

A weak upward elevational shift in the distributions of breeding birds in the Italian Alps

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ABSTRACT

Aim To test whether bird assemblages are shifting upwards in their elevational distribution in synchrony with current climate warming and/or habitat changes.

Location A gradient of elevation in the Italian Alps (Alta Valsessera, Piedmont).

Methods We used data from two recent atlas surveys performed on a 1 × 1 km grid at an 11-year interval (1992–94 and 2003–05). We modelled the elevational gradient of avifaunal composition, using a sample-based approach, in an effort to detect evidence for an upward elevational shift of bird zonation. Changes in species richness were controlled for. The results from this analysis were compared with those obtained using a species-based approach. Changes in climate and landscape between the two surveys were assessed using local meteorological data and Corine Land Cover maps, respectively.

Results We detected small avifaunal changes between the two surveys: (1) mean elevations increased for the majority of species, but the average change was not significantly different from zero; (2) the species richness increased, but this was mainly due to an increase in sampling effort; and (3) a change in species composition was detected, which was at the limit of significance and corresponded on average to a 29-m upward elevational shift in the distribution of the avifauna. The shift was the same for open land and forest bird communities. During the same period, the mean temperature increased by c. 1 °C in the area, and a slight trend towards vegetation closure by woody plants was detected.

Main conclusions The use of fine-scale breeding bird atlases in mountainous regions, together with ordination methods, provides a sensitive tool to test and measure elevational shifts in species ranges, but the results have to be interpreted carefully. In our case, the observed elevational shift in the distributions of the avifauna cannot unambiguously be attributed to climate warming. This shift is smaller than expected from the regional increase in temperature, which raises the question of how closely bird distributions match climate change.

Keywords

Atlas data, bird assemblages, climate warming, correspondence analysis, elevational gradient, Italy, landscape change, species distribution, species range shifts.

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INTRODUCTION

Numerous studies have demonstrated the impact of recent climate warming on the distributions of specific groups of plants (Grabherr *et al.*, 1994; Pauli *et al.*, 2001; Klanderud & Birks, 2003; Lesica & McCune, 2004; Sturm *et al.*, 2005;

Walther *et al.*, 2005; Beckage *et al.*, 2008; Lenoir *et al.*, 2008), invertebrates, for example butterflies (Parmesan *et al.*, 1999; Thomas *et al.*, 2001; Warren *et al.*, 2001; Hill *et al.*, 2002; Konvicka *et al.*, 2003; Franco *et al.*, 2006; Wilson *et al.*, 2007) and Odonata (Ott, 2001; Paulson, 2001; Hickling *et al.*, 2005), and vertebrates, including anurans (Pounds *et al.*, 1999), fishes

(Roessig *et al.*, 2004; Perry *et al.*, 2005; Wynn *et al.*, 2007), mammals (Frey, 1992; Beever *et al.*, 2003) and birds (see below). Data from these studies, together with the even larger literature on climate-induced changes in phenology, have been used in meta-analyses. Parmesan & Yohe (2003) estimated an average northward latitudinal shift in the Northern Hemisphere of $6.1 \text{ km decade}^{-1}$ for the northern range limits of 99 species (i.e. alpine plants, $n = 9$; butterflies, $n = 31$; birds, $n = 59$). This often quoted value is based on four studies: Grabherr *et al.* (1994, 1995) for plants, Parmesan *et al.* (1999) for butterflies and Thomas & Lennon (1999) for birds. Using a wider selection of published studies, Root *et al.* (2003) also showed an 'overall fingerprint' of climate warming on biodiversity. Most of the cited studies concerned birds and referred to modifications in phenologies and densities. Those referring to range modifications of birds were Thomas & Lennon (1999) for Europe and Pounds *et al.* (1999) for tropical birds.

Evidence of changes in bird distribution patterns that correlate with patterns of current climate warming is essentially based on the approach of Thomas & Lennon (1999). These authors showed that the northern range limits of southern species in the UK had shifted northwards by 18.9 km in 20 years, but they did not observe any shift in the southern margins of northerly species in the same area. Brommer (2004) and Hitch & Leberg (2007) found very similar results, using the same method in Finland and North America, respectively. La Sorte & Thompson (2007) also found similar results for winter ranges of North American birds. Nevertheless, the generality of climate-induced shifts in bird distributions has to be taken with caution, as shown by La Sorte & Thompson (2007) who highlighted possible confounding effects, especially anthropogenic habitat changes.

In order to test for changes in species distribution, elevational gradients can be useful as they can constitute a fine-scale substitute for latitudinal gradients. As 'internal limits' of species distributions (Gaston, 2003), elevational limits are likely to be more dependent on local environmental factors and less influenced by global population dynamics and the dispersal ability of species than are latitudinal limits (Beckage *et al.*, 2008). Substituting one gradient for the other does not imply a strict homology of elevational and latitudinal patterns, although it is often considered that 1 m in elevation is roughly equivalent to 1 km in latitude (Parmesan & Yohe, 2003). Yet there are still only a few studies of changes in the elevational distributions of birds (see Archaux, 2004; Shoo *et al.*, 2006), and only two of them are conclusive in showing an upward shift (Pounds *et al.*, 1999; Tryjanowski *et al.*, 2005).

