

Alpine bird distributions along elevation gradients: the consistency of climate and habitat effects across geographic regions

Dan Chamberlain¹ · Mattia Brambilla^{2,3} · Enrico Caprio¹ · Paolo Pedrini² · Antonio Rolando¹

Received: 1 September 2015 / Accepted: 19 April 2016 / Published online: 30 April 2016
© Springer-Verlag Berlin Heidelberg 2016

Abstract Many species have shown recent shifts in their distributions in response to climate change. Patterns in species occurrence or abundance along altitudinal gradients often serve as the basis for detecting such changes and assessing future sensitivity. Quantifying the distribution of species along altitudinal gradients acts as a fundamental basis for future studies on environmental change impacts, but in order for models of altitudinal distribution to have wide applicability, it is necessary to know the extent to which altitudinal trends in occurrence are consistent across geographically separated areas. This was assessed by fitting models of bird species occurrence across altitudinal gradients in relation to habitat and climate variables in two geographically separated alpine regions, Piedmont and Trentino. The ten species studied showed non-random altitudinal distributions which in most cases were consistent across regions in terms of pattern. Trends in relation to altitude and differences between regions could be explained

mostly by habitat or a combination of habitat and climate variables. Variation partitioning showed that most variation explained by the models was attributable to habitat, or habitat and climate together, rather than climate alone or geographic region. The shape and position of the altitudinal distribution curve is important as it can be related to vulnerability where the available space is limited, i.e. where mountains are not of sufficient altitude for expansion. This study therefore suggests that incorporating habitat and climate variables should be sufficient to construct models with high transferability for many alpine species.

Keywords Altitude · Climate change · Model performance · Model transferability · Variation partitioning

Introduction

Many species have shown recent shifts in their distributions in response to environmental change, in particular climate change (Parmesan and Yohe 2003; Chen et al. 2011), mostly towards higher latitudes and/or altitudes (Walther et al. 2002). Investigating the effect of climate change on biodiversity and ecosystems has thus become a key ecological research area, often underpinned by modelling approaches that seek to determine relationships between species occurrence or population dynamics and climate, and to predict the future response to climate change (Bellard et al. 2012). Such approaches have been frequently applied to species distributions, which may be affected by a range of factors, but in particular by climatic variation and habitat availability. The effect of environmental factors such as climate, topography and land-cover are often considered for modelling species distributions (Guisan and Thuiller 2005), typically using correlative models, which

Communicated by Ola Olsson.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-016-3637-y) contains supplementary material, which is available to authorized users.

✉ Dan Chamberlain
dan.chamberlain99@gmail.com

- ¹ Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Via Accademia Albertina 13, 10123, Turin, Italy
- ² Museo delle Scienze di Trento, Sezione Zoologia dei Vertebrati, Corso del Lavoro e della Scienza 3, 38122 Trento, Italy
- ³ Fondazione Lombardia per l'Ambiente, Settore Biodiversità e Aree Protette, Largo 10 Luglio 1976, 1, 20822 Seveso, MB, Italy

relate the occurrence of a species to a set of environmental predictors, allowing for the re-projection of species occurrence under new, future environmental conditions. A critical issue in this approach is represented by the extent to which a given model can be generally applied over different spatial and temporal contexts (i.e. model transferability). As it is impossible to test predictions on future data, model performance could be evaluated by means of a space-for-time substitution (Araújo and Rahbek 2006), using data from different regions and cross-checking models (e.g. Randin et al. 2006).

In mountain environments, where species distributions are often limited by temperature, increased warming has been accompanied by upward shifts in the distributions of many species, e.g. plants (Lenoir et al. 2008; Harsch et al. 2009), butterflies (Wilson et al. 2005), birds (Tryjanowski et al. 2005; Reif and Flousek 2012) and small mammals (Moritz et al. 2008). For several cold-adapted species, and in particular for those living in high-altitude open habitats, such shifts may lead to a reduction in range as areas of suitable climate and habitat become smaller and more fragmented as they are pushed towards mountain summits. Such effects may in the future have serious consequences for mountain biodiversity (Sekercioglu et al. 2008; Dirnböck et al. 2011; Chamberlain et al. 2013; Maggini et al. 2014; Brambilla et al. 2015), and indeed there is evidence that birds of high altitude are already showing declines (Lehikoinen et al. 2014; Flousek et al. 2015). It should, however, also be acknowledged that mountain biodiversity may be under other anthropogenic pressures (Chamberlain et al. 2016), such as changes in grazing regimes (Laiolo et al. 2004) and increasing disturbance (Caprio et al. 2011), although evidence for the effects of these factors, either positive or negative, on mountain bird population trends is so far lacking.

Patterns in species occurrence or abundance along altitudinal gradients often serve as the basis for detecting changes (e.g. Maggini et al. 2011; Pernollet et al. 2015) and assessing future sensitivity (Chamberlain et al. 2013) of mountain species to climate change. Generally speaking, investigating elevational range limits is critical to understanding distributional patterns, and is needed to predict the likely effects of (and responses to) climate change in mountain species (Gifford and Kozak 2012). The altitudinal transect approach is useful for studying potential climatic effects on species distributions, because the altitudinal gradient provides a space-for-time substitution when considering conditions along the gradient (Hodkinson 2005), while complications involving broader-scale biogeographic processes, evident in geographic distribution shift studies, are also largely avoided (Rahbek 2005). However, given that conditions change rapidly over fine spatial scales along altitudinal gradients, data collected need to be of a sufficiently high resolution to be useful for monitoring and modelling

distribution shifts (Chamberlain et al. 2012). In areas with strong altitudinal gradients, the use of models developed at finer spatial scales is required to avoid overestimation of habitat loss due to climate change (Randin et al. 2009).

Birds are undoubtedly a well-studied group in terms of the impacts of environmental change generally. However, relative to other habitats, the factors that dictate bird distributions, population sizes and population trends in mountains are less well known (EEA 2010), largely due to the logistical constraints of working in such an environment (Chamberlain et al. 2012). Even basic, but nonetheless essential, information on species distributions along altitudinal gradients is scarce. In Europe, there is very little information on variations in bird distributions along altitudinal gradients in mountains, with a few exceptions (ring ouzel *Turdus torquatus*, marsh tit *Poecile palustris* and bullfinch *Pyrrhula pyrrhula*, Maggini et al. 2011; water pipit *Anthus spinoletta*, Melendez and Laiolo 2014; ptarmigan *Lagopus muta*, Pernollet et al. 2015). There is therefore a need to quantify the distribution of more species along altitudinal gradients in order to act as a fundamental basis for future studies on environmental change impacts. Furthermore, if models of altitudinal distribution are to be used for drawing inferences on the wider impacts of environmental change, then it is necessary to know the extent to which altitudinal trends in occurrence are consistent across geographically separated areas, and therefore the extent to which a model derived from one area can be used to make predictions in another (i.e. model transferability; Whittingham et al. 2007; Schaub et al. 2011). Finally, it would be useful to know whether relatively simple models based on altitude alone are sufficient to describe bird distributions along the gradient, or whether environmental variables (habitat and climate) are essential elements to modelling elevational distributions of birds.

