 species out of the 95 (i.e. for 35%), a significant upward shift was identified in at least one of the reference points along the response curve. That proportion increases when considering only sedentary species, 12 out of 27 species (44%). For the remaining species, 28 presented a significant downward shift and 34 species no significant change. Significant shifts, either upward or downward, were not linked to a particular habitat. According to the changes that occurred at the five reference points, different patterns could be identified and attributed to the theoretical patterns described in Fig. 2. Concerning the change patterns of the 33 species presenting a significant upward shift, 3 were leading edge expansions (pattern A), 2 trailing edge retractions (pattern B), 6 range expansions (pattern C), 1 optimum shift (pattern D), 2 expansions (pattern E), 5 retractions (pattern F), 5 complete upward shifts (pattern G) and in 9 cases the curve was truncated and contained only two reference points (either OBL–CBL or CBR–OBR). The latter are curves belonging to lowland species, whose abundance decreases with elevation (left column of Fig. 2), or alpine species, whose abundance increases with elevation (right column of Fig. 2). Range expansions were mainly linked to rare species with very low abundances throughout the elevational gradient. Upward retractions in their broad sense (i.e. patterns B and F confounded) were mainly linked to species nesting in the forest (six species over seven). Forest birds were also the most represented (four cases over five) among species having completely shifted upwards (pattern G). The mean shift at the five reference points for the 33 species presenting a significant upward shift was of 82 m for the OBL, of 52 m for the CBL, of 40 m for the optimum, of 91 m for the CBR and of 94 m for the OBR.

As an illustration, the response curves of three species with a significant change between the two periods are shown in Fig. 5. The Marsh Tit (*Parus palustris*), a common lowland passerine, has started to move upwards with a significant shift of the optimum (OPT) and the central border right (CBR). However, the shift at the outer border right (OBR) is not significant. Thus, the change mainly consists in a retraction (type F) from low elevations with so far no significant upward shift at the leading edge of the distribution. The change for the Ring Ouzel (*Turdus torquatus*) is quite similar but occurs at higher elevations. The change is significant for the OBL, CBL and OPT points, but not for the CBR. As the curve is truncated on the right, the situation for the OBR can thus not be assessed. This species is therefore mainly retracting from the lower elevations of its elevational range. For the Eurasian Bullfinch (*Pyrrhula pyrrhula*) the changes are significant and positive for all five reference points and thus represent a case of complete upward shift (type G). In Fig. 5, the potential distribution of the abundance is also shown for the three species during the first (1999–2002) and the second period of assessment (2004–2007). The potential distribution is here determined solely as a function of elevation and does not include any other predictor.

3.2.2. Population trends at the leading and trailing edge

The change in the shape of the response curve at the trailing and leading edges of the same three focus species between the two periods with their population trends below the CBL and above the CBR respectively is presented in Fig. 6. For the species character-