In this paper we analyse a bird data set obtained by repeated sampling of a valley in the Italian Alps at an 11-year interval. Using ordination methods, we look for any change in the composition of species assemblages (i.e. the lists of the species present in each sample) that would indicate a change in the elevational zonation of birds. By averaging species responses, our sample-based approach has the double advantage: (1) of a lower sensitivity to truncated distributions, compared with

species-based approaches that particularly require knowledge of the lower and upper distributional limits (see Gaston & Blackburn, 1996); and (2) of a lower sensitivity to the variability of range boundaries (La Sorte & Thompson, 2007), as it takes account of all the presence data available along the gradient. We completed this approach by an analysis of the change in the mean elevation of the range of each species. Changes in the elevational distributions of the avifauna were finally compared with changes in climate and landscape in the study area over the same time interval.

MATERIALS AND METHODS

Sampling resolution

The patterns of change in species composition are highly dependent on the sampling resolution, and two opposing pitfalls can be pointed out. On the one hand, adopting too fine a resolution, such as that provided by traditional point counts, would give too much weight to small changes in vegetation structure to the detriment of coarse-scale effects such as climate (Archaux, 2004). On the other hand, adopting too coarse a resolution, such as the classical $10 \times 10 \text{ km}$ atlas grids, would not permit the correct modelling of elevational gradients in topographically complex areas (Shoo *et al.*, 2006). We thus used a $1 \times 1 \text{ km}$ grid, which is an intermediate resolution that has been used in an increasing number of atlas studies. Compared with point counts, this resolution reduces the weight of the vegetation structure by increasing the probability of including several vegetation types in a single sampling unit. Compared with coarser atlas grids, this resolution is to be preferred for the representation of elevational changes, as showed empirically by Dejaifve (1995) in the eastern Pyrenees.

Study area and field work

The study area, the Alta Valsessera, is an alpine valley in the Italian Piedmont. It can be included in a $14 \times 10 \text{ km}$ rectangle (between $45^{\circ}39'11.0'' \text{ N}$, $7^{\circ}59'2.8'' \text{ E}$ in the south-west and $45^{\circ}45'45.7'' \text{ N}$, $8^{\circ}11'29.0'' \text{ E}$ in the north-east), and extends from 550 to 2556 m a.s.l., with a mean elevation of 1370 m a.s.l. (Fig. 1). Each of the 101 square kilometres of the area was surveyed during the breeding season by a single observer; the first time between 1992 and 1994 (Bordignon, 1997) and again in 2003–05 (Bordignon, 2007). This resulted in one of the rare diachronic data sets of European bird assemblages at this resolution, with a mean interval of 11 years between the two periods. The overall durations of the censuses in the two study periods were 702 and 748 h, respectively. The sampling effort was as equally distributed as possible according to elevation (Table 1). However, in the case of elevation the sampling effort also depended on local species richness (decreasing with elevation), species detectability (increasing with habitat openness) and the accessibility of squares. Presence or absence of a species was recorded according to the usual methodology in