This paper has three aims: (1) to describe the distributions of birds along altitudinal gradients in the European Alps at relatively high altitude (c. 1700–3100 m) and to determine whether they vary between two geographically separated regions; (2) to assess the performance of models derived across the whole study area in order to determine whether bird distributions can be better explained by variations in altitude, habitat cover or climate, or combinations of these, along the gradient; and (3) to assess the extent of unexplained variations attributable to regional differences (i.e. whether combinations of habitat and climate are sufficient to explain regional differences).

Materials and methods

Fieldwork was undertaken in two geographically distinct alpine areas in northern Italy, Piedmont and Trentino

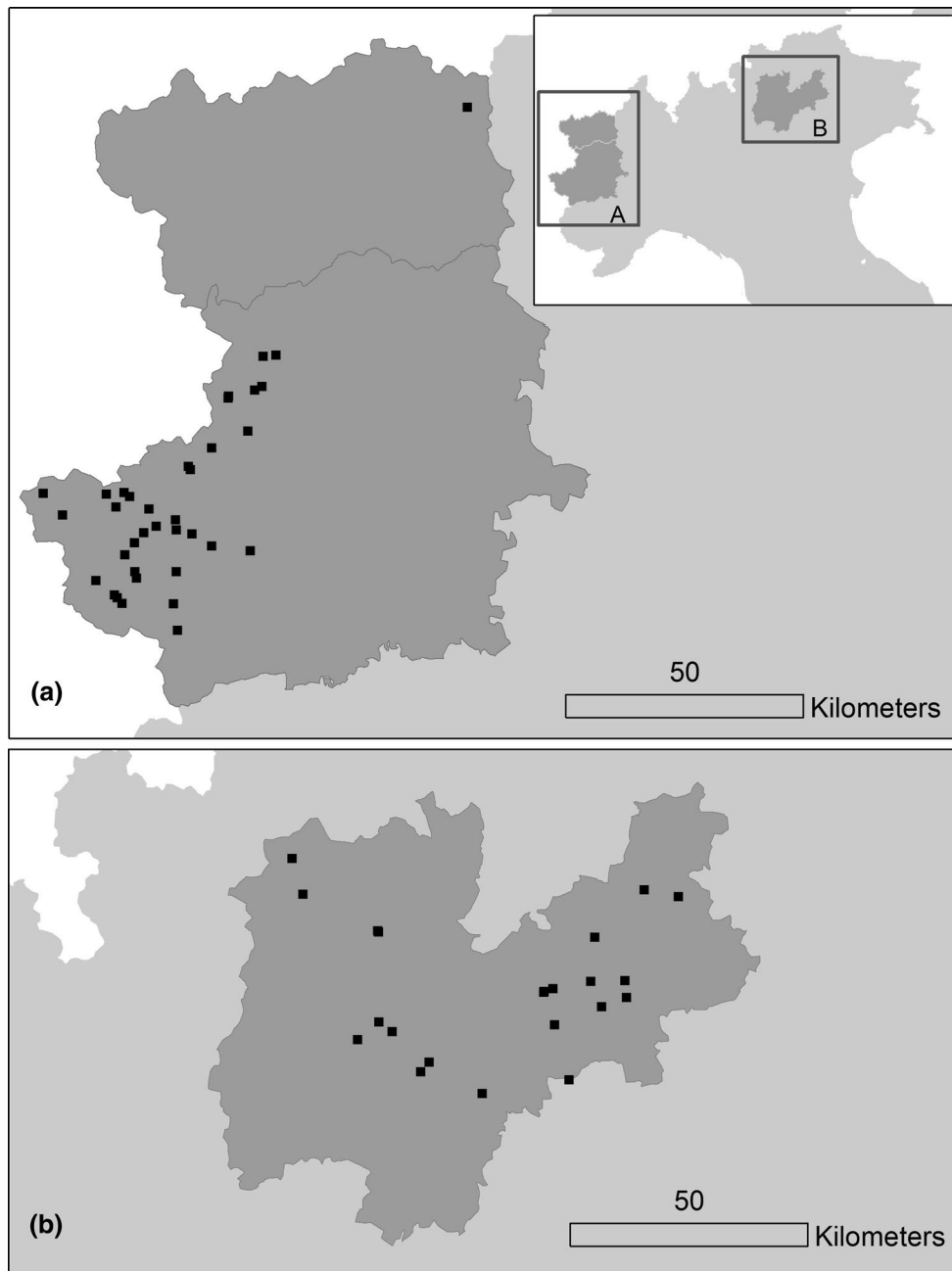


Fig. 1 Location of the transects in the provinces of Turin (Piedmont) (a) and Trentino (b)

(Fig. 1). In both areas, dominant shrub species are typically juniper *Juniperus communis* and *Rhododendron* spp. The natural treeline occurs at around 2200–2300 m, although this varies depending on local conditions. Furthermore, in many areas, the treeline is lower due to the impacts of livestock grazing. Grasslands occur throughout both areas, consisting of seasonal pastures and higher-altitude alpine meadows. Scree and rocky areas are common, especially at higher altitudes, and are typically dominant above c. 2700 m. In Piedmont, the dominant tree species is European

larch *Larix decidua*, whereas in Trentino it is spruce *Picea abies*. In general, trends in the cover of major habitat types were similar between the two regions, although there were some notable differences, e.g. greater forest cover at lower altitudes (c. 1700–1900 m), and higher rock cover throughout the gradient in Trentino (Fig. S1 in the Electronic Supplementary Material, ESM). There was little difference in temperature between the two regions, although there was markedly higher precipitation in Piedmont (Fig. S2 in the ESM).

