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RESEARCH PAPER

The drivers of avian abundance: patterns in the relative importance of climate and land use

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ABSTRACT

Aim Climate and land use can have important effects on the local abundances of species, but few studies have investigated the relative impacts of these factors. Here, we quantify the relative importance of climate, land use and surrounding population size in determining the abundances of birds across a continent.

Location Europe.

Methods We used species abundance models to identify the relative importance of different environmental predictors for estimating the local abundances of 342 species of European breeding birds. Models controlling for phylogeny were used to relate species life history and ecological traits to the climate:land use importance ratio. The mean of this ratio, across all species occurring in a given area, was mapped to explore spatial variation in the major drivers of abundance.

Results At the scale examined, climate is generally more important than land use in determining species abundances. However, the abundance of species in neighbouring areas is also a major correlate. Among climate variables, temperature is of greater importance than moisture availability in determining abundances. The relative importance of these variables varies with latitude, with temperature being most important in the north, and moisture availability in the south. Differences in the importance of specific drivers are related to species ecological traits: climate is more important for determining the abundance of species that have larger global ranges or a smaller body mass.

Main conclusions Abundances of species occurring in northern Europe, an area predicted to experience climatic changes of high magnitude, are most sensitive to climate, particularly temperature. Given the greater confidence in future projections of temperature than precipitation, this increases confidence in projections of the impacts of climate change on species in the north, whilst attempts to predict future populations in central and southern Europe may be dependent on less predictable changes in land use and precipitation.

Keywords

Abundance modelling, climate, European birds, land use, relative variable importance, spatial variation, species traits.

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INTRODUCTION

Climate change has been implicated as a major driver of recent variations in the distributions and abundances of birds (Green *et al*., 2008; Gregory *et al*., 2009; Illán *et al*., 2014). However, species responses to climate change are highly variable in both their magnitude and rate (Walther *et al*., 2002). Understanding the relative effects of climate and concurrent land use changes on population changes of species is challenging, yet is vital for conserving species in future. Regional variations in the extent of

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recent land use changes are increasingly pronounced (Kaplan *et al.*, 2012) with, for example, large differences between eastern and western Europe (Donald *et al.*, 2001). By contrast, the greatest recent changes in temperature have been observed towards the poles, a trend that is projected to continue through the current century (IPCC, 2013). Regional disparities in expected climate change, and differential species responses to climate change, mean that it is important to understand the extent to which the abundances of species in different areas are driven by climate.

Climate is often regarded as the primary, albeit indirect, driver of avian population dynamics (Thuiller *et al.*, 2004). As a result, ecologists frequently use climate projections to predict, through species distribution modelling (SDM), the risks that species face under particular climate change scenarios (Elith *et al.*, 2010). However, species that are affected by human activities are unlikely to be in equilibrium with climatic conditions (Thuiller *et al.*, 2004), a pre-requisite for understanding species–climate relationships (Pearson & Dawson, 2003). For example, the intensification of agricultural practices across Europe during the last quarter of the 20th century led to widespread changes in the abundance and distribution of many farmland bird populations (Donald *et al.*, 2001). To account for such confounding issues, land use variables have been incorporated into SDMs and shown to improve their explanatory power significantly (Thuiller *et al.*, 2004). However, few studies (Eglington & Pearce-Higgins, 2012; Renwick *et al.*, 2012) have directly assessed the relative roles of climate and land use when modelling the abundance, rather than the distribution, of a species, and none has done so at a continental scale. Furthermore, the relative role of climate and land use may vary not only between species but also spatially. Beale *et al.* (2014) demonstrated that the influence of climate on the distribution of a species varied across the species' range. To understand the susceptibility of species to climate change, we must first disentangle the relative importance of climate and land use in determining abundance at a scale encompassing the large majority, if not the entirety, of a species' range.

The large-scale declines in the populations of some European birds (Vickery *et al.*, 2014; Inger *et al.*, 2015) are of growing concern, among both scientists and politicians. Although specific regional declines (for example, those of farmland bird populations in Britain) have been primarily attributed to agricultural intensification (Chamberlain *et al.*, 2000; Donald *et al.*, 2001), it is unclear whether climate or land use is the primary driving factor behind large-scale variations in populations of European birds (Thuiller *et al.*, 2004; Green *et al.*, 2008; Eglington & Pearce-Higgins, 2012; Vickery *et al.*, 2014). It has been suggested that there exists a hierarchical scheme of environmental controls on species distributions, whereby climatic variables operate over the largest scale, with geology and land use determining species distributions at smaller scales (Thuiller *et al.*, 2004). It has also been suggested that, by modelling abundance, we can distinguish finer-scale variations in habitat quality that may not have been evident in distribution modelling (Howard *et al.*, 2014); this might enable more accurate assessments of the relative importance of land use and climate for species at a continental scale.