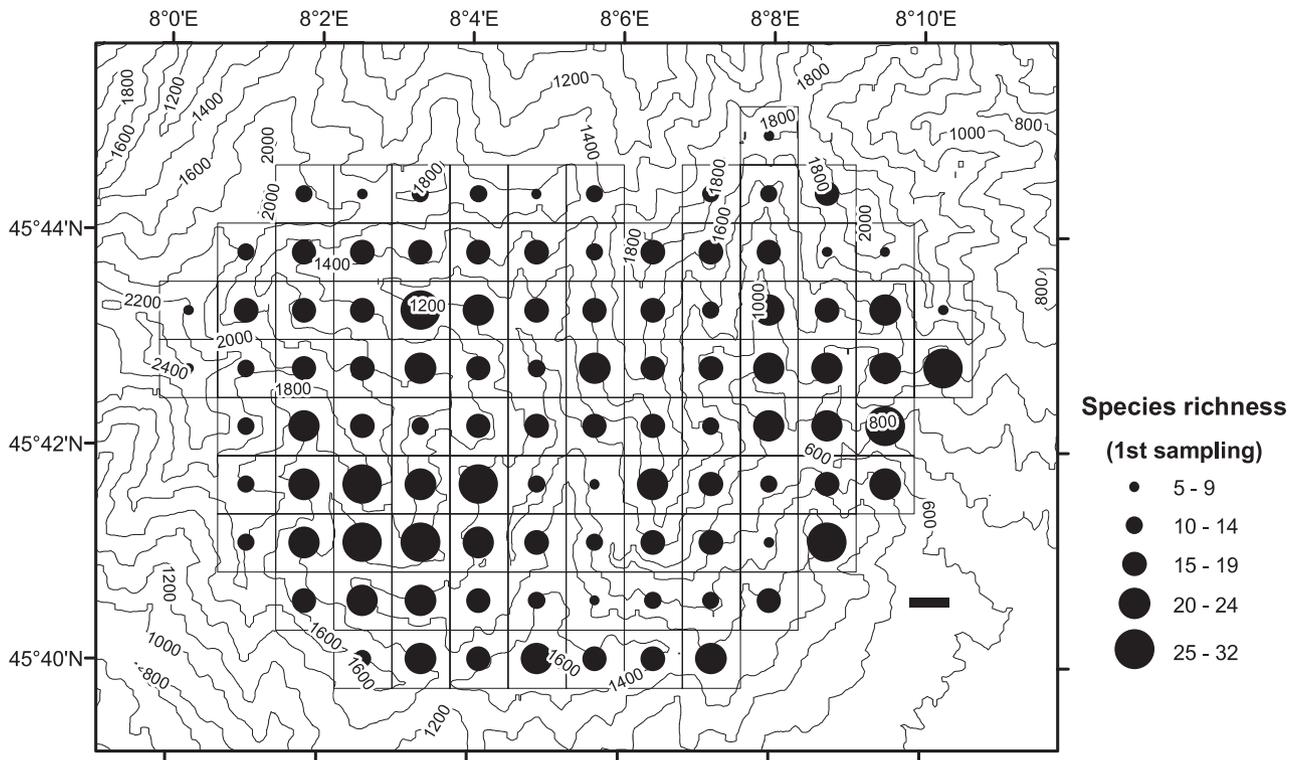


Figure 1 Map of the Alta Valsessera, Italian Alps, showing the grid of the atlas, the topography (isometric curves in m a.s.l), and the distribution of bird species richness across the valley.

Table 1 Between-year distribution of the sampling effort (in hours) of birds in the Alta Valsessera, Italian Alps, and its variations according to elevation (in m), with the corresponding number of squares sampled (No. squares).

Years	Hours	Elevation (m)	Hours	No. squares
First survey				
1992	225	< 1000	180	11
1993	246	1000–2000	418	86
1994	231	> 2000	104	4
	702		702	101
Second survey				
2003	254	< 1000	194	11
2004	245	1000–2000	435	86
2005	249	> 2000	119	4
	748		748	101

atlas surveys. The two surveys recorded 75 species in total, of which 68 species were common to both surveys [the raw data are given in Appendix S1 in Supporting Information; nomenclature follows IOC World Bird Names (Gill *et al.*, 2009)]. We assumed that the distributions of the birds in the atlas corresponded to their breeding distribution. As this assumption is uncertain for species with large home ranges, 13 of them were excluded (*Tachymarpis melba*, *Ptyonoprogne rupestris* and the 11 raptors). A fourteenth species, the elusive wallcreeper (*Tichodroma muraria*), was also excluded because of its

particularly low detectability, which makes its observed elevational range highly variable. The list of species recorded is given in Appendix S2, with the number of squares occupied by each species, and an elevation index \bar{E} (weighted mean inside the available elevation range of the data), taking into account the unequal distribution of the squares at different elevations (high-elevation squares were less numerous). According to the following formula, \bar{E} is based on the mean elevation \bar{e}_i of the 100-m-wide elevational bands in which a species was present, i being the number of the elevation band (from 7 = 700–800 m, to 22 = 2200–2300 m), weighted by the frequency f_i of this species in each band:

$$\bar{E} = \left(\sum_{i=7}^{22} f_i \right)^{-1} \sum_{i=7}^{22} \bar{e}_i \times f_i.$$

The change in the species mean elevations \bar{E} between the two surveys was tested using a Wilcoxon test for paired samples. To examine whether birds in different habitats were shifting differently, the interaction between survey and habitat (forest versus non-forest species, see Appendix S2) was tested using ANOVA.

Considering the possibility that local changes in species ranges may simply result from larger-scale changes in species abundance, we used the 'short-term slope' of species yearly indices at the European scale (period 1990–2005) provided by the Pan-European Common Bird Monitoring Scheme of the European Bird Census Council (EBCC) (Klvanova & Vorisek,

2007) (Appendix S2). This ‘short-term slope’ is the average percentage change per year of the indices over the time period considered. A slope value > 1 means a positive trend; if the slope value is < 1 the trend is negative (Klvanova & Vorisek, 2007). An overall expansion or contraction of the European distributions was tested using a two-sided *t*-test, the null hypothesis being 1 (no change). In order to control for the effect of expansions and contractions of the European distributions of species on their mean elevations in the study area, we regressed the changes in the latter: (1) against the change in number of atlas unit squares occupied by each species (local abundance), and (2) against the short-term trend given by the EBCC (large-scale abundance).

Gradient modelling

We used correspondence analysis (CA) to model the elevational gradient of species composition. This method is well adapted to high beta-diversity gradients (no species range covers our whole elevational gradient) (Prodon & Lebreton, 1994). The two data sets corresponding to the two surveys were merged. Because we wanted to test whether the species observed in the first survey collectively moved upwards in elevational distribution, the five species detected on the second survey (a full list is given in Appendix S2) were excluded from the analysis (the effect of this exclusion on the results was controlled for in a subsequent analysis). The resulting presence–absence matrix [$101 \times 2 = 202$ samples (= squares) $\times 56$ species] was submitted to CA. The scores of the squares on the first axis of the analysis (hereafter *F1*) were regressed against elevation. Because this relationship was nonlinear and heteroscedastic, the *F1* scores were log-transformed: $F1' = \log(-F1 + 1)$. We tested the average shift of the squares on the first axis of the CA between the two dates ($\overline{\Delta F1'}$) against the null hypothesis (no upward shift) by analysis of covariance (ANCOVA), with *F1'* as the dependent variable, and the elevation of the squares (continuous) and the time (coded 0 for the first survey and 1 for the second) as independent variables. A systematic elevational shift in species composition, if any, would be revealed by a significant effect of time. As the hypothesis of an upward shift was directional, we used one-sided tests.