Bird and environmental data

Sampling took place over 3 years in Piedmont (2010–2012), and in a single year, 2011, in Trentino. Identical field survey methods were undertaken in each region. Point counts were carried out along transects, which were selected based on accessibility, and which were usually (although not always) along footpaths. Transects were separated by at least 1 km. A minimum altitude of 1700 m was defined in both areas. In the field, the start of each transect was the closest suitable point above 1700 m in altitude. Suitable points were those without any obvious disturbance (e.g. occupied human habitation, livestock) or where detectability may have been affected (e.g. large cliffs, noisy streams in spate) within 100 m. Point locations were recorded on a handheld Garmin GPS. The next selected point along the transect was then the next suitable location after a minimum distance of 200 m (i.e. to ensure no adjacent points were overlapping). While a random selection of points was not practically feasible, this systematic technique at least avoided any possible selection based on the birds themselves.

Point counts (Bibby et al. 2000) were carried out from mid-May to mid-July, using a 10-min count period preceded by a 5-min settling period. At each point, the observer recorded all birds seen and heard within a 100-m radius (estimated with the aid of a laser range finder). Simple habitat data were also collected at each point, including the percentage cover of canopy (i.e. vegetation above head height), shrubs (woody vegetation below head height), open grassland (i.e. no canopy), bare rock (including scree and other unvegetated areas) within a 100-m radius, and the number of mature trees (approximately greater than 20 cm in diameter) within a 50-m radius (in forested areas, it was not possible to count trees at a greater distance). Point counts commenced 1–1.5 h after sunrise and continued until 1300 hours. No surveys were undertaken in wet or excessively windy conditions. A total of 453 points were surveyed on 56 transects: 271 points from 34 transects in Piedmont and 182 points from 22 transects in Trentino.

Climate data were extracted from WorldClim (Hijmans et al. 2005), including five temperature variables and five precipitation variables. The temperature variables were: mean annual monthly temperature, maximum and minimum monthly temperature over the whole year, mean monthly temperature for the breeding season and mean monthly temperature for the winter. The precipitation variables were: total annual precipitation, maximum and minimum monthly precipitation over the whole year, mean monthly precipitation for the breeding season and mean monthly precipitation for the winter. Topographic data (aspect and slope) were extracted from a digital terrain model of northern Italy at a 1-ha scale, and determined at

the point level by calculating mean values of the squares overlapping each 100-m-radius point count location. Both easting and northing were considered, which were expressed as an index equal to $\cos(A)$, where A is the aspect (east or south) expressed in radians (following Bradbury et al. 2011); a value of 1 represents facing directly south or east, and -1 represents facing directly north or west. Altitude (expressed in m) at each point was recorded by the GPS in the field. Slope was measured in degrees. (A full list of environmental variables considered in the modelling procedure is presented in Table S1 in the ESM.) All variables were standardised to a mean of zero prior to analysis. All analyses were carried out in R 3.01 (R Development Core Team 2013).

General modelling approach

The presence of a given species detected at each point count location was used to analyse the distribution of alpine birds along the altitudinal gradient. Initial analyses suggested that species with occurrence rates $<15\%$ had consistently poor model performance (see below) and, often, problems with model fitting (e.g. lack of convergence), and therefore a species was only considered if it occurred on at least 15% of the sample for the relevant open or closed habitat type. For each species, we considered only the likely nesting habitat, which we defined broadly into ‘closed’ and ‘open’ habitats following Chamberlain et al. (2013). The former was defined as any habitat where the cover of canopy + shrubs > 0 . Open habitats were defined as any habitat where the number of mature trees was zero; these species to some extent tolerate some woody vegetation (e.g. young trees, shrubs), but tend to avoid mature trees and other vertical structures. Applying this ‘habitat mask’ had the advantage of focussing just on likely breeding habitat (and thus omitting isolated records of non-breeding and/or dispersing individuals) and omitting redundant zeros which may cause model-fitting problems (Zuur et al. 2009). Black redstart *Phoenicurus ochrurus* was recorded in a range of habitats, so, for this species, the entire dataset was considered.

Bird distributions were analysed using logistic regression with the lme4 package in R (Bates et al. 2015). Multiple visits were made to some points in Piedmont, which was accounted for by using a successes/failures syntax (Crawley 2013). Transect was fitted as a random factor in all models to account for non-independence of points along the same transect. In all cases, model fitting was preceded by a procedure to detect and reduce the effect of collinearity between the variables. This was done by calculating variance inflation factors (VIFs) for the variables and sequentially deleting the variable with the highest VIF, as

described by Zuur et al. (2009), using a cut-off value of 3.0. The final variable sets, with minimal levels of collinearity, were used for model averaging and variation partitioning (see below).

Modelling altitudinal trends across regions (aim 1)

In order to determine variations in species distributions in relation to altitude and region, a statistical hypothesis testing framework was adopted, with the null hypothesis that bird species were distributed randomly in relation to altitude and region. Both linear and quadratic terms were included in the models. ‘Region’ was included as a two-level factor (Piedmont or Trentino). The interactions between region and both altitude and altitude² were included in the initial model for each species, in which significant interactions indicate differing trends along the gradient between regions. These initial models were subject to a model reduction procedure whereby non-significant terms were sequentially dropped from a model until only significant ($p \leq 0.05$) terms remained.

Assessing model performance (aim 2)

Altitude may be a proxy for a multitude of effects operating at various scales (Hodkinson 2005). The extent to which either habitat, climate or altitude, either alone or in combination, could predict bird distributions was assessed by testing the performance of different models derived from a randomly selected dataset from 70 % of observations against the observed distributions from the remaining 30 % of observations. Models were derived from the model dataset (i.e. 70 % of the observations) for altitude (ALT), habitat (HAB; habitat cover and topographic variables), climate (CLIM; temperature and rainfall) and combined habitat and climate (HAB + CLIM) variables for each species (see Table S1 in the ESM for a complete list of variables in each set). In each case, variables causing inflated VIFs (see above) were omitted. Non-linear effects were included in models following visual assessment of scatterplots (following Zuur et al. 2009). Altitude and temperature and altitude and precipitation (which were highly collinear) were not modelled together. In total, there were ten climate variables considered, and there was also a high level of collinearity within this dataset. A preliminary step was therefore undertaken to select the best fitting temperature and best precipitation variable for each species by comparing univariate models (i.e. only one climate variable at a time) using AIC. The climate variables used in CLIM and HAB + CLIM

models were then those whose univariate models had the lowest AIC (see the ESM for further details).

For each model type (ALT, HAB, CLIM, HAB + CLIM), a model averaging approach, considering all combinations of models, was used to derive parameter estimates using the shrinkage method with the MuMIn package in R (Bartoń 2013). These were then used to predict the probability of presence in the test dataset (i.e. 30 % of observations). Observed presences were compared with the probability estimates from the model, and AUC was calculated from the package PresenceAbsence (Freeman 2007) to test the ability of the models to correctly predict observed presence. Models with $AUC < 0.70$ are considered to have limited predictive capacity (e.g. Swets 1988). To aid interpretation, we further classified models as having adequate ($0.70 \leq AUC < 0.80$) and good ($AUC \geq 0.80$) predictive capacity.