Here, we assess the relative roles of climate and land use in determining the local abundance of breeding-birds across Europe. We examine whether the relative contribution of climate and land use varies among species in relation to ecological traits. Our working hypothesis, following previous research (Barbet-Massin *et al.*, 2012; Virkkala & Lehikoinen, 2014) on determinants of the ecological niche, is that climatic influences will dominate at poleward regions in Europe and that land use will be more important in determining abundance patterns in the more heterogeneous landscapes of central and southern Europe. Specific traits, such as mass and range size (Angert *et al.*, 2011; Buckley & Kingsolver, 2012), have been linked to the characteristics of species climatic niches. For example larger-bodied and wider-ranging species occur more frequently in colder climes (Ashton, 2002). Based on energy conservatism in endotherms, we might expect large-bodied organisms to be less closely tied to climate than smaller species (due to surface area:volume ratios). Species-specific traits including breeding range size and migratory distance have also been linked to habitat specialization (Reif *et al.*, 2015). Our goal here is to identify those traits that indicate whether a species is most likely to be sensitive to the impacts of climate change (those whose abundance is most strongly related to climatic variation) or habitat modification (those whose abundance is most strongly related to land use). In addition, we investigate spatial patterns in the role of different drivers of abundance, identifying those areas of Europe in which birds are likely to be more susceptible to change in climate or land use. Given that species northern range limits are often thought to be determined by their thermal tolerances (Woodward, 1987; Addo-Bediako *et al.*, 2000), we might predict that climate will be of greater importance at higher latitudes.

METHODS

Species data

Spatial abundance data for 496 species of breeding birds within Europe were obtained from the EBCC (European Bird Census Council) Atlas of European breeding birds (Hagemeijer & Blair, 1997). The EBCC atlas provides, for many countries across Europe, a population size estimate for each species in the *c.* 50 km × 50 km squares of the Universal Transverse Mercator (UTM) grid. Population size estimates, principally relating to the period 1985–88, are based on a seven-point scale (including zero and six logarithmically scaled categories: 1–9, 10–99, 100–999, 1000–9999, 10,000–99,999, ≥ 100,000 breeding pairs). For Russia, parts of Belarus, Ukraine and the Caucasus republics, the data in the species records were primarily qualitative; therefore, these areas were excluded from the analysis. Likewise, some areas in western Europe recorded only qualitative presence–absence data, so were excluded from analyses (Fig. S1 in Supporting Information). From the initial 496 species, we excluded introduced species and species which spend a significant proportion of their time at sea because their abundance is unlikely to be strongly linked to terrestrial climate and land use. Due to model-building limitations, particularly when undertaking data splitting for model validation, those species recorded in fewer than 20 grid cells were also omitted. The remaining 342 species were used for all subsequent analyses.

Bioclimatic data

Climatic data were derived from the global compilation made by New *et al.* (1999) for the 30-year interval 1961–90, the latter part of which corresponds to the period of EBCC bird abundance data collection. Following the formulation of Prentice *et al.* (1992), three bioclimatic variables were calculated for each UTM grid cell: mean temperature of the coldest month (MTCO); growing degree-days above 5 °C(GDD5); and the annual ratio of actual to potential evapotranspiration (APET) (Fig. S2). Through both direct and indirect effects on vegetation, prey, predators, competition or diseases (Gregory *et al.*, 2009), these variables can limit species ranges and populations. Previously, these variables have been widely and successfully used in models to describe both the range extents (Thuiller *et al.*, 2004; Huntley *et al.*, 2007; Oliver *et al.*, 2012) and abundance patterns (Green *et al.*, 2008; Gregory *et al.*, 2009; Howard *et al.*, 2014) of European birds.

Land use data

Land use data were compiled at the same resolution as the species data. The land use for each cell was derived from an aggregation of the Pan-European Land Cover (PELCOM) 1-km resolution database (Mucher *et al.*, 2000); these land–use classifications being based on NOAA-AVHRR satellite data. The PELCOM database was chosen over similar finer-scale land use datasets due to its complete spatial coverage of the study area and the homogeneity of the methods used for land cover classification (Thuiller *et al.*, 2004; Araújo *et al.*, 2005). Eight land use classifications were used: forest, grassland, urban, arable, wetland, coastal, shrubland and barren. The percentage coverage of each of these eight classes was calculated for each UTM grid cell (Fig. S3).

Surrounding local abundance

Spatial autocorrelation (SAC) refers to the greater degree of similarity between more proximate samples and can occur through distance-related biological processes and spatially structured environmental processes (Dormann, 2007). Methodologies assessing the effects of SAC have shown that it may influence both coefficients and inference in statistical analyses through the violation of the independence assumption, autocorrelated residuals and, hence, inflation of type 1 errors (Legendre, 1993). Segurado *et al.* (2006) recommend the inclusion of an autocovariate term as the most effective means of dealing with spatial autocorrelation. Therefore, we account for potential spatial autocorrelation in our models by calculating an indicator of surrounding abundance for each UTM grid cell using equation 1:

$$L = \log_{10}\left(\frac{1}{n}\sum_{i}^{n}\frac{1}{2}(10^{A_i})\right) \tag{1}$$

where L is the surrounding local abundance, n is the number of adjacent cells, A is the categorical abundance scale is the categorical abundance scale and i is the abundance category index. In the formula, the log-scaled integer estimates of abundance in the adjacent cells are back-transformed and divided by two to give an absolute abundance for each cell relating to the midpoint of the abundance category. The mean of these estimates of surrounding absolute abundances across cells is log-transformed to enable direct comparison with the original abundance values on the existing ordinal scale.