The change in observed species richness between the two surveys was tested using a Wilcoxon test for paired samples. As the number of squares varied with elevation, the consistency of the observed pattern of species richness was controlled for using rarefaction methods with ESTIMATES (Colwell, 2005). We considered consecutive 100-m-wide elevational bands, within which the atlas squares were considered as spatial replicates. Heterogeneity in detection probabilities was taken into account using the Chao estimator (Chao, 1987; Walther & Martin, 2001). ESTIMATES gives random resampled accumulation curves for both the rarefaction method and the estimator. As the number of pooled samples depended on the elevational band considered, we chose to fix a common threshold of three random replicates in each band for the

estimations to be comparable from one band to the other, thus excluding the highest bands (above 1900 m) for which there were fewer than three squares. Wilcoxon tests for paired samples were also computed on the estimators between the two dates.

As open land and forest bird assemblages may show different responses to warming (Jiguet *et al.*, 2006), we also tested the changes in species composition separately for two groups of squares: (1) 28 squares that have more than 50% of the surface area as open land; and (2) 73 squares with more than 50% of closed habitats (i.e. shrublands and woodlands). We computed the surfaces of open versus closed vegetation using the Corine Land Cover map (©EEA, Copenhagen, 1990; available at: <http://dataservice.eea.europa.eu/dataservice/>), including the categories 322 ‘Moors and heathlands’ and 324 ‘Transitional woodland scrub’ in the closed habitats.

Climate and landscape data

Four stations close to the Valsessera area (Albano, Masserano, Varallo, Oropa) provided a complete series of climatological records for the periods 1992–94 and 2003–05. We computed mean monthly temperatures, mean monthly maximum temperatures, mean monthly minimum temperatures and total rainfall per month for the breeding period (March–July). We evaluated the significance of the climate changes between the two sampling periods using three-way ANOVA with station/elevation, month and survey as additive variables. These short-term results were compared with changes over a longer period, using a continuous series for 1970–95 (Cortemiglia, 1999). We evaluated the landscape changes that occurred between 1990 and 2000 using the Corine Land Cover data (©EEA, Copenhagen, 1990, 2000; available at: <http://dataservice.eea.europa.eu/dataservice/>). The resolution was 5 ha (i.e. 1/20th of an atlas-square unit). All analyses were carried out using R software (R Development Core Team, 2005) with the ADE-4 package for ordination methods (Thioulouse *et al.*, 1997).

RESULTS

Climate and landscape changes

The meteorological data restricted to our two sampling periods showed significant increases in mean temperatures ($+1.0$ °C, $P < 0.01$, SE = 0.3) (Fig. 2) and maximum temperatures ($+1.4$ °C, $P < 0.01$, SE = 0.35), but a non-significant increase in minimum temperatures ($+0.5$ °C, $P = 0.06$, SE = 0.28). There was also a significant 40% decrease in the mean monthly rainfall (-57 mm, $P < 0.01$, SE = 17.2). Over the longer period (1970–95), a mean increase in spring temperature of 0.7 °C decade⁻¹ was observed at Torino, while the rainfall in the neighbouring cities of Biella and Varallo showed increases of 2 mm decade⁻¹ and 7 mm decade⁻¹, respectively. Regarding vegetation, comparison of the Corine land-cover data for our two surveys showed a slight trend towards habitat closure on 1.7% of the area, of which 12% resulted from a transition

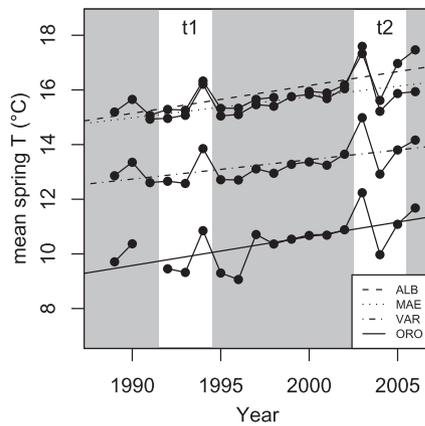


Figure 2 Increase in March–July mean temperature over the period 1989–2006 at four meteorological stations near the Alta Valsessera, Italian Alps (Albano, Masserano, Varallo and Oropa at 155, 243, 470 and 1162 m a.s.l., respectively). Lines are linear regressions. White areas correspond to the time periods of the two surveys (t1 and t2).

from ‘natural grasslands’ to ‘moors and heathlands’ and 88% from the latter categories to ‘forests’.