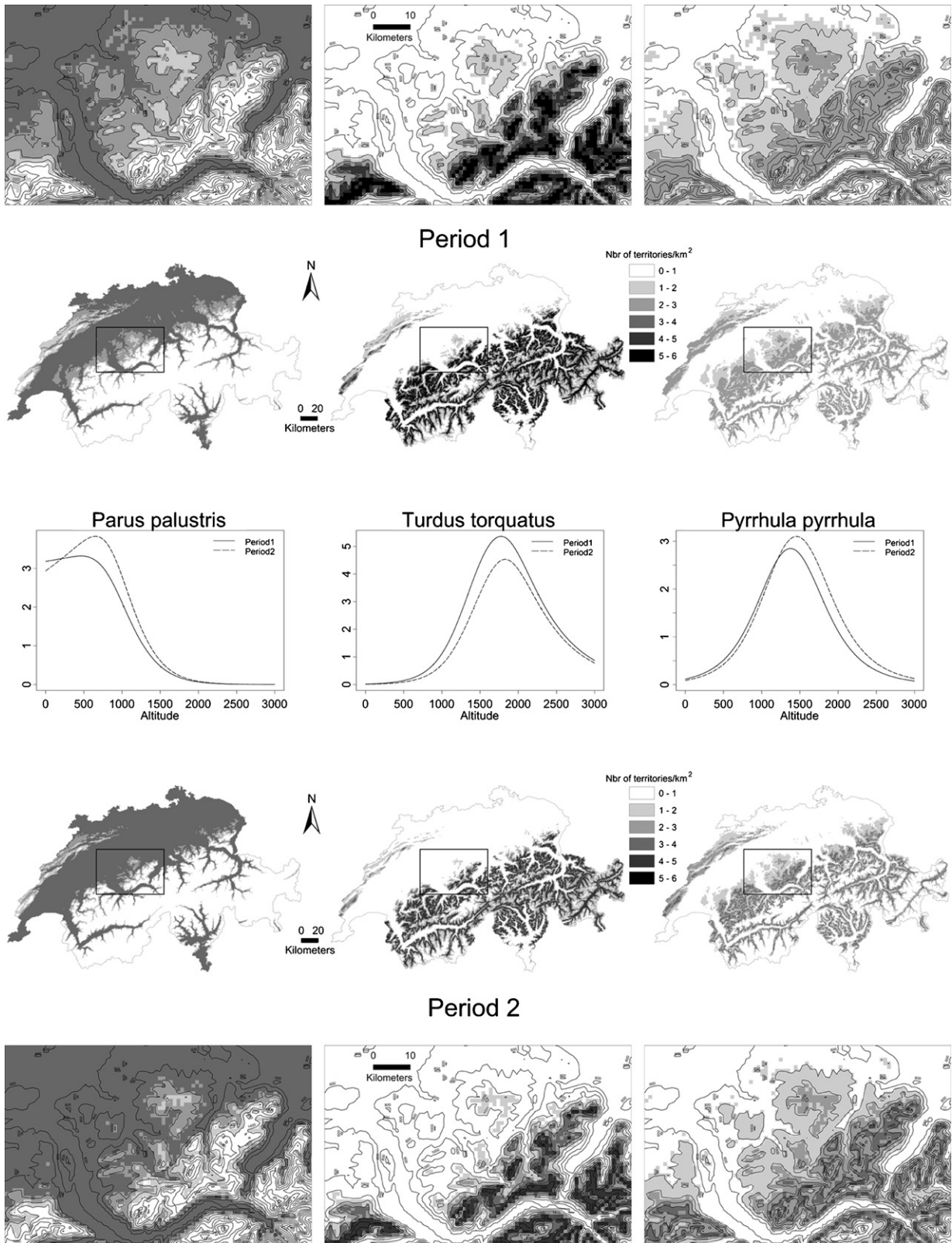


Fig. 5. Response curve shapes of the modelled abundance as a function of elevation for the period 1999–2002 (solid line) and 2004–2007 (dashed line) for three species presenting different patterns in the upward-shifting process. The potential abundance-based distribution across Switzerland is determined for each species and for the two periods as a function of elevation solely (spatial prediction for period 1 on the top, spatial prediction for period 2 below). The change of the elevational distribution toward higher elevations can be appreciated in the zoomed areas.