Variation partitioning (aim 3)

The categorical variable ‘region’ was added to HAB + CLIM models from the above procedure; these models containing habitat, climate and region were defined as ‘full’ models. Variation partitioning for generalized linear models (e.g. Ficetola et al. 2007) was then carried out on the full models in order to assess the amount of variation explained by HAB and CLIM variables, and by the categorical variable region. A large amount of variation attributable to region indicates that overall differences between regions are not attributable to the other model variables (i.e. HAB and CLIM). Marginal R^2 values (fixed effects) for generalized linear mixed effects models (Nagakawa and Schiezzeth 2013) were calculated for the full model, and for HAB variables, CLIM variables, region, and combinations of these for each species using the r.squareGLMM command in R package MuMIn (Bartoń 2013). The variation attributable to each component was determined using the approach outlined by Legendre (2008). Altitude was not considered in this analysis due to strong collinearity with climate variables.

Results

The occurrence rates for the commonest species (present on 15 % of points in both regions) are shown in Table 1, along with the classification into ‘open’ and ‘closed’ habitat species. There were 10 species that were recorded on at least 15 % of points in both regions (for a total of 847 records relative to those species).

Table 1 Species occurrence (proportion of points where present) for species which occurred on at least 15 % of points in at least one region

Species	Habitat	Total	<i>n</i>	Piedmont	<i>n</i>	Trento	<i>n</i>
Water pipit <i>Anthus spinoletta</i>	Open	0.46	246	0.57	140	0.30	106
Wren <i>Troglodytes troglodytes</i>	Closed	0.22	305	0.26	191	0.17	114
Dunnock <i>Prunella modularis</i>	Closed	0.30	305	0.20	191	0.46	114
Robin <i>Erithacus rubecula</i>	Closed	0.15	305	0.15	191	0.18	114
Black redstart <i>Phoenicurus ochrurus</i>	All	0.21	453	0.24	271	0.16	182
Wheatear <i>Oenanthe oenanthe</i>	Open	0.35	246	0.45	140	0.22	106
Chiffchaff <i>Phylloscopus collybita</i>	Closed	0.21	305	0.18	191	0.25	114
Coal tit <i>Periparus ater</i>	Closed	0.28	305	0.27	191	0.28	114
Willow tit <i>Poecile montanus</i>	Closed	0.30	305	0.37	191	0.18	114
Chaffinch <i>Fringilla coelebs</i>	Closed	0.42	305	0.54	191	0.21	114

Species were defined according to general nesting habitat (see text for details). Species occurrence is based on the total points surveyed per habitat. *n* is the number of points for each habitat and region

Altitudinal trends across regions (aim 1)

All ten species considered showed significant variation in probability of occurrence in relation to altitude (Fig. 2). Two, robin *Erithacus rubecula* and willow tit *Poecile montanus*, showed a significant interaction between region and altitude. Robin showed significant linear decreases in probability of occurrence with altitude in both regions, although the decrease was steeper in Trentino compared to Piedmont (Fig. 2d). Willow tit showed a non-linear relationship with altitude in Piedmont, occurrence peaking at c. 1900 m, but a decline in Trentino (Fig. 2i). Overall probability of occurrence varied significantly between regions for several species and was higher for water pipit, wheatear *Oenanthe oenanthe* and chaffinch *Fringilla coelebs* in Piedmont and higher for dunnock *Prunella modularis* and robin in Trentino. In general, therefore, trends across the elevation gradient were similar for most species in the two regions, although overall occurrence rates often varied.

Based on Fig. 2, the species can be broadly defined into lower altitude species (those showing a decline along the gradient), transition zone species (those showing a non-linear trend with a peak in probability of occurrence around the treeline) and open habitat species (either showing a peak in probability of occurrence in open grassland or an increase with altitude). The majority of species were closed habitat species showing a significant decrease with altitude: wren *Troglodytes troglodytes*, robin, chiffchaff *Phylloscopus collybita*, coal tit *Periparus ater* and chaffinch (Fig. 2). In addition to willow tit in Piedmont, dunnock also showed an intermediate peak at the transition zone (c. 1900 m; Fig. 2c). Both open habitat species considered showed a non-linear trend, with a peak in probability of occurrence at intermediate altitudes: water pipit (c. 2205 m; Fig. 2a) and wheatear (c. 2350 m; Fig. 2f). Black redstart was the only species considered initially to be a

habitat generalist and therefore analysed across all habitats. This species showed a peak in probability of occurrence at relatively high altitudes (c. 2650 m; Fig. 2e) suggesting it was more of an open habitat species. However, when the species was analysed considering only open habitats, there was no significant effect of altitude, suggesting that the significant variation in Fig. 2e is largely driven by the contrast in species occurrence between open and closed habitats.

Model performance (aim 2)

AUC values for ALT, HAB, CLIM, and combined habitat and HAB + CLIM models are given in Table 2 (details of the highest ranked model for each species are given in Table S2 in the ESM). For black redstart, model fits were considered inadequate (AUC < 0.70) for all models. There were also three species, dunnock, wheatear and chiffchaff, for which no models were classified as 'good'. Forest species tended to have better performing models than species of more open habitats. Considering the best performing model (i.e. the highest AUC value, regardless of classification) for each species, it was clear that models which included habitat were better than those without, and in particular combinations of habitat and climatic variables (HAB + CLIM models) tended to have relatively high AUC values (Fig. 3a). When considering models classified according to AUC (i.e. poor, adequate or good), again it was clear that HAB + CLIM models tended to perform best, followed by HAB models. ALT and CLIM models performed less well (Fig. 3b).