Distributional changes: species-based analysis

The number of species whose mean elevation increased ($n = 42$) was higher than the number whose mean elevation decreased ($n = 19$), but the overall upward shift was not significantly different from zero (Wilcoxon test for paired samples, $P = 0.31$) (results by species are given in Appendix S2). The ANOVA of the mean elevations of species confirmed that the survey effect on elevation was non-significant ($P = 0.72$) and showed no interaction with species habitat (open land versus forest) ($P = 0.66$).

At the European scale, no overall expansion or contraction of the distributions of the studied species was detected, according to the EBCC indices (t -test, $P = 0.34$). The second ANOVA showed that changes in species mean elevations could not be explained by the specific European trends ($P = 0.66$) or by the changes in the numbers of squares occupied by each species ($P = 0.71$).

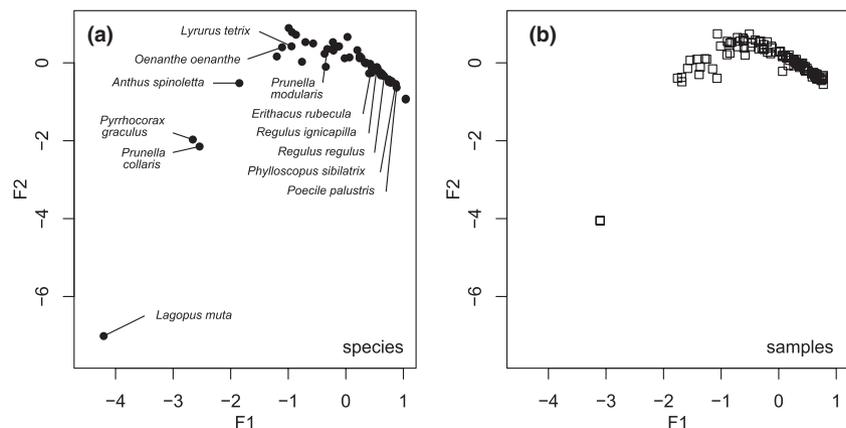
Distributional changes: sample-based analysis

The first CA axis accounted for 20.8% of the total inertia (eigenvalue $\lambda_1 = 0.44$). This axis corresponded to a well-marked and monotonic gradient from low-elevation species (e.g. *Poecile palustris* and *Phylloscopus sibilatrix*) to high-elevation species (e.g. *Lagopus muta* and *Pyrrhonorax graculus*) (Fig. 3a). The second CA axis ($\lambda_2 = 0.23$) showed an arch effect (Fig. 3a,b) characteristic of a strong environmental gradient on the first axis. The scores of the squares on the first axis were significantly correlated with their mean elevation ($r^2 = 0.80$, $P < 0.001$) but the relationship was not linear and the variability in $F1$ increased with elevation (Fig. 4a). After log-transformation of the scores ($F1'$), the relationship was linear and homoscedastic ($r^2 = 0.87$, $P < 0.001$) (Fig. 4b). From the first to the second survey, there was a -0.07 unit shift on the log-transformed axis (Table 2), which means that, at a given elevation, the avifauna gained species of lower elevations and/or lost species of higher elevations. This effect of time on the species composition of the squares was significant (one-sided test, $P = 0.03$). The regression of elevation against $F1'$ (Table 2) showed that this shift on the CA axis was equivalent to a mean upward shift of 29.4 m in the distribution of the avifauna.

The observed species richness showed a decreasing but hump-shaped pattern with elevation in the two surveys. This pattern was correlated with the number of squares at each elevation ($r = 0.88$) (Fig. 5a,b). Nevertheless, rarefaction methods and the Chao estimator showed that this pattern was highly consistent in the interval 700–1900 m a.s.l., even when controlling for the number of samples by elevational band (Fig. 5c,d). Furthermore, the observed richness for three samples according to rarefaction curves represented 83% of the total richness estimate given by the Chao estimator, which suggests that the sampling effort per grid cell was satisfactory. The observed average richness of the squares significantly increased from the first to the second survey ($\overline{\Delta S} = +2.09$ species, $P < 0.001$), and was consistent with the estimated values ($\overline{\Delta S}_{\text{rarefaction}} = +2.10$, $P < 0.01$; $\overline{\Delta S}_{\text{Chao}} = +2.01$, $p = 0.06$).

Similar results were obtained from the subset of open land squares, which corresponded mostly to high elevations (mean

Figure 3 (a) Ordination of the bird species in the Alta Valsessera, Italian Alps, on the two-first axes of the correspondence analysis, highlighting 12 indicative species among 56, from low-elevation (e.g. *Poecile palustris* and *Phylloscopus sibilatrix*) to high-elevation (e.g. *Lagopus muta* and *Pyrrhonorax graculus*) species. (b) Ordination of the 101 atlas squares (first survey only) in the same space. The first axis ($F1$) shows the gradient of elevation (increasing from right to left), the second axis ($F2$) is a quadratic artefact of the first axis (arch effect).