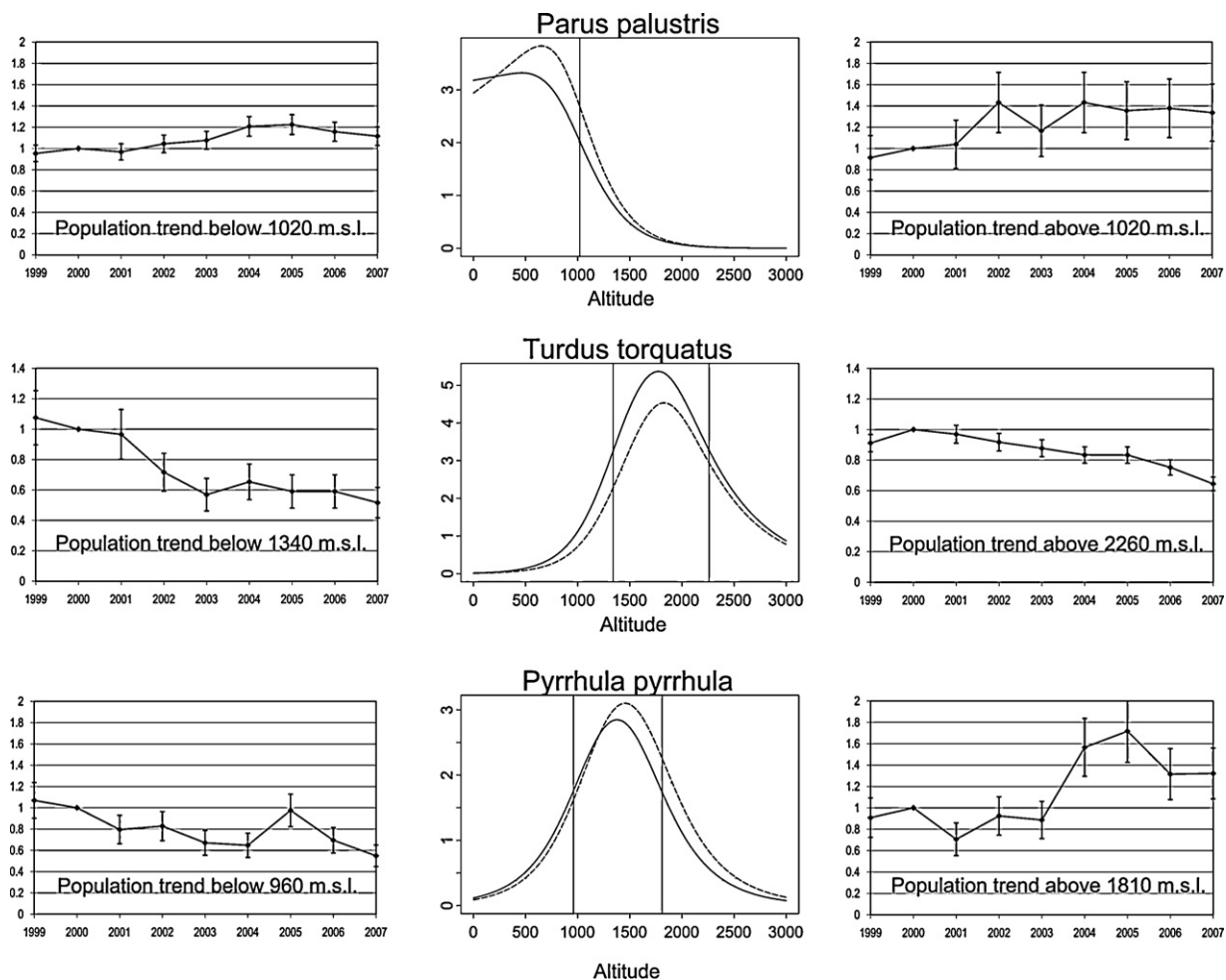


Fig. 6. Response curve shapes of the modelled abundance as a function of elevation for the period 1999–2002 (solid line) and 2004–2007 (dashed line) for three species presenting different patterns in the upward-shifting process. Graphics on the left and on the right represent population trends in the elevational bands below the CBL and above the CBL of each species respectively (vertical solid lines). On these graphics, populations in 2000 are set as reference (value 1) and populations for other years are expressed proportionally to this reference value.

ized by a complete shift – the Eurasian Bullfinch (*Pyrrhula pyrrhula*) – the population trend significantly decreased at the trailing edge ($p < 0.01$) and it significantly increased at the leading edge ($p < 0.01$). The Ring Ouzel (*Turdus torquatus*) retracted from the lower elevations of its range with no significant change in the upper limit. This pattern is combined with an overall decrease in abundance. The population trend at the leading edge is therefore negative ($p < 0.01$) as it is at the trailing edge ($p < 0.01$). The curve for the Marsh Tit (*Parus palustris*) is truncated, therefore population trends were calculated above and below the same point, i.e., the CBL. Like the Ring Ouzel, the Marsh Tit is retracting from the lower elevations, but this pattern is combined with an overall increase in the modelled abundance. The two trends are therefore positive ($p < 0.01$).

3.2.3. Temperatures trends over the study period

Trends for the daily mean temperature in Switzerland for the period 1999–2007 and per elevational band are presented in Fig. 7. The lowland band (<700 m asl) includes 34 weather stations of the automatic meteorological network of Switzerland (SwissMetNet). The montane (700–1500 m asl), subalpine (1500–2300 m asl) and alpine-nival (>2300 m asl) bands include 14, 15 and 4 stations respectively. Altogether mean daily temperature tends to increase over the considered period. Results of the GLMM are significant for the montane ($p < 0.05$) and subalpine ($p < 0.01$) elevational belts. For the montane belt, mean daily temperature averaged over a year

and over the 14 weather stations increased from 6.46 °C in 1999 to 7.25 °C in 2007, thus a mean increase of 0.79 °C. For the sub-alpine belt the mean increase was of 0.84 °C. The general shape of each trend remains however similar at each elevational band