Variation partitioning (aim 3)

Variation partitioning was used to assess the contribution of each of HAB variables, CLIM variables and region in the

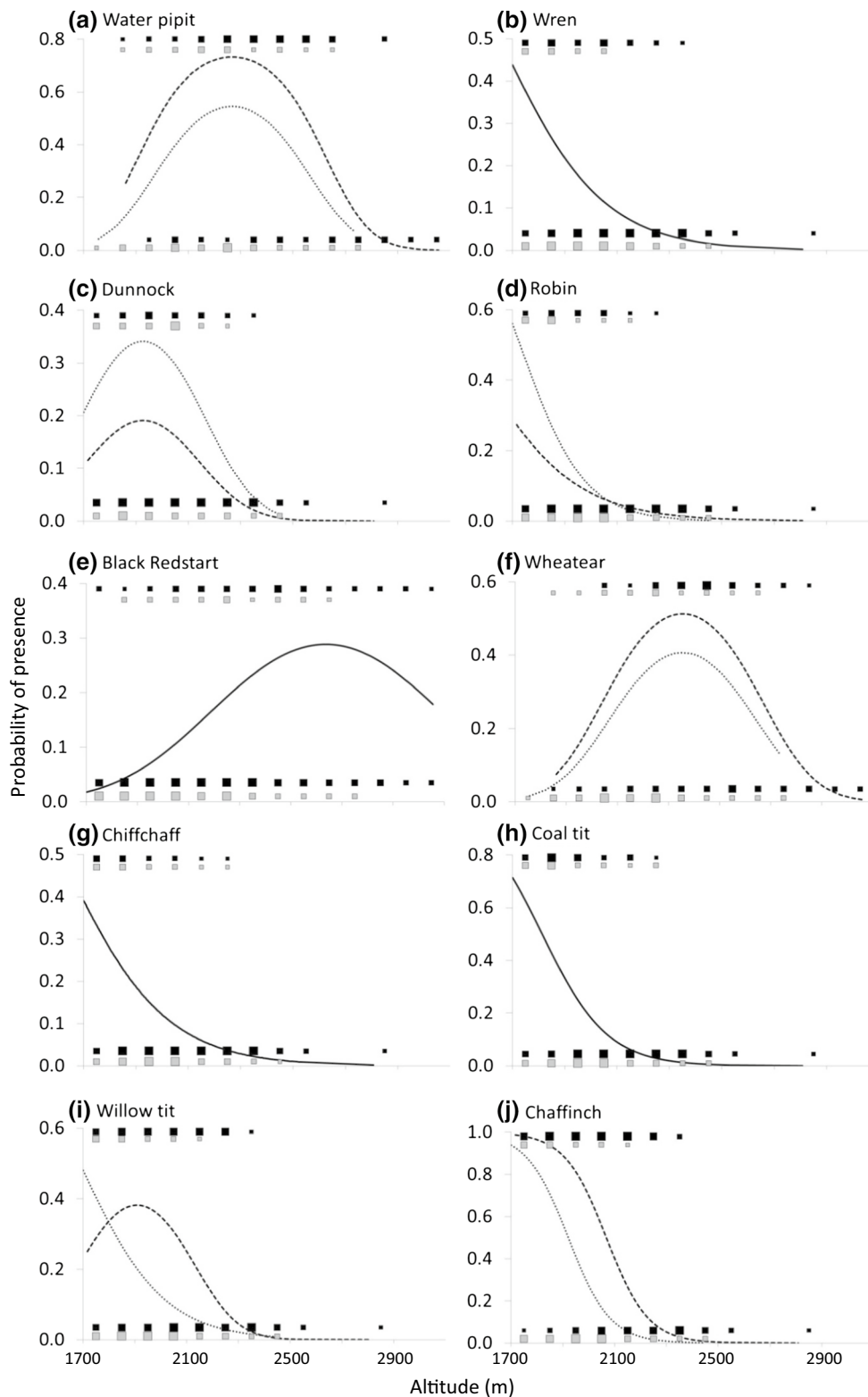


Fig. 2 Trends in the probability of occurrence in relation to altitude. Where there was an effect of region, or where a species was analysed in only one region, *dashed lines* indicate Piedmont and *dotted lines* indicate Trentino. A *solid line* indicates a trend fitted from both regions combined (i.e. where there was no significant difference). Observed presences and absences are shown as *black squares*

(Piedmont) and *grey squares* (Trentino) on the y-axis maximum and minimum, respectively. These are summarised into frequencies for each category (region and presence/absence) calculated at each 100 m interval. *Symbol size* is representative of the number of points, divided into five groups, where 1 (i.e. the smallest) = 1 point, 2 = 2–5 points, 3 = 6–10 points, 4 = 11–15 points and 5 = 16 points or greater

Table 2 Performance of different models describing probability of occurrence of species along altitudinal gradients

Species	ALT	HAB	CLIM	HAB + CLIM
Water pipit	<i>0.74 ± 0.06</i>	<i>0.74 ± 0.06</i>	<i>0.79 ± 0.05</i>	0.84 ± 0.05
Wren	<i>0.71 ± 0.06</i>	0.67 ± 0.07	0.68 ± 0.07	0.57 ± 0.07
Dunnock	0.65 ± 0.06	0.56 ± 0.06	<i>0.75 ± 0.05</i>	<i>0.76 ± 0.05</i>
Robin	<i>0.78 ± 0.06</i>	<i>0.76 ± 0.07</i>	0.64 ± 0.07	<i>0.77 ± 0.06</i>
Black redstart	0.59 ± 0.05	0.67 ± 0.05	0.65 ± 0.06	0.64 ± 0.06
Wheatear	<i>0.74 ± 0.06</i>	0.51 ± 0.08	<i>0.75 ± 0.06</i>	0.65 ± 0.07
Chiffchaff	0.60 ± 0.07	<i>0.76 ± 0.06</i>	0.60 ± 0.06	<i>0.74 ± 0.06</i>
Coal tit	0.87 ± 0.04	0.83 ± 0.05	<i>0.77 ± 0.05</i>	0.89 ± 0.05
Willow tit	0.68 ± 0.06	0.87 ± 0.04	0.59 ± 0.06	0.84 ± 0.04
Chaffinch	0.69 ± 0.06	0.90 ± 0.04	<i>0.77 ± 0.05</i>	0.91 ± 0.03

Values presented are AUC ± SE. AUC is coded according to thresholds of inadequate (normal), adequate (italics) and good (bold) model performance

ALT includes altitude and altitude²; *HAB* includes habitat and topographic variables (after variable reduction according to VIF); *CLIM* includes climate variables (temperature and precipitation). *HAB + CLIM* includes both habitat and climate variables

full models (parameter estimates are given in Table S3 in the ESM). There was a wide range of variation explained by the fixed effects of the full model, from 0.20 in water pipit to 0.75 in robin (Table 3). Much of the variation was attributable to habitat variables, and to a lesser extent climate (with the notable exception of robin). The pure effect of region was very low in most models, suggesting regional differences (e.g. Fig. 2) could be explained largely on the basis of habitat and climate. The variation attributable to interactions between region and climate variables was, however, reasonably high, and likely arose due to the sometimes marked differences in climate between the two regions (Fig. S2 in the ESM).