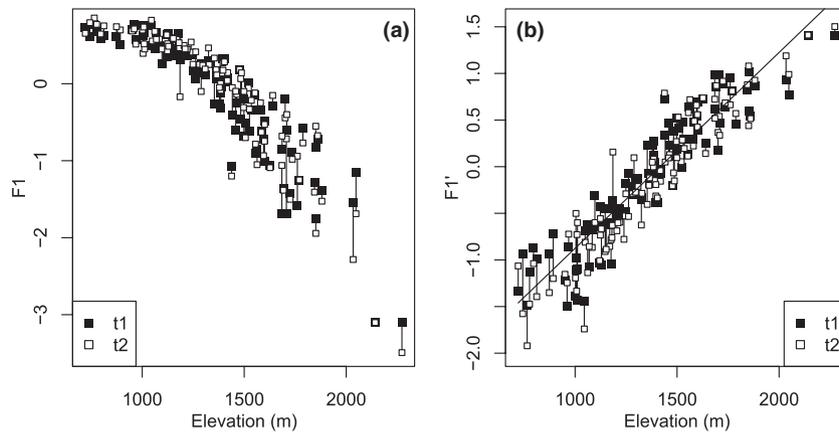


Figure 4 (a) Trajectories of the F1 scores of the atlas squares of the Alta Valsessera, Italian Alps, from the first survey (t1, filled squares) to the second (t2, empty squares), as a function of their respective mean elevation. The relationship is nonlinear, and the variability of F1 increases with elevation. (b) The same relationship linearized: $F1' = \log(-F1 + 1)$. The line shows the linear regression of $F1'$ against elevation ($r^2 = 0.87$). The trajectories of the squares (black to white) show that on average, for a given square/elevation, the avifauna has become less alpine, i.e. has included more low-elevation species.

Table 2 Results of the models used (a) to estimate and test a potential difference in bird species composition between the two surveys (1992–94 and 2003–05) in the Alta Valsessera, Italian Alps, and (b) to estimate the equivalence in elevation (m) of this change in composition.

Variables	Estimate	SE	<i>t</i> -value	<i>P</i> -value
(a) Change in composition with time				
Formula: $F1' \sim \text{elevation} + \text{time}$				
d.f. = 199; $r^2 = 0.87$				
Intercept	-2.98	8.40×10^{-2}	-35.4	$< 2 \times 10^{-16}$
Elevation	2.10×10^{-3}	5.81×10^{-5}	36.1	$< 2 \times 10^{-16}$
Time	-7.12×10^{-2}	3.77×10^{-2}	-1.89	0.03
(b) Correspondence elevation composition				
Formula: $\text{elevation} \sim F1'$				
d.f. = 200; $r^2 = 0.87$				
Intercept	1425.261	8.535	166.98	$< 2 \times 10^{-16}$
$F1'$	412.253	11.478	35.92	$< 2 \times 10^{-16}$

elevation 1681 m a.s.l.), and from the forested squares, which corresponded to lower elevations (mean elevation 1252 m a.s.l.). For open land squares, the effect of time on the species composition was equivalent to a mean upward elevational shift in the distribution of the avifauna of 26.0 m, but it was not significant (ANCOVA, $n = 28$, one-sided $P = 0.15$). For forested squares, the time effect corresponded to an upward shift of 30.7 m, and this was significant ($n = 73$, one-sided $P = 0.02$).

Including the five species that were only detected in the second survey in the analyses did not qualitatively change these results.

DISCUSSION

Main results

Mean temperature in the breeding season increased by +1 °C between the two surveys. In the same time period, the mean

elevation of the majority of the bird species increased. At the community level, a significant overall shift of 29 m towards higher elevations was measured, and the species richness seems to have increased. However, Corine land-cover data also suggest a slight trend towards vegetation closure in the area, which does not allow the bird shift to be interpreted as an unambiguous climatic effect.

Species versus sample approach

Our species-based analysis showed that the species-specific shifts in elevational range between t1 and t2 are non-significant as a whole. This is not surprising because: (1) the data set is small (101 square units only), so some species are only present in a few records; (2) the relatively large within-square altitudinal ranges blur the elevational profiles; and (3) the truncation of many ranges renders their interpretations difficult (Gaston & Blackburn, 1996; Thomas & Lennon, 1999; Parmesan & Yohe, 2003). The main advantage of a