In those cases where neighbouring cells included marine habitats, the categorical abundance was included in the above calculation as a zero (alternatively, including these cells as missing data had no impact on our findings; Fig. S4). We included information only from neighbouring cells immediately adjacent to the focal cell (i.e. first-order neighbours; Dormann *et al.*, 2007); higher orders of neighbouring cells were considered, but model fit was best when only first-order neighbours were included (Fig. S5).

Statistical analyses

Random forests (RF) were used to model species abundance and to provide estimates for the relative importance of predictor variables. This machine learning technique is a bootstrap-based classification and regression tree (CART) method (Cutler *et al.*, 2007). Robust to over-fitting, it is widely recognized to produce good predictive models; hence, it is increasingly applied to species distribution modelling (Cutler *et al.*, 2007). RF models were preferred to ordinal regression techniques because they make fewer assumptions about the distribution of predictor and response variables (Cutler *et al.*, 2007).

Models were fitted using 10-fold cross validation to reduce SAC between training and test data and to minimize over-fitting. To improve stability, each model was built using 1000 classification trees fitted to a random sample of the observations (approximately 63% of the available data). The remaining 'out-of-bag' observations (OOB; a term used with RF models to describe the semi-independent test data not used initially for model fitting) were then cross-validated against the resulting trees to estimate model performance (Cutler *et al.*, 2007) using a threshold independent measure of model performance, namely AUC, the area under the receiver operating characteristic (ROC) curve (Manel *et al.*, 2001). Previous evaluation has shown that these models perform well when assessed using other measures of model discrimination and calibration, in addition to AUC (Howard *et al.*, 2014). These previous analyses also demonstrated that RF models substantially reduced residual SAC relative to that present in the raw data.

The importance of individual variables was calculated using a permutation-based measure of the normalized difference in prediction accuracy for the OOB data when the predictor variable is included as originally observed, versus when the predictor variable is randomly permuted. Higher values of AUC indicate a greater degree of association between the variable and the response (Cutler *et al.*, 2007). To account for potential correlations among predictor variables, a conditional permutation approach, proposed by Strobl *et al.* (2008), was applied using the 'party' package in R (Liaw & Wiener, 2002; R Development Core Team, 2012). Using this approach, the underlying correlation structure is preserved by permuting the predictor variable only within groups of observations. This method provides a fair means of comparison, identifying the relevant predictors and mostly eliminating the preference for correlated variables (Strobl *et al.*, 2008). To enable comparisons between species, relative variable importance was calculated by dividing the importance of each individual variable by the summed importance across all variables for each species. Relative variable importance for each species was aggregated for each of the two broad categories of driver: climate and land use (Ishwaran, 2007). The aggregated importance of climate variables was then divided by the aggregated importance of land use variables. This ratio was taken to give a measure of the relative importance of climate and land use for each species (Table S1).

A phylogenetic generalized least squares (PGLS) approach was used to test both for relationships between species-specific traits and the relative importance of climate to land use (hereafter termed 'relative climate importance') and for relationships between species-specific traits and the importance of spatial autocorrelation for a species, whilst controlling for phylogenetic non-independence (Freckleton, 2009). Species traits were taken from BirdLife International & NatureServe (2012) and included mean body mass, generation length, primary habitat association, migratory strategy and average and maximum natal dispersal distances. Global range size, a measure of the geographic scale over which the drivers of abundance operate, was also included, and was derived from BirdLife International species range polygons (BirdLife International & NatureServe, 2012). Prevalence within the study area, which represents the quantity of available data, was calculated as the proportion of UTM squares that were occupied (from Hagemeijer & Blair, 1997). Phylogeny was based on a consensus tree built using 5000 trees sub-sampled from the global phylogeny built by Jetz *et al.* (2012). We compared the Akaike information criterion (AIC) corrected for small sample size (AICc) for all subsets of the global model, selecting all models within six ΔAICc of the best performing model. To avoid selecting overly complex models, all models with a better-performing simpler nested model were disregarded (Richards, 2008). Diagnostic plots were examined for the final model for each analysis to check for heteroscedasticity, non-normal errors and outliers. Phylogenetic analyses were carried out in the 'caper' package in R (Orme *et al.*, 2012; R Development Core Team, 2012).

Spatial variation in relative variable importance was investigated by calculating the mean ratio of importance of climate versus land use for all species present within a UTM grid cell. This was applied to all cells where more than 75% of the species present were represented by quantitative data (Fig. S1). In total, this accounted for 47.5% of the UTM grid cells across Europe. As we found little variation in the performance of models for species located in different parts of Europe, these ratios were not corrected for model fit. To test for spatial variation in these ratios, an ordinary least squares regression (OLS) was used to examine the relationship between the mean ratio of importance of climate versus land use for all species present in a UTM grid cell against the latitude and longitude of the cell. Species richness and heterogeneity of land use (the latter measured using Shannon's diversity index; Forman, 1995) within each UTM grid cell were also included in these OLS models and an ANOVA used to identify differences in the explanatory power of variables.