Discussion

Altitudinal trends

Alpine bird species show marked patterns in distribution along altitudinal gradients. For the widely distributed species considered (i.e. those occurring relatively commonly in both Piedmont and Trentino), these patterns were generally consistent across regions (wren, chiffchaff, coal tit), although there were some species for which overall rates of occurrence varied, but the shape of the relationship between probability of occurrence and altitude was the same between regions (water pipit, dunnock, wheatear, chaffinch). This has important implications for modelling species distributions, as it suggests model transferability for several species, i.e. a model derived from one region could be used to project relative elevational shifts in a wider area. There were two species that showed significant

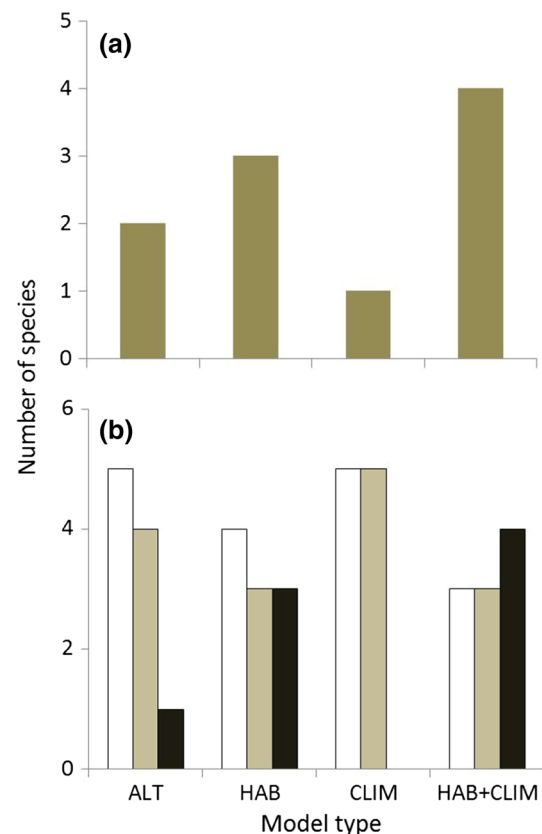


Fig. 3 Performance of different models measured by AUC. **a** Number of species for which a given model had the maximum value of AUC. **b** Number of species for which a given model was classified as having inadequate (AUC < 0.70, white bars), adequate (0.70 ≤ AUC < 0.80, grey bars) and good (AUC ≥ 0.80, black bars) predictive capacity. *ALT* altitude only, *HAB* habitat only, *CLIM* climate variables only, *HAB + CLIM* combined habitat and climate variables

Table 3 Variation partitioning based on R^2 for generalised linear models (Nagakawa and Schiezzeth 2013) derived from the fixed effects of full models, i.e. including habitat variables (*HAB*), climate variables (*CLIM*) and region (*REG*)

Species	Full	REG	CLIM	HAB	REGHAB	CLIMHAB	REGCLIM	3-WAY
Water pipit	0.200	0.004	0.028	0.114	−0.001	0.011	0.054	−0.010
Wren	0.299	0.001	0.022	0.148	0.002	0.119	0.128	−0.121
Dunnock	0.471	0.001	0.117	0.105	0.009	0.094	0.248	−0.103
Robin	0.755	0.061	0.309	0.107	0.028	0.328	0.278	−0.356
Black redstart	0.522	0.016	0.008	0.374	−0.018	0.137	0.124	−0.119
Wheatear	0.321	0.000	0.113	0.161	0.000	0.022	0.047	−0.022
Chiffchaff	0.429	0.015	0.069	0.180	0.016	0.138	0.165	−0.154
Coal tit	0.549	0.022	0.154	0.171	−0.009	0.217	0.202	−0.208
Willow tit	0.394	0.047	0.051	0.119	−0.012	0.164	0.177	−0.152
Chaffinch	0.648	0.004	0.030	0.200	−0.004	0.274	0.414	−0.270

The variation attributable to each individual group of variables is given by REG, CLIM and HAB. The variation attributable to interacting pairs of variables is given by *REGHAB* (region and habitat), *CLIMHAB* (climate and habitat) and *REGCLIM* (region and climate). The variation attributable to the interaction between all three variables is given as 3-WAY. Negative values are interpreted as zeros (Legendre 2008)

differences in altitudinal trend between region, robin and willow tit. Differences in habitat, and in particular the number of trees, may explain these patterns, especially for willow tit, where the patterns in species occurrence match very closely with trends in the number of trees across the two regions (compare Fig. 2i and Fig. S3A in the ESM).

Observer effects may be important in such surveys (e.g. Sauer et al. 1994; Farmer et al. 2014), and we cannot rule out that these may have influenced overall between-region differences for some species. However, we believe such effects are likely to have been minimised as methods were identical in the two areas, the species involved were relatively easily identifiable by song, and the use of a fairly course measure, presence/absence, will have reduced subjectivity that might arise from making estimates of abundance. It is also notable that differences were not uni-directional—there were some species with higher occurrence rates in Trentino (dunnock, robin) and others with higher occurrence rates in Piedmont (water pipit, wheatear, willow tit, chaffinch). There were also differences in survey effort between regions in that many points were subjected to two or more visits in Piedmont, but there was only a single visit in Trentino. However, there was no evidence that this affected the outcome of the results (Fig. S4 in the ESM).

Model performance across regions

Altitude correlates with gradients in habitat cover and with trends in climate, and is therefore thought to be a good general surrogate for the multiple environmental variables that are likely to dictate species distributions (e.g. Hodkinson 2005) and therefore to be a good basis for studying environmental, and in particular climate, change (Shoo et al. 2006). Although the species here showed clear variations along the altitudinal gradient, altitude models with a simple

habitat mask (i.e. removing unsuitable nesting habitat prior to modelling) did not perform especially well (only coal tit had an altitude model considered ‘good’; Table 2). Schaub et al. (2011), working across a longer, but lower, altitudinal gradient, also found only weak evidence that altitude was a good predictor of farmland bird density. Similarly, climate-only models performed relatively poorly, and there was no species that had a ‘good’ climate model (Table 2). For both climate and altitude models, there were several species whose models were considered adequate, so it should not be concluded that such models, masked for wholly inappropriate habitats, are of no value. However, it is clear that incorporation of habitat cover in the models resulted in improved model performance in many species. Whilst models using climate alone have proved useful in estimating species distributions at broad scales (e.g. Huntley et al. 2007), in many situations (and particularly when considering finer scales), climate and bird distributions are unlikely to be very tightly linked when vegetation distribution is subject to other limiting factors (in particular, grazing by domestic livestock), and when complex topography may mean strong influences of microclimatic conditions. Data derived from relatively broad scales may therefore be inadequate to model distributions over steep altitudinal gradients where mean climates can change over short distances. Climatic data collected in the field at scales more appropriate to the activity of the birds (e.g. delimited by territory size, foraging range or nest site) may therefore provide the basis of more informative climate-only models. However, given the effort involved in collecting such data, it is difficult to envisage a situation where simple habitat variables modelled in conjunction with larger-scale climate variables would not prove to be the best option in terms of both effort and model performance.