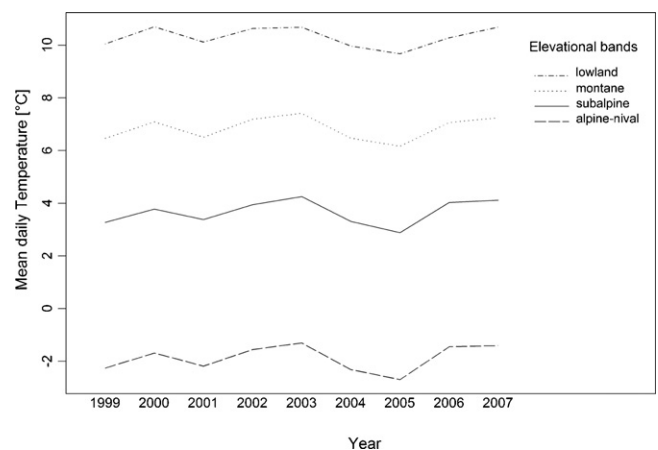


Fig. 7. Trends for the mean daily temperature in Switzerland between 1999 and 2007 within the elevational bands. The figure is based on the measurements of 67 fixed weather stations of the automatic meteorological network of Switzerland (SwissMetNet).

with synchronized yearly ups and downs. Similar trends were also observed for the maximum daily temperature and partly for the minimum daily temperature (graphs not shown). The maximum daily temperature trends were significant and positive for the montane ($p < 0.001$) and the subalpine ($p < 0.001$) belt. Maximum daily temperature increased on average by 1.03°C between 1999 and 2007 for the montane belt and by 1.12°C for the subalpine belt. Results of the GLMM for the minimum daily temperature were significant and negative for the lowland belt ($p < 0.01$) and positive for the subalpine belt ($p < 0.05$). Although exhibiting a negative trend, the averaged minimum daily temperature increased by 0.3°C for the lowland belt between the beginning (1999) and the end (2007) of the study period. The increase for the subalpine belt was 0.68°C .

The general model linking mean temperature (calculated from daily mean temperature averaged over a year) to elevation allowed defining a general rate of change in mean temperature with elevation for Switzerland of $-0.52^\circ\text{C}/100\text{m}$. The general model was calibrated using the data of the 9 years and the ensemble of the 67 weather stations selected for the study. A similar model was calibrated considering only data for the year 1999 and a second considering only data for the year 2007; the difference in the intercept of the two models informing about the increase in mean temperature between the beginning and the end of the study period. The difference between the two intercepts was 0.60, which corresponds to a global increase of 0.6°C . The slope of the two regression lines was very similar but not identical (-0.0053 versus -0.0052 for 1999 and 2007, respectively). This indicates that the increase in mean temperature was not the same throughout the elevational gradient, but that it was more important at higher elevations, which confirms the results obtained by the analysis per elevational band. A t-test performed over bootstrapped model indices (1000 times) confirmed that slope and intercept were significantly different between 1999 and 2007.

4. Discussion

4.1. Proposed methodology

The general methodology we have proposed here could be efficiently applied to the data of the Swiss breeding bird survey and proved to be effective in assessing in a quantitative manner the extent of the shifts that have occurred at five reference points defined along the response curve of the modelled distribution. Furthermore, the change at these five reference points and the resulting code allowed the identification of the type of shift pattern. All the shift patterns defined in our conceptual catalogue were found in real data either in their full or in their truncated form. The short time period covered by the data indirectly supports the hypothesis that the theoretically defined patterns correspond in this case to transitional patterns in an ongoing upward-shifting process, but as mentioned in Section 2.1 similar patterns can be determined by factors other than climate change, e.g. barriers, land use change, competition or different warming rates at different elevations.

Studies assessing climate change impacts generally compare distinct periods separated by several decades (Thomas and Lennon, 1999; Wilson et al., 2005; Lemoine et al., 2007; Lenoir et al., 2008). Such studies are even more likely to benefit from the proposed methodology to assess changes over these long periods. Furthermore, the proposed methodology can be applied to gradients other than elevation. The simplest example would be the latitudinal gradient to assess poleward shifts. Our approach can be compared to the methodologies of Thomas and Lennon (1999), Hitch and Leberg (2007) or Hill et al. (2002), which are essentially based on the average of the 10 northernmost/southernmost latitudes. Assessing shifts