RESULTS

The relative importance of abundance drivers

RF models of the abundance of the 342 species of European breeding bird generally performed well, with a mean AUC score of 0.97 (SE ± 0.001). An ANOVA comparing the relative importance of the two aggregated variable types (climate and land use) and the spatial autocovariate term across the species models, whilst controlling for species as a random effect, showed an overall significant difference between the three variable types ($F_{2,1023} = 4442$, $P < 0.01$; Fig. 1a). Specifically, despite the models including more land use variables than climate variables and only one SAC term, Tukey's post-hoc analysis revealed that climate was significantly more important than land use ($P = 0.05$) in explaining the abundance of species. Further, the importance of each of the climate variables in isolation was greater than that of any of the land use variables. Perhaps unsurprisingly, given the spatial coherence of most species distributions, the SAC term appeared to be significantly more important than both climate and land use ($P < 0.01$).

There were also significant differences in the relative importance of individual variables among species ($F_{11,341} = 168.4$, $P < 0.01$; Fig. 1b). In general, within the climatic variables, temperature variables have a much greater impact on species abundances than moisture availability. Both GDD5 and MTCO were significantly more important than APET (Tukey's post-hoc analysis, $P < 0.01$ for both). The importance of individual land use variables in modelling abundances also differed significantly. In addition, the prevalence of a land use type across Europe was positively correlated with the mean relative importance of that variable ($r^2 = 0.89$) in the models of species abundance. For example, forest, arable, coastal and inland wetland land uses were all significantly more related to species abundances than the grassland, urban, shrubland and barren land use types (Tukey's post-hoc analysis, $P \leq 0.05$ for each comparison). The most important land use variables for a species were those directly related to its primary habitat association (e.g. arable

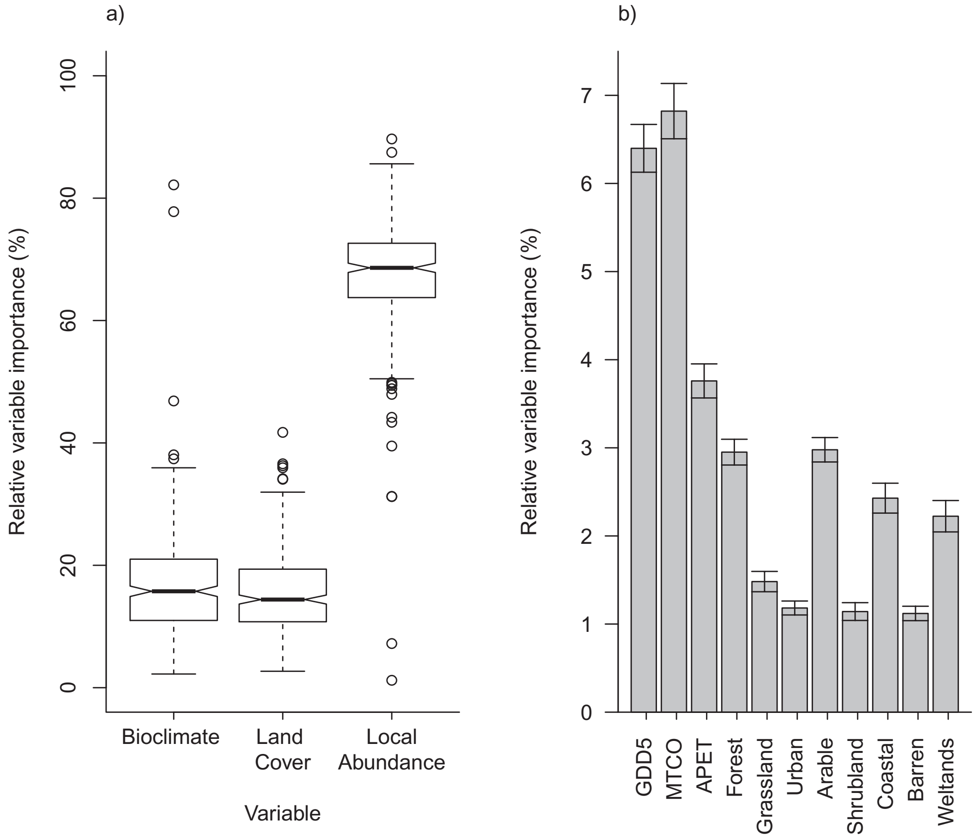

Figure 1 Mean relative importance (± SE) of climatic and land use variables along with spatial autocorrelation for 342 species in determining species local abundance, for both aggregated variables (a) and individual variables (b). Notches indicate the 95% confidence intervals of the median, with a lack of overlap indicating a significant difference at the 5% level. Circles indicate outliers.

land coverage was the most important variable determining the abundance of farmland species) (Fig. S6).

Between-species variation in relative variable importance

When testing the relationship between the ratio of the relative importance of climate versus land use variables for species and species-specific traits, a PGLS model retained four variables. These were: a species' primary habitat association, its global range size, its log body mass and its prevalence across Europe (Table 1). This model explained 18% of the observed variance in relative climatic importance. A highly significant positive relationship was found between global range size and the relative climatic importance, whilst body mass and prevalence were significant negative covariates. The relative importance of climate appeared to be unaffected by primary habitat association, with the exception of coastal species, for which climate was less important than for other species (Table 1).