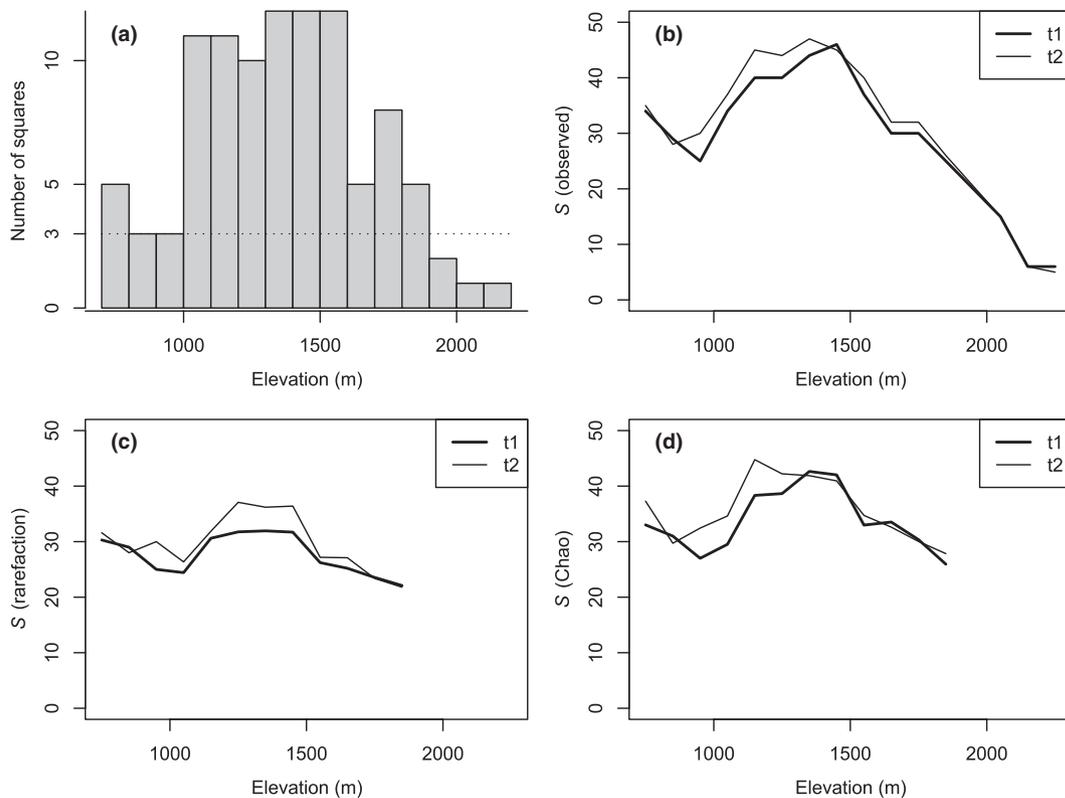


Figure 5 (a) Distribution of the atlas squares in the Alta Valsessera, Italian Alps, according to elevation. The dotted line shows the threshold adopted for the bird species richness estimations (replicates of three squares) that led to the exclusion of the three highest 100-m-wide elevational bands. (b) Total observed species richness (S), by 100-m-wide elevational band (lines) for each survey (t1 and t2). Estimated bird species richness by elevational band, calculated for $n = 3$ random samples, by rarefaction (c), and by the Chao estimator (d).

sample-based approach via ordination methods is the precision gain due to the averaging at the sample scale. We think that the smallness of the elevational shift of the bird zonation justifies this approach. The sample-based approach is also affected to a certain extent by range truncation, but is less sensitive to this problem thanks to the averaging properties of CA (Hill, 1973). We did not use detrended correspondence analysis because of theoretical (Wartenberg *et al.*, 1987, Legendre & Legendre, 1998) as well as empirical (Hirst & Jackson, 2007) controversy, especially concerning the underlying hypothesis of constant turnover along the gradient. Our approach is closely related to the method used by Wilson *et al.* (2007), except that in our case the ordination precedes the regression, whereas in their canonical correspondence analysis (CCA) the regression (linear constraint of the axes by elevation and time) precedes the ordination. However, CCA allows transformations of the environmental variables only, while our log-transformation of axis scores permitted the linearization of the relationship between the scores of the squares and their elevation, making the relationship between species composition changes and elevation more tractable analytically.

Species richness and sampling effort

The increase in species richness between the two surveys may result from several non-exclusive causes: (1) an upward shift of

the species richness gradient as a function of the upward shift of the avifauna (richness globally decreases with elevation); (2) a range expansion of most of the species in the study area; and (3) an increase in sampling effort within squares. Given the smallness of the elevational shift we measured, the first hypothesis alone cannot explain the 14.7% increase in mean species richness in the atlas-square units that we observed from the first to the second survey. The second hypothesis is also unlikely: although the species expansions or contractions in the study area were correlated with their European trends, the overall expansion of the species within the study area from the first to the second survey could not be explained only by larger-scale trends. Although we had no detailed measure of the sampling effort by square, we think that the increase in richness in the second survey is principally due to an increase in sampling efficiency. Variations in sampling effort can have many origins (Ferrer *et al.*, 2006), but in our case they probably resulted from the increased duration of the fieldwork (+6.6%) and from the increased efficiency and knowledge of the area of the observer in the second survey. Sampling effort can bias diversity estimates (Field *et al.*, 2002) and estimated shifts in species range margins (Hill *et al.*, 2002; Shoo *et al.*, 2006). In our case, the overall expansion of species ranges within the study area is likely to be a consequence of increased sampling effort, together with larger-scale trends. But the elevational shift measured is unlikely simply to result from this

increase in richness because: (1) changes in species mean elevations (in the species approach) were not correlated with changes in the numbers of squares occupied by these species; (2) CA is relatively insensitive to variation in species number, except for very large increases in richness (Dargie, 1986); and (3) the potential bias that could result from the interaction between an increase in sampling effort and the theoretical decrease of species richness with elevation (resulting in a larger probability of detection of low-elevation species in the second sampling) seems negligible. Indeed, the real pattern of species richness with elevation is hump-shaped (increasing below 1500 m a.s.l. and then decreasing; Fig. 5). Furthermore, the elevational extent of the squares is too small to create large differences in species richness inside the squares.

