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Population responses of bird populations to climate change on two continents vary with species' ecological traits but not with direction of change in climate suitability

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Abstract
Climate change is a major global threat to biodiversity with widespread impacts on ecological communities. Evidence for beneficial impacts on populations is perceived to be stronger and more plentiful than that for negative impacts, but few studies have investigated this apparent disparity, or how ecological factors affect population responses to climatic change. We examined the strength of the relationship between species-specific regional population changes and climate suitability trends (CST), using 30-year datasets of population change for 525 breeding bird species in Europe and the USA. These data indicate a consistent positive relationship between population trend and CST across the two continents. Importantly, we found no evidence that this positive relationship differs between species expected to be negatively and positively impacted across the entire taxonomic group, suggesting that climate change is causing equally strong, quantifiable population increases and declines. Species' responses to changing climatic suitability varied with ecological traits, however, particularly breeding habitat preference and body mass. Species associated with inland wetlands responded most strongly and consistently to recent climatic change. In Europe, smaller species also appeared to respond more strongly, whilst the relationship with body mass was less clear-cut for North American birds. Overall, our results identify the role of certain traits in modulating responses to climate change and emphasise the importance of long-term data on abundance for detecting large-scale species' responses to environmental changes.

1 Introduction

Correlational studies over large numbers of species, regions and taxonomic groups have revealed clear associations between recent climate change and observed changes in geographical range and abundance of many plant and animal taxa (Hickling et al. 2006; Parmesan and Yohe 2003; Spooner et al. 2018; Stephens et al. 2016). The evidence for positive changes in species abundance and distribution in response to beneficial recent climate change (i.e. in regions where this will lead to abundance increases and range extensions) is generally perceived to be stronger and more plentiful than for populations expected to be negatively impacted (e.g. Frishkoff et al. 2016; Parmesan et al. 1999; Parmesan and Yohe 2003; Root et al. 2003; Thomas et al. 2006; Thomas and Lennon 1999). However, this effect may be an artefact, particularly if there are time lags in the responses of populations to climate change, or if range retractions are more difficult to detect than expansions. For example, climate change may adversely affect an animal species through changes in vegetation affecting the suitability of its habitat, which take time to occur, leading to an extinction debt (Kuussaari et al. 2009). Such time lags may act in the opposite direction too, resulting in instances where beneficial effects, and therefore, the responses of species predicted to benefit may be delayed (Menéndez et al. 2006), but this would not explain the suggested excess of positive relative to negative effects on species distribution and population changes.

Range retractions may be more difficult to detect than expansions, particularly when occurrence is mapped at a coarse scale. Range expansion requires successful colonisation of a new site beyond the current range by a small number of individuals, whilst range retraction may require the extinction of many local populations (Thomas et al. 2006; Brommer et al. 2012). Furthermore, the biological process of extinction may constitute a longer-term process than colonisation, which may not be detected in the relatively short time periods considered by many studies of range change (Brommer et al. 2012). Finally, attributing range retractions solely to climatic change is difficult. Range expansion in areas of degraded habitat can easily be attributed to improving climatic conditions. However, apportioning the cause of range retractions among a suite of threatening processes, including habitat degradation and invasive species, is much harder (Thomas et al. 2006). Despite some evidence for the negative effects of climate change on populations (Lehikoinen et al. 2019), there is still no consensus on whether the reported difference in strength and quantity of evidence for positive relative to negative effects of climate change is an artefact or a true reflection of species' responses. A large-scale, multispecies assessment of the positive relative to negative effects of climate change on species' populations would provide important insights into the cause of this apparent disparity.

In some studies investigating the impacts of climate change, species distribution models (SDMs) relating geographical distribution to climatic variables are combined with annual meteorological data to estimate the direction and magnitude of changes in climate suitability over a given time period for different species or regions (Engler et al. 2017; Stephens et al. 2016). Variation in observed population changes, both among species in a given area and among regions for a given species, can then be compared to the modelled differences in climate suitability trend. A positive relationship between observed and expected change is taken as correlational evidence of a probable population-level response of distribution and/or abundance to climatic change (although see Clavero et al. 2011). Such studies have found positive relationships between climate suitability and population trend, as expected, but have also identified substantial residual variation in the observed changes in distribution and abundance that is not accounted for statistically by measures of climatic change (Green et al. 2008; Stephens et al. 2016).

Species' populations and distributions are influenced by many factors other than climate (e.g. Clavero et al. 2011), and local climate adaptation may lead to different responses in different parts of a species' range (Visser et al. 2003), so such unexplained variation is unsurprising. Ecological factors might lead to interspecific variation in spatial patterns of sensitivity to climatic change, regardless of the expected direction of change in suitability (Pearce-Higgins et al. 2015). The phenological mismatch hypothesis is a good example of this, where the prevalence and magnitude of species' sensitivity to changes in life-cycle phenology relative to the phenology of prey or other resources (Franks et al. 2018) may vary because of differences in habitat, diet or migratory behaviour (Both et al. 2010). Changes, unrelated to climate change, in the suitability of habitats or impacts of environmental factors on demographic rates, such as changes in agricultural practices, land cover or pollution, may also counteract and mask the effects of climate change to a different extent for some groups of species (Clavero et al. 2011; Herrando et al. 2014; Kampichler et al. 2012). However, to our knowledge, the potential role of ecological traits in affecting species' responses to recent climatic change has not been explored comprehensively.