A PGLS model testing relationships between the importance of SAC for each species and species-specific traits retained only primary habitat association and log body mass. A highly significant negative relationship was found between body mass and the importance of SAC, whilst SAC was less important for species associated with Mediterranean or tundra and moorland habitats than for species with other primary habitat associations (Table S2).

Spatial patterns in the importance of climate and land use

There are clear spatial patterns in relative climatic importance across Europe (Fig. 2). A regression analysis revealed a significant positive relationship between the mean relative climatic importance for all species present in a UTM grid cell and the latitude of that cell ($F_{1,1716} = 2585$, $P < 0.01$); this indicates that the relative importance of climate for determining the abundance of species increases from southern to northern Europe. Significant relationships were also identified between mean relative climatic importance of a UTM grid cell and the longitude, species richness and land use heterogeneity of that cell. However, the proportion of variance explained by these variables was low (1.20, 2.37 and 0.76%, respectively), particularly when compared with the proportion of variance explained by latitude (57.50%; Table S3). Spatial patterning is also evident in the relative importance of individual climatic variables (e.g. see the contrast between a temperature

Table 1 Species traits and the relative importance of climate and land use. Estimated coefficients from AIC selected phylogenetically corrected GLS regression models of the ratio of the relative importance of climatic and land use variables for determining the abundance of species on species-specific traits. *P*-values significant at the 5% level are shown in bold.

	Effect size	Standard error	*t*-value	*P*-value
Intercept (habitat generalists)	0.66	1.15	0.58	0.57
Primary habitat association:				
1. Coastal	–0.95	0.31	–3.09	**<0.01**
2. Inland wetland	–0.22	0.18	–1.22	0.22
3. Tundra, mires and moorland	0.01	0.22	0.06	0.95
4. Boreal and temperate forest	0.32	0.18	1.78	0.08
5. Mediterranean	0.48	0.34	1.41	0.16
6. Agriculture and grassland	–0.06	0.18	–0.33	0.74
7. Montane grasslands	–0.35	0.38	–0.92	0.36
Log (body mass)	–0.17	0.07	–2.34	**0.02**
Prevalence across Europe	–1.61	0.27	–5.98	**<0.01**
Log (global range size)	0.23	0.06	3.56	**<0.01**

Lambda = 1. Residual standard error: 0.509 on 265 degrees of freedom. Adjusted *R*-squared = 0.173.

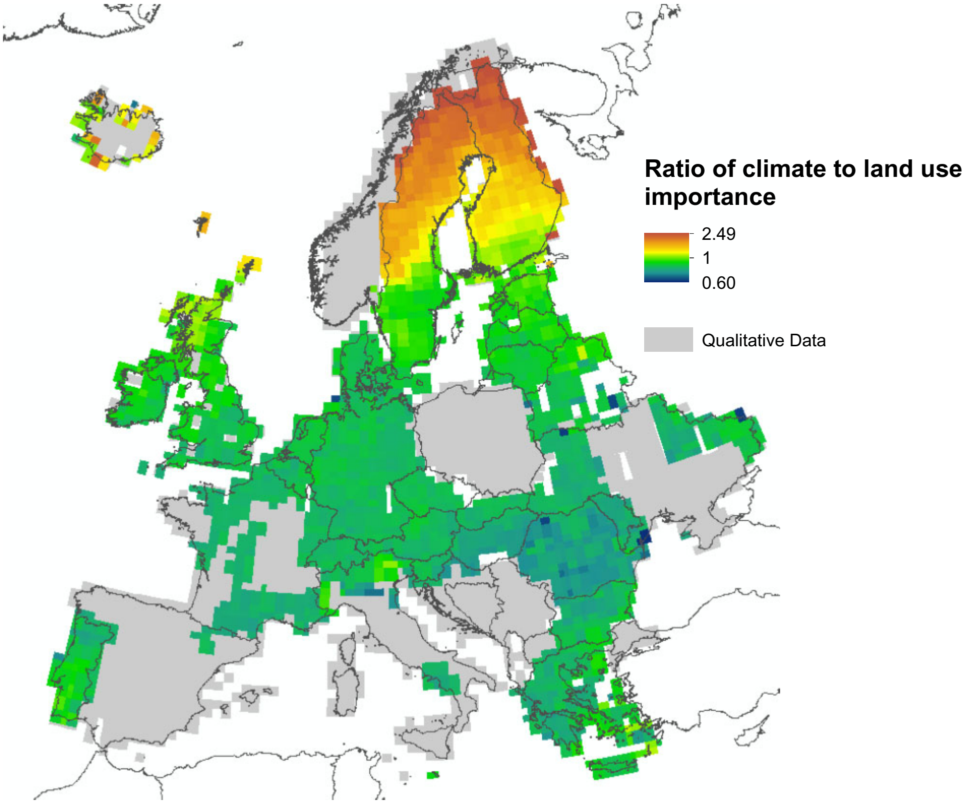

Figure 2 Spatial distribution of the ratio of the relative importance of climate to land use for determining the abundance of European bird species present within each UTM grid cell. Grey regions indicate areas omitted from analysis due to paucity of quantitative data (see Methods).