directly at range margins is always risky because occurrence in this part of the distribution is often the result of isolated dispersal events which may result in non-lasting populations (Shoo et al., 2006). Moreover, an improvement in the detection probability between the two periods of assessment can lead to a spurious conclusion of a range expansion and this is particularly true when only range margins are assessed (Hitch and Leberg, 2007). It is therefore recommended to assess changes at margins in a substantial range. In order to use an established definition, for our methodology we adopted the outer border and central border characteristics described in Heegaard (2002), which are defined with respect to the centre and not to the margin of the distribution. Our methodology could also be used to explore the time dimension in order to assess phenological shifts. It can then be compared to trends in the first arrival date (Donnelly et al., 2009), the quantile approach (Van Buskirk et al., 2009) or the first-versus-mean arrival date (Miller-Rushing et al., 2008). For the same reasons pointed out for range margins in the spatial dimension, range margins in the temporal dimension could also be misleading. The methodology we propose would therefore clearly perform better than the use of the first arrival date and would be more accurate than the single point of reference represented by the mean arrival date. On the other hand, the quantile approach would give very similar results. We believe also that our approach could be useful to explore other environmental gradients composing the environmental niche of a species such as water, energy or other resources. In the context of the study of resource sharing of competing plant species, a similar approach was used by Heikkinen and Mäkipää (2010) in order to assess plant response curves along a C/N gradient. Curves were described by three measures: the optimum, the niche width and the curve skewness. Similarly to our approach, the latter two measures were determined according to Heegaard's central border but were used in order to define the ecological amplitude of the species and the degree of overlap with competing species while we used them in order to position the curves along the gradient.

Species are generally distributed within their range according to a central-margin (C-M) gradient, with the centre supporting the highest population density (Guo et al., 2005). This pattern can well be modelled by a bell-shaped distribution. Previous studies have employed generalized linear models (GLMs) with a quadratic term in order to model the elevational distribution of species (Wilson et al., 2007; Lenoir et al., 2008). This parametric method forces however the response to fit the predefined quadratic shape. Generalized additive models (GAMs) are more flexible, follow the data more closely and are therefore particularly suited for skewed or multimodal response curves or those characterized by a plateau (e.g. Yee and Mitchell, 1991). In our case, we limited the number of degrees of freedom of the smoothing functions to two. The resulting simplification of response curves was necessary in order to be able to compare the curves for the two periods.

4.2. Shifts in the elevational distribution of breeding birds in Switzerland

Estimates of elevation shifts in animal distribution due to recent climate change are still rare in the literature to allow direct comparison, particularly for birds (Parmesan, 2006; Shoo et al., 2006; Sekercioglu et al., 2008). As a first indication, the meta-analysis performed by Parmesan and Yohe (2003) over more than 1700 species of different (plant and animal) taxa documented significant upward range shifts averaging 6.1m per decade. In the French Alps, Archaux (2004) recorded the greatest shift for the European Robin (*Erithacus rubecula*) with an upward shift of 114m over a 30-years period. In Switzerland this species does not seem to have significantly changed its distribution, either up- or downwards, during the 9 years considered. Shifts of similar importance in the optimum of

the distribution have however been modelled in Switzerland for the Marsh Tit (*Parus palustris*) (Fig. 5), the Song Thrush (*Turdus philomelos*) and the Garden Warbler (*Sylvia borin*) (results not shown). The shift pattern for these species is of type F according to our catalogue, i.e., mainly a retraction from low elevations. In their assessment in an alpine valley in Italy, Popy et al. (2009) found that the mean elevations increased for the majority of species over the considered period of 11 years, but that the average change was not significantly different from zero. However, a significant upward shift of 29 m of the bird zonation could be identified. Over the same period, mean temperature in the area (mean values over four nearby stations) increased by 1 °C and maximum temperature by 1.4 °C. The increase for the minima was of 0.5 °C although not significant. For Switzerland we were able to assess temperature increases of the same order of magnitude for the subalpine belt (+0.84 °C for mean, +1.12 °C for the maximum and +0.68 °C for the minimum daily temperature), but in our case elevational shifts were significant. For the 33 species presenting a significant upward shift, the mean upward shift at the five reference points was of 82, 52, 40, 91 and 94 m from left (OBL) – trailing edge – to right (OBR) – leading edge. The general model linking mean daily temperature to elevation allowed defining an approximate rate of change in mean temperature with elevation for Switzerland of $-0.52\text{ °C}/100\text{ m}$ (rate calculated with the data of 67 weather stations of SwissMetNet over the study period). According to this rate, the overall increase of 0.6 °C that we assessed for the mean temperature between 1999 and 2007 would correspond to an upward shift of 115 m. The mean upward shifts we assessed for the CBR and OBR, 91 and 94 m respectively, are quite consistent with this expectation. However, we are aware that the temperature increase occurred over the study period is probably not the one that caused the observed elevational shift in bird distributions (assuming there is a causal relationship). Indeed, there is a certain inertia in population dynamics related to the lag over which effects on survival or reproduction become noticeable in population totals. So it may well be that the observed changes in the bird distributions are the effects of a warming process that started before the study period.