A small elevational shift

Our study suggests a small but real upward elevational shift of the bird zonation. This shift is likely to be a response to the 1 °C increase in mean temperature and/or to the change in the vegetation cover between the two surveys. It is smaller than would be expected from 'climatic envelope' models, which suppose a strong and direct relationship between temperature and bird distribution (Pearson & Dawson, 2003; Huntley *et al.*, 2007, 2008). This 1 °C increase in temperature would be equivalent to *c.* 200 m in elevation, based on an average gradient of -0.5 °C per 100 m, whereas the observed effect on the avifauna is four to eight times lower. The observed increase of 1 °C over the period 1992–2005 (*c.* 0.9 °C decade⁻¹) was, however, exacerbated by the 2003 heat wave. The world mean increase in temperatures was about +0.07 °C decade⁻¹ for the last century (IPCC, 2007), and only about +0.15 °C decade⁻¹ in the Alps for the period 1906–2005 [source: Coarse Resolution Subregional Mean climate time series of the Greater Alpine Region (CRSM), available at <http://www.zamg.ac.at/alp-imp/>, accessed 25 August 2008]. However, warming has accelerated since 1970, and is slightly greater in spring. The mean increase in temperatures was actually +0.60 °C decade⁻¹ in the breeding period (March–July) in the Alps for the period 1970–2005 (CRSM). The increase in temperature that we observed in the Valsessera area is thus in the same order of magnitude.

Concerning habitat, despite the low precision of the Corine land-cover data, we observed a slight trend towards vegetation closure in our study area. Field observations also showed that the grass was growing taller in ungrazed meadows. This trend towards vegetation closure may also contribute to an upward elevational shift in the bird zonation. In this context, the smallness of the shift we observed can be explained by several non-exclusive hypotheses. First, the elevational ranges of birds may be mostly constrained by the minimum temperatures, particularly in early spring, since we showed that the minima had changed much less than the maxima between the two surveys. Second, the avifauna response may be time-lagged, as shown for butterflies (Hill *et al.*, 1999; Burton, 2003; Fleishman & Mac Nally, 2003; Wilson *et al.*, 2005). This may be the case if bird species are more limited by their

habitat than by their climatic requirements, which could be wider than currently observed. The ecotones between different habitat types along the elevational gradient, in particular the upper forest limit, may constitute barriers that hinder rapid shifts in bird ranges. Several studies have shown time-lags in the response of the vegetation to climate change (Davis, 1989; Payette *et al.*, 1989; Wardle & Coleman, 1992; Grabherr *et al.*, 1994; Keller *et al.*, 2000; Kullman, 2001; Sato *et al.*, 2007), especially for long-lived trees and for ubiquitous plants (Lenoir *et al.*, 2008). However, when we considered the open land and the forests separately, the upward shift was similar in the two compartments. The upper limit of trees is thus unlikely to be the main factor controlling the elevational shift of birds in our area.

The range shifts described in the literature are usually stated in metres per year or decade, although measurements in metres per degree Celsius would make the comparisons between different time periods easier. The shift that we measured, about 29.4 m for 1 °C and for 11 years (i.e. *c.* 26.7 m decade⁻¹), is congruent with the upward shifts measured in plants (27.8 m decade⁻¹ in Walther *et al.*, 2005; 29 m decade⁻¹ in Lenoir *et al.*, 2008), but two to three times smaller than the shifts observed in butterflies (*c.* 85 m decade⁻¹ in Wilson *et al.*, 2007). If we accept the rule of thumb that 1 m in elevation is equivalent to 1 km in latitude (Parmesan & Yohe, 2003), our shift is also consistent with the recent northward shifts measured for birds: 9.5 km decade⁻¹ for the UK in Thomas & Lennon (1999), 15.7 km decade⁻¹ for Finland in Brommer (2004) and 23.5 km decade⁻¹ for North America in Hitch & Leberg (2007). These values concerned northern limits of distributions; southern limits seem to change more slowly, if at all. La Sorte & Thompson (2007) found similar results for winter ranges in North America (4.5 and 14.8 km decade⁻¹, respectively, for the species centres of occurrence and for their northern boundary).

CONCLUSIONS

Our study shows that fine-scale atlas data can be invaluable in assessing species range shifts resulting from environmental change. Furthermore, this kind of analysis offers possibilities for the construction of synthetic indicators of distribution changes at a regional scale. With this aim, it is worth repeating the surveys at 10- to 20-year intervals, carefully controlling for changes in sampling effort and in habitat. For the time being, the response of birds to warming seems to be less strong and/or rapid than expected from climatic models. Until a better understanding of the underlying mechanisms is achieved, predictions based only on 'climatic envelope' models should be either validated or considered cautiously (Araújo *et al.*, 2005; Beale *et al.*, 2008).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Raw presence–absence data on bird species from the two atlas surveys in the Valsessera, Italian Alps

(1992–94 and 2003–05), used for the community and for the species approaches.

Appendix S2 List of the bird species considered in the ordinations, together with the number of squares they occupied in the two surveys; their mean elevation index \bar{E} , computed from the available data (see Materials and Methods); their European trends according to the EBCC Pan-European Common Birds Monitoring Scheme; and their classification as forest and non-forest species.

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