and a moisture-related variable, Fig. 3). There were significant positive relationships between the relative importance of both temperature-related variables and latitude (regression of the mean importance of an individual climate variable across all species present in a UTM grid cell against latitude: GDD5, $F_{1,1716} = 7118$, $P < 0.01$; and MTCO, $F_{1,1716} = 11{,}353$, $P < 0.01$; Fig. 3a,b, Table S3). Conversely, the relative importance of APET in explaining abundance declined with latitude [regression (as above): $F_{1,1716} = 3618$, $P < 0.01$; Fig. 3c, Table S3].

DISCUSSION

At the spatial scale examined, the abundances of the vast majority of terrestrial European birds are more strongly influenced by climate than by land use. We demonstrate, for the first time,

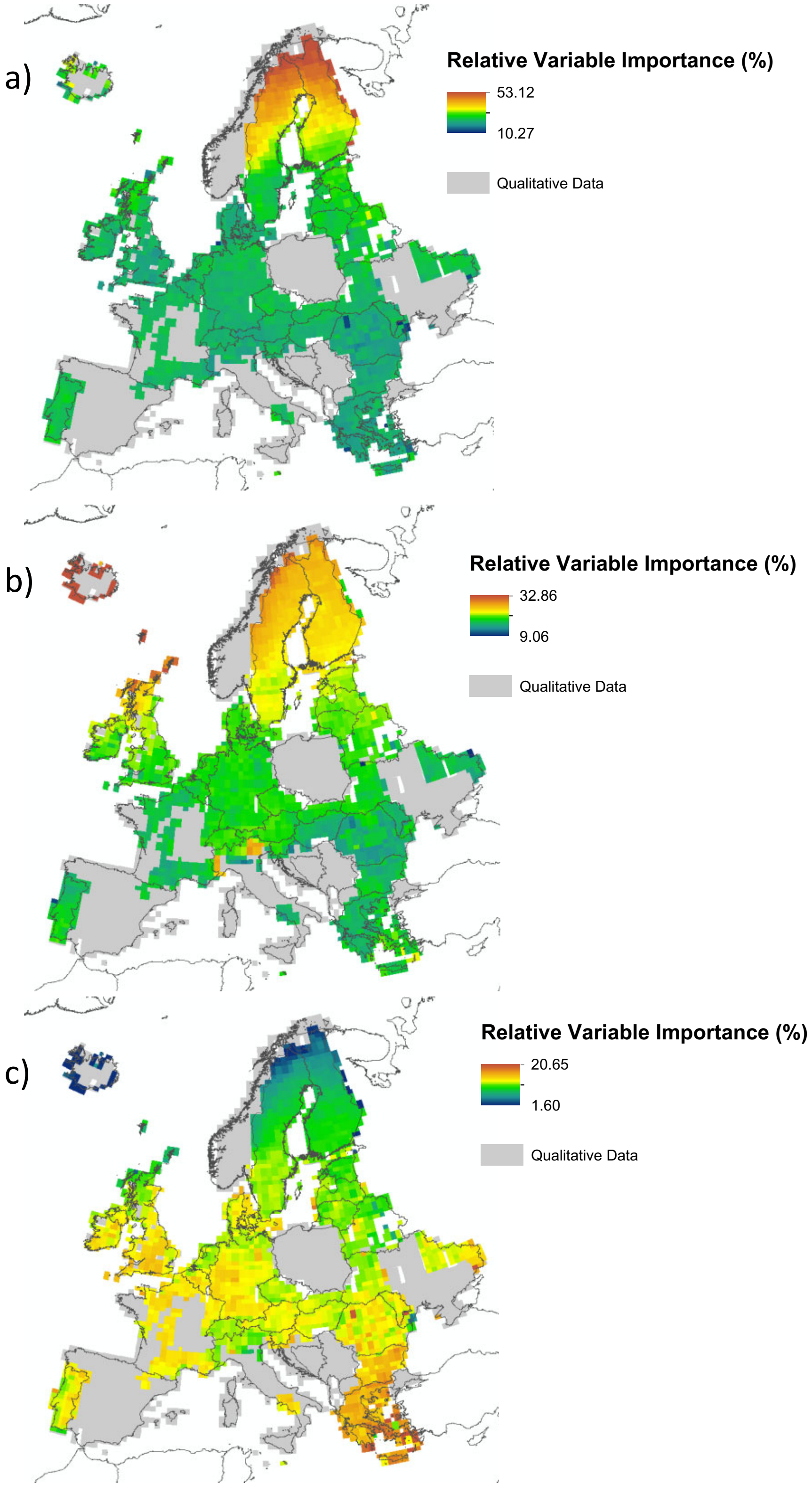

Figure 3 Spatial distribution of relative importance for determining the abundance of European birds of measures of: (a) mean temperature of the coldest month; (b) growing degree-days above 5 °C; and (c) actual to potential evapotranspiration ratio. Grey regions indicate areas omitted from analysis due to paucity of quantitative data (see Methods). Note the different scales for each plot.

substantial spatial variation in the relative importance of factors driving local abundance. We discuss these results in the light of three key findings: (1) the substantial differences between land use, climate and neighbouring abundance in their relative importance for determining local species abundance; (2) the strong spatial patterns in variable importance; and (3) the specific traits that predispose a species to the influence of either climate or land use.