There was very little variation attributable to region compared to climate and habitat variables. This is likely

because most of the variation caused by region (e.g. Fig. 2) is in fact due to habitat and climatic differences already taken into account in the models, so inclusion of region in addition to climate does not add any useful information. This is further evidence (along with the consistency in altitudinal trends) that habitat and climate act on species distributions in a consistent way across geographic regions. It also implies that other unmeasured differences, such as geology, soil type, current and past land management, and disturbance (e.g. through winter sports or hunting), are either unimportant in dictating bird distributions or they do not vary sufficiently across regions. Of course, we would caution against assuming such relationships are consistent across other regions with widely differing environmental pressures. Our results suggest model transferability for the Southern Alps for several widespread species, but it would be worthwhile to repeat the study on distribution data from regions in different countries.

Wider implications

The relatively poor performance of climate-only models (models were ‘adequate’ for five species and inadequate for the rest) implies that climate alone does not have a major role in directly limiting species distributions along the altitudinal gradient. Habitat, or a combination of habitat and climate, showed better performing models, suggesting that habitat management can be used to some extent to improve conditions, potentially mitigating the negative effects of climate change for some species (Braunisch et al. 2014). Habitat degradation and loss are often considered to be the key threats to biodiversity, rather than climate change per se (e.g. Sala et al. 2000; Jetz et al. 2007; Chamberlain et al. 2016), and indeed in an alpine context there are a number of environmental pressures which are likely to affect habitat quality (e.g. winter sports, Rolando et al. 2007; land abandonment, Laiolo et al. 2004), but whose effects could be ameliorated via habitat management. Nevertheless, climate change is also a major driver of habitat change in the Alps, in particular via effects on shifts in vegetation zones (e.g. Cannone et al. 2007) which may have consequences in the future for bird distributions (Chamberlain et al. 2013). While climate apparently plays a relatively minor role in limiting current species distributions at the altitudes and at the fine spatial scale considered here, it is very likely to be of greater importance over broader contexts—a longer altitudinal gradient and/or a broader spatial scale may well have revealed a greater importance of climate in the models. Although not the goal of this paper, identifying the point along the altitudinal distribution at which climate becomes limiting would help to improve longer-term forecasts of potential effects of climate change.

Although overall occurrence rates often varied between regions, the species studied showed non-random altitudinal distributions which for most species were consistent across regions in terms of pattern, which is a key finding in terms of the evaluation of the potential effects of climate change and associated habitat shifts (Araújo and Rahbek 2006). The shape and position of the altitudinal distribution curve is important as it can be related to vulnerability where the available space is limited, i.e. where mountains are not of sufficient altitude for expansion (e.g. Chamberlain et al. 2014; Pernollet et al. 2015). This study therefore suggests general consistency in response in terms of the shape of the curve, and that regional differences are largely driven by habitat and climate. Incorporating these variables should be sufficient to construct models with high transferability for many alpine species, a particularly relevant finding in terms of modelling species response to habitat characteristics and environmental change (Randin et al. 2006). However, despite adequate model performance in many cases, there was nonetheless often a large amount of unexplained variation, suggesting that there is considerable scope for further improving model performance. We suggest that further detailed autecological studies of alpine bird species are needed in order to improve our ability to describe their distributions, in particular in terms of understanding what specific factors mostly affect their occurrence. This would help to understand the capacity of bird species to buffer the effects of climate change by means of (micro-) habitat selection (Moritz and Agudo 2013). Such knowledge would contribute to evaluating species’ sensitivity (Chamberlain et al. 2013) and adaptation potential (Bellard et al. 2012), and ultimately to building more precise models on which to base future scenarios of environmental change and conservation planning. This is particularly compelling for alpine habitats and species, as fine-scaled modelling is highly desirable in areas with strong altitudinal gradients, where coarse models may overestimate the potential habitat loss due to climate change (Randin et al. 2009).

Acknowledgments The research in Piedmont was partly funded through a Grant to DEC from the People Programme (Marie Curie Actions) of the European Union’s Seventh Framework Programme FP7/2007–2013/. The research in Trentino was partially supported by Accordo di programma PAT, 2010–2013 and MUSE 2011–2012; we are grateful to Franco Rizzolli and Francesco Ceresa for field work in Trentino. We are grateful to Ola Olsson and an anonymous referee for their constructive comments on an earlier version of the manuscript.

Author contribution statement All authors contributed significantly to the conception and planning of the paper. DEC took a lead in analysing the data and writing the paper. MB and EC carried out data extraction in GIS. PP and AR managed fieldwork in Trentino and Piedmont, respectively.

