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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.

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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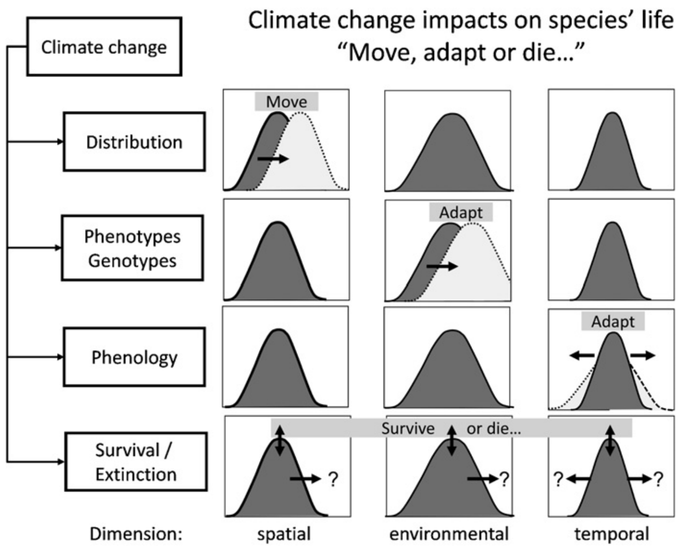

Fig. 1. "Move, adapt or die". Individuals can adapt to climate change by either shifting their distribution in the geographic space or adapting in the environmental or temporal space. Populations that are not able to adapt in one of these dimensions or adapt fast enough can drive their species to extinction.

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