Differences in the relative importance of climate, land use and spatial autocorrelation

There is substantial evidence for the individual impacts that changes in both climate and land use have on European bird populations (Lemoine *et al.*, 2007; Vickery *et al.*, 2014), and conflicting opinions about which is the most important factor affecting avian populations (Thuiller *et al.*, 2004; Vickery *et al.*, 2014). Here, despite evidence of variation in their importance among species and across space, we show that climate is usually more influential than land use in driving abundance patterns within a species' range. Previous studies (Thuiller *et al.*, 2004) suggested that climate is a better predictor of range extent than land use but here, for the first time, we demonstrate that, within a species' range, climate is also the dominant factor in determining abundance patterns at this larger, landscape scale.

Species distributions are thought to be determined by a hierarchical scheme of environmental controls, with climatic variables operating over the largest range, and factors such as land use, geology and topography operating at increasingly finer scales (Thuiller *et al.*, 2004). This hierarchy may also operate on abundance, favouring a greater importance of climate than land use at a coarse spatial scale. Despite this, we have also shown the importance of land use variables independently of the variability described by climate. Widespread land uses, whose occurrence may not be closely tied to local climate, such as arable land, forestry and inland wetlands, were important determinants of abundance patterns. Surprisingly, we also identified more localized land use variables, such as shrubland and urban environments, as important predictors of the abundance of some species. This contrasts with previous studies investigating the perceived role of land use variables on range extent (Thuiller *et al.*, 2004), where the importance of more localized land use variables was less evident. One explanation for this difference may lie in the difference between presence–absence models (as used by Thuiller *et al.*, 2004) and our abundance models. Specifically, by considering abundance, our models can reflect finer-scale differences in habitat quality than can presence–absence models (Howard *et al.*, 2014). Abundance models might, therefore expose finer-scale species–habitat relationships than those detected by presence–absence modelling. However, this does not mean that climate and/or land use models are sufficient to explain spatial variations in abundance patterns for all species.

By using a conditional inference framework and permutation-based approach to assess variable importance, we also showed that the majority of spatial variation in species abundance can be related to the abundance of the same species in neighbouring cells. This term partly reflects the degree of spatial aggregation in climate and land use, as well as in the bird abundance data themselves. This could result in estimates of the importance of climate and land use being more conservative than if SAC had not been accounted for. Also incorporated in this term are the effects of unknown spatial processes, such as biotic interactions. The apparent importance of SAC suggests that species' dispersal abilities may be an important factor in determining local abundance, which may in turn indicate potential difficulties in establishing new breeding areas separated from current distributions (Tilman & Kareiva, 1997; Dormann *et al.*, 2007). Our finding that this variable can, in some instances, explain 70% or more of the spatial variation in abundance of a species indicates the importance of accounting for spatial autocorrelation when modelling abundance (Segurado *et al.*, 2006). Techniques such as hierarchical partitioning can help us understand the extent to which some of the variation in SAC is related to spatial patterning in the other predictor variables, but this approach cannot be applied to RF models.

When climate variables are considered individually, our results indicate that temperature-related variables are much more important than moisture availability in determining abundances across Europe. This is important, as the highest degree of predictive uncertainty for future climates occurs with precipitation forecasting (Theis *et al.*, 2005). With the exception of the Mediterranean region, where precipitation is shown to be an important determinant of abundance, our results suggest that uncertainty around precipitation forecasts may affect projections of future European species range extents to a much lesser extent than currently expected and, thus, that projections of future climate suitability for most species may be more reliable than is currently supposed.

Spatial variance in the role of land use and climate in determining abundances

Spatial patterns in the relative importance of climate and land use indicate that the abundances of species that occur at higher latitudes in Europe are more strongly dictated by climate variables. Despite the correlative nature of the models, their high predictive ability on spatially independent data indicates that our findings are robust. Our results, therefore, could have important ramifications with regard to future climate change. Future changes in climate are projected to be greatest in more northerly latitudes of Europe (Virkkala *et al.*, 2008; IPCC, 2013), and in a direction unfavourable to most northerly species (Huntley *et al.*, 2007). Whilst the past is not necessarily a good predictor of the future, bioclimate models have been shown to have some power in predicting future population changes (Green *et al.*, 2008; Gregory *et al.*, 2008). The strong dependence of avian abundance in these areas on climate means that constituent species will not only be exposed to some of the strongest climate changes in future but also that their populations will be among the most sensitive to such changes. Previous studies have identified that boreal and arctic species are vulnerable to climate change as a result of projected future declines in range size (Virkkala *et al.*, 2008). Given, in addition, that the abundances of these species are particularly strongly related to climatic factors, all other things being equal, populations are likely to be subject to more substantial declines than currently anticipated from considerations of range extent alone.