References

- Araújo MB, Rahbek C (2006) How does climate change affect biodiversity? *Science* 313:1396–1397
- Bartoń K (2013) MuMIn: Multi-model inference. R package version 1.9.0 ed
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. *Ecol Lett* 15:365–377
- Bibby CJ, Burgess ND, Hill DA, Mustoe SH (2000) *Bird census techniques*, 2nd edn. Academic, London
- Bradbury RB, Pearce-Higgins JW, Wotton S, Conway GJ, Grice PV (2011) The influence of climate and topography in patterns of territory establishment in a range-expanding bird. *Ibis* 153:336–344
- Brambilla M, Bergero V, Bassi E, Falco R (2015) Current and future effectiveness of Natura 2000 network in the central Alps for the conservation of mountain forest owl species in a warming climate. *Eur J Wildl Res* 61:35–44
- Braunisch V, Coppes J, Arlettaz R, Suchant R, Zellweger F, Bollmann K (2014) Temperate mountain forest biodiversity under climate change: compensating negative effects by increasing structural complexity. *PLoS ONE* 9:e97718
- Cannone N, Sgorbati S, Guglielmin M (2007) Unexpected impacts of climate change on alpine vegetation. *Front Ecol Environ* 5:360–364
- Caprio E, Chamberlain DE, Isaia M, Rolando A (2011) Landscape changes caused by high altitude ski-spites affect bird species richness and distribution in the Alps. *Biol Conserv* 144:2958–2967
- Chamberlain D, Arlettaz R, Caprio E, Maggini R, Pedrini P, Rolando A, Zbinden N (2012) The altitudinal frontier in avian climate change research. *Ibis* 154:205–209
- Chamberlain DE, Negro M, Caprio E, Rolando A (2013) Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. *Biol Conserv* 167:127–135
- Chamberlain DE, Negro M, Caprio E, Rolando A (2014) Shifting habitats in the Alps and potential future consequences for birds. In: *Proceedings of the BOU's 2014 annual conference, ecology and conservation of birds in upland and alpine habitats*. Published Online <http://www.bou.org.uk/bouproc-net/uplands/chamberlain-et-al.pdf>
- Chamberlain DE, Pedrini P, Brambilla M, Rolando A, Girardello M (2016) Identifying key conservation threats to Alpine birds through expert knowledge. *Peer J* 4:e1723
- Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026
- Crawley MJ (2013) *The R book*, 2nd edn. Wiley, Chichester
- Dirnböck T, Essl F, Babitsch W (2011) Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Glob Change Biol* 17:990–996
- EEA (2010) Europe's ecological backbone: recognising the true value of our mountains. EEA Report 6/2010. European Environment Agency, Copenhagen
- Farmer RG, Leonard ML, Flemming JEM, Andersen SC (2014) Observer aging and long-term avian survey data quality. *Ecol Evol* 4:2563–2576
- Ficetola GF, Thuiller W, Miaud C (2007) Prediction and validation of the potential global distribution of a problematic alien species—the American bullfrog. *Divers Distrib* 13:476–485
- Flousek J, Telensky T, Hanzelka J, Reif J (2015) Population trends of Central European montane birds provide evidence for adverse impacts of climate change on high-altitude species. *PLoS ONE* 10:e0139465
- Freeman E (2007) PresenceAbsence: an R package for presence-absence model evaluation. USDA Forest Service, Ogden
- Gifford ME, Kozak KH (2012) Islands in the sky or squeezed at the top? Ecological causes of elevational range limits in montane salamanders. *Ecography* 35:193–203
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models? *Ecol Lett* 8:993–1009
- Harsch MA, Hulme PE, McGlone MS, Duncan RP (2009) Are tree-lines advancing? A global meta-analysis of treeline response to climate warming. *Ecol Lett* 12:1040–1049
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978
- Hodkinson ID (2005) Terrestrial insects along elevational gradients: species and community responses to altitude. *Biol Rev* 80:489–513
- Huntley B, Green RE, Collingham YC, Willis SG (2007) *A climatic atlas of European breeding birds*. Lynx, Barcelona
- Jetz W, Wilcove DS, Dobson AP (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol* 6:e157
- Laiolo P, Dondero F, Ciliento E, Rolando A (2004) Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *J Appl Ecol* 41:294–304
- Legendre P (2008) Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *J Plant Ecol* 1:3–8
- Lehikoinen A, Green M, Husby M, Kålås JE, Lindström Å (2014) Common montane birds are declining in Northern Europe. *J Avian Biol* 45:3–14
- Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768–1771
- Maggini R, Lehmann A, Kéry M, Schmid H, Beniston M, Jenni L, Zbinden N (2011) Are Swiss birds tracking climate change? Detecting elevational shifts using response curve shapes. *Ecol Model* 222:21–32
- Maggini R, Lehman A, Zbinden N, Zimmerman NE, Bollinger J, Schröder B, Foppen R, Schmid H, Beniston M, Jenni L (2014) Assessing species vulnerability to climate and land use change: the case of the Swiss breeding birds. *Divers Distrib* 20:708–719
- Melendez L, Laiolo P (2014) The role of climate in constraining the elevational range of the Water Pipit *Anthus spinoletta* in an alpine environment. *Ibis* 156:276–287
- Moritz C, Agudo R (2013) The future of species under climate change: resilience or decline? *Science* 341:504–508
- Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322:261–264
- Nagakawa S, Schiezh H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42
- Pernollet CA, Korner-Nievergelt F, Jenni L (2015) Regional changes in elevational distribution of the Alpine Rock Ptarmigan *Lagopus muta helvetica* in Switzerland. *Ibis* 157:823–836
- R Development Core Team (2013) *R: A Language and Environment for Statistical Computing* 3.01. R Foundation for Statistical Computing, Vienna
- Rahbek C (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol Lett* 8:224–239

- Randin CF, Dirnböck T, Dullinger S, Zimmermann NE, Zappa M, Guisan A (2006) Are niche-based species distribution models transferable in space? *J Biogeogr* 33:1689–1703
- Randin CF, Engler R, Normand S, Zappa M, Zimmermann NE, Pearson PB, Vittoz P, Thuiller W, Guisan A (2009) Climate change and plant distribution: local models predict high-elevation persistence. *Glob Change Biol* 15:1557–1569
- Reif J, Flousek J (2012) The role of species' ecological traits in climatically driven altitudinal range shifts of central European birds. *Oikos* 121:1053–1060
- Rolando A, Caprio E, Rinaldi E, Ellena I (2007) The impact of high-altitude ski-runs on alpine grassland bird communities. *J Appl Ecol* 44:210–219
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Lee-mans R, Lodge DM, Mooney HA, Oesterhel M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774
- Sauer JR, Peterjohn BG, Link WA (1994) Observer differences in the North American Breeding Bird Survey. *Auk* 111:50–62
- Schaub M, Kéry M, Birrer S, Rudin M, Jenni L (2011) Habitat-density associations are not geographically transferable in Swiss farmland birds. *Ecography* 34:693–704
- Sekercioglu CH, Schneider SH, Fay JP, Loarie SR (2008) Climate change, elevational range shifts and bird extinctions. *Conserv Biol* 22:140–150
- Shoo LP, Williams SE, Hero J-M (2006) Detecting climate change induced range shifts: where and how should we be looking? *Aust Ecol* 31:22–29
- Swets JA (1988) Measuring the accuracy of diagnostic systems. *Science* 240:1285–1293
- Tryjanowski P, Sparks TH, Profuc P (2005) Uphill shifts in the distribution of the white stork *Ciconia ciconia* in southern Poland: the importance of nest quality. *Divers Distrib* 11:219–223
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- Whittingham MJ, Krebs JR, Swetnan RD, Vickery JA, Wilson JD, Freckleton RP (2007) Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. *Ecol Lett* 10:25–35
- Wilson RJ, Gutiérrez D, Gutiérrez J, Martínez D, Agudo R, Monserrat VJ (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecol Lett* 8:1138–1146
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York