If we consider the analogy between latitudinal and elevational shifts, we can transpose some assumptions concerning the mechanisms occurring at the edges of the distribution. According to Hampe and Petit (2005) the main processes at the leading and trailing edges of the distribution in response to a given environmental change are migration, persistence or extinction. Within the context of climate change, migration depends mostly on populations at the colonization front. Indeed, it is at the leading edge that isolated long-dispersal events occur and potentially lead to exponential population growth (Thuiller et al., 2008). As a consequence, the population trends at the leading edge of a shifting distribution are in principle positive. In our study, this was confirmed in the case of the Eurasian Bullfinch. Its elevational change being a complete shift, the population trend was positive at the leading edge and negative at the trailing edge. This seems to be consistent with findings of Foden et al. (2007) who suggest that population trends calculated for the range boundaries are a sensitive and relevant indicator of incipient range changes. However, general population trends normally observable during a shifting process can be modulated by an overall increase or decrease in abundance due to other confounding factors. According to our conceptual framework, this would correspond to an interaction between the main types of shift patterns (A–G) and pattern H (change in abundance). The pattern displayed by the Ring Ouzel is an example of such an interaction. As suggested by Thuiller et al. (2008), one of the future challenges in species distribution modelling will be the incorporation of demographic parameters that provide information about the probability of local extinction or population increase. This remains a difficult exercise since it requires quantitative information about the rela-

tionship between demography and environment. Range limits, by latitude or with elevation, have received increasing interest lately (e.g. Gaston, 2009), particularly with the increasing research on the impacts of climate change. Also, population trends are today combined with projections of future distribution ranges in order to define vulnerability indexes for species (Gregory et al., 2009).

4.3. Conservation implications

Opinions differ as to whether conservation actions should focus on the centre or on the edges of species distributions. Dispersal is often risky for the individuals and the long-term survival of newly implanted populations depends on having a critical number of individuals that move and assemble together in suitable breeding habitats (Kokko and Lopez-Sepulcre, 2006). From this point of view, conservation efforts should therefore be concentrated at the leading edge of the distribution in order to create suitable habitats along the expansion route. These are not necessarily to be envisaged as corridors, but more likely as ‘stepping stones’ sufficiently close to each other to lie within the species’ dispersal capability (Huntley et al., 2006). Environmental conditions at the centre of the range are the most favourable and therefore support populations with the highest densities according to the centre-periphery hypothesis. Being less susceptible to environmental and demographic stochasticity, core populations are likely to be more persistent than marginal ones. Conservation should thus focus on core populations if the aim is to ensure the long-term persistence of the species (Thomas et al., 2008). Trailing edges have been largely underestimated in the past, but recent findings in phylogeography suggest that populations at trailing edges play an essential role in maintaining long-term stores of genetic diversity and in promoting speciation (Hampe and Petit, 2005). Even though relict populations may show reduced intra-population diversity because of their small size and isolation, high levels of genetic diversity are observable between populations thus leading to high levels of regional diversity (Hampe and Petit, 2005). These are elements that should be considered for an evolutionarily enlightened management strategy (Ashley et al., 2003). Finally, according to Araujo and Williams (2001), complementary hotspots for conservation are to be found within the margins of species’ ranges. Conservation areas at the intersection of several species range margins allow protecting several species at a time. This is especially favourable for species with narrow ranges, i.e. endemic and rare species.

5. Conclusions

The proposed methodology was efficiently applied to the data of the Swiss breeding bird survey and proved to be effective in assessing in a quantitative manner the extent and the type of elevational shift. All seven theoretical patterns described in our catalogue were found in real data either in their full or truncated form. A significant upward shift was identified between the two periods of assessment for 33 breeding bird species out of 95. Changes in mean temperature were observed over the same period even if the cause and effect relationship was not directly established. Further investigations are needed to disentangle the effect of other potential confounding factors that could lead to similar patterns. These factors are for instance habitat barriers, land use/land cover change, species competition or different warming rates along the elevational gradient. Next steps will consider repeating this assessment in a few years’ time in order to see whether change patterns have evolved towards their theoretical final pattern (type G – complete shift). This will probably be the case within homogeneous habitats, but intermediate patterns are likely to persist in situations influenced by other factors. Finally, it would be interesting to apply and

validate our approach for other gradients, taxa and regions of the world.

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