The relative importance of individual climatic variables also shows spatial patterns, with temperature-related variables more important in the north, and moisture availability more important in the south. These findings are in line with the water–energy hypothesis, in which the key factor determining richness variation switches from moisture availability at the equator to energy-related variables towards the poles (Hawkins *et al.*, 2003; Whittaker *et al.*, 2007), and match latitudinal gradients in the temporal variation in bird populations to both temperature and precipitation (Pearce-Higgins & Green, 2014). In those areas where energy inputs are low, such as at higher latitudes, temperature constrains species richness and abundance (Brown & Maurer, 1989); by contrast, where temperatures (and hence energy input) are higher, moisture availability constrains richness and abundance (Hawkins *et al.*, 2003).

The importance of land use in determining abundance is more evident for species present in the southern regions of Europe. In this context, there are parallels with the apparent climate sensitivity of more northerly species, discussed above. Specifically, the future impacts of land use change in southern Europe may be compounded by the prevalence of land use specialists (as defined by Moreira & Russo, 2007) in these regions. The Mediterranean regions where such species are principally located are also the regions where land use change is likely to be greatest in future (Jetz *et al.*, 2007), potentially accelerating rates of population change.

Some countries wholly (Norway and Poland), mostly (Spain) or partly (Italy, France and Iceland), did not provide quantitative spatial estimates of species abundance for the EBCC atlas (Hagemeijer & Blair, 1997). This includes some southern regions that are highly heterogeneous in both land use and temperature (Sanderson *et al.*, 2002; Barnagaud *et al.*, 2012). Whilst it is possible that a paucity of data in these areas may bias the importance of variables towards those regions where data are more fully represented, for example mid and northern Europe, given that we were able to incorporate data from Iberia, southern France, Italy and Greece in the south, and Scotland, Iceland, Sweden and Finland in the north, the full range of variation across both climate and land use is adequately represented in the data. Looking forward, several countries omitted from our analyses have subsequently initiated standardized population monitoring (PECBMS, 2009), providing the potential for future analyses to be applied to the entire region. As with all correlative modelling, our predictive ability does not extend to novel regions of parameter space. For example, the introduction of novel land uses to an area could, through a novel combination of climate and land use variables, create a previously unmodelled habitat niche. This is particularly the case for those land uses governed by anthropogenic factors (rather than climatic variables), such as arable or urban land use, which, if introduced to new regions of northern Europe, could create novel conditions.

Species characteristics and the drivers of abundance

A range of ecological characteristics, such as body mass, range size and gene frequency, have all been linked to the climate sensitivity of species (Buckley & Kingsolver, 2012; Parmesan *et al.*, 2013). Our results provide further evidence for trait–climate relationships. First, our analyses identify a negative relationship between body mass and the importance of climate. This is perhaps unsurprising, given the lower surface area to volume ratio of larger-bodied organisms, which renders them less susceptible to climate (Peters, 1986). Second, we show a negative relationship between prevalence of a species across Europe and the importance of climate. This is consistent with the idea that an extensive prevalence indicates that a species is adapted to a wide range of climatic conditions (and vice versa) (Addo-Bediako *et al.*, 2000; Ohlemuller *et al.*, 2008). Although there are good reasons to expect negative relationships between the importance of climate and both body mass and prevalence, attributing causal relationships is vexed in this case. This results from the positive association between body mass and prevalence, as well as the fact that both of these traits are known to increase with increasing latitude (Brown & Maurer, 1989).

CONCLUSIONS

Here, we present the first comprehensive analysis of the factors determining spatial variation in abundance of a continental avifauna. We compare the relative importance of climate and land use variables in determining the abundance of species, taking into account the importance of spatial autocorrelation. Overall, the importance of climate variables outweighs that of land use in determining species abundances; furthermore, across Europe, the importance of variables related to temperature outweighs those related to moisture, increasing our confidence in projections of the impact of future climate change on European bird species. Spatial variation in relative variable importance shows that climate variables are particularly important for those species present in northern Europe. This knowledge, combined with predictions of high-magnitude climatic changes in these areas, indicates that northern bird species in Europe are likely to be amongst those most vulnerable to future impacts of climate change on their populations.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Study area.
Figure S2 Bioclimate variable data.

Figure S3 Land-use variable data.
Figure S4 Model performance when including/excluding marine cells.
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Figure S7 Spatial distribution of the relative importance of land use types.
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Table S1 Species values of the relative importance of climate to land use.
Table S2 Species traits and the importance of spatial autocorrelation.
Table S3 Summary of ANOVA results.

BIOSKETCHES

Christine Howard, **Philip A. Stephens** and **Stephen G. Willis** are members of the Conservation Ecology Group at Durham University (http://www.conservationecology.org). The research of the group centres around questions related to the conservation of species and improving our understanding of ecological systems.

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All authors are interested in the ecological processes driving changes in species distributions and abundances. All authors were involved in the design of these analyses. Analyses were carried out by C.H. C.H. wrote the first draft of the manuscript, and S.G.W., P.A.S. and J.W.P.H. contributed substantially to revisions.

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