In this paper, we address these two issues—the apparent difference in response between species expected to benefit or be negatively impacted by climate change, and the role of ecological traits in influencing the relationship of population change to climate suitability trend. First, we examine the strength of the relationship between species- and region-specific population trends and trends in climate suitability using two of the best global datasets of recent long-term population changes for 525 bird species from Europe and the USA. Second, we investigate how species' responses to changing climatic suitability vary with ecological traits, specifically body mass, migratory behaviour and habitat association. We hypothesise that, should all three trait variables be upheld as important, we might expect to see a more positive mean annual population trend (r) vs. CST regression slope for (i) species with smaller body mass, whose populations are likely to be favoured by the higher temperatures inherent in climatic change (Millien et al. 2006; Sheridan and Bickford 2011); (ii) species associated with habitats more immediately-responsive to climate change (i.e. wetlands), which might be expected to undergo more rapid population changes as a result of climate-driven habitat degradation or improvement (Erwin 2009; Foden et al. 2009) and (iii) long-distance migrants which may be more vulnerable to phenological changes on their breeding grounds (Both et al. 2010; Mayor et al. 2017; Vickery et al. 2014).

2 Materials and methods

2.1 Bird population trends

We obtained information on changes over time in breeding bird population size in Europe during the period 1980–2009 for 145 common species in 20 nation states (termed 'states' henceforward) from the Pan-European Common Bird Monitoring Scheme (PECBMS 2012; Online Resources 1 and 2). For the USA, information on changes in breeding population size during the same period was obtained for 380 bird species in the 48 states of the contiguous USA (also termed 'states') from the US Breeding Bird Survey (Sauer and Link 2011; Online Resources 3 and 4). For a given species, the information consisted of annual indices of population in the state derived from counts conducted annually using comparable methods at survey sites in all European or all US states. The methods used to derive the annual

population indices from the count data are given by PECBMS (2012) and Sauer and Link (2011) for Europe and the USA respectively. The number of species for which annual indices was available for a given state ranged from 36 to 104 species (Europe, Online Resource 2) and from 66 to 215 species (USA, Online Resource 4). The duration of the time period of the data series used to calculate a population trend ranged from 10 to 30 years, depending on state and species (Online Resource 5, PECBMS 2012; Sauer and Link 2011).

Datasets were checked to eliminate state-level trends for species that (i) were of limited temporal extent or (ii) displayed anomalously large inter-annual population fluctuations, possibly indicative of extensive population movements among states or of less robust population estimates. To do this, we applied the following rules. First, state-wide indices of abundance for any species were included only if that species had been monitored since 2000 at the latest. Second, state-level abundance index series for any species that displayed population fluctuations too large to reflect local population processes, such as annual changes of a factor > 10, were excluded (Gregory et al. 2009; Stephens et al. 2016). For Europe, this left 1686 species-state combinations with population data available for analysis, with 6760 species-state combinations available for the USA. For each species and state, a mean annual population trend (r) was calculated as the slope of the ordinary least squares regression of the natural logarithm of the population index on calendar year, using the results for all years for which an eligible population index was available (Online Resource 5).

2.2 Ecological traits

In examining the relationship between bird population trends and trends in climate suitability, we wished to account for ecological traits of species. We used information on three traits previously reported as important predictors of population trends and for which data could be summarised with a high level of confidence at the state-level for both European and North American species: mean body mass, breeding-season habitat association and migratory behaviour (Angert et al. 2011; Buckley and Kingsolver 2012). These traits are correlated with drivers of population trend (e.g. land-use change; Sanderson et al. 2006), and may act as proxies for other ecological traits (e.g. diet, clutch size, brain size, degree of habitat specialisation; Millien et al. 2006).

Body mass was obtained as the mean of the mean masses of male and female birds (g), or of unsexed birds where sex-specific information was not available. Mass data came from Cramp et al. (1977–1994) for European species, and from BirdLife International's World Bird Database for US species (BirdLife-International 2014). We used the natural logarithm of this mean body mass (Lmass) in analyses (Online Resources 1 and 3).

Species were assigned to one of four breeding-season habitat categories (HAB; Online Resources 1 and 3). For Europe, species were assigned a primary breeding habitat, based on information from PECBMS (2012), Gregory et al. (2009), Tucker and Evans (1997) and expert opinion. For the USA, broad habitat use could not be differentiated at state level, so continent-wide habitat preferences were obtained from BirdLife-International (2014) and Poole (2005). Species were allocated to habitat categories if more than 50% of the population in each state used that particular habitat during the breeding season (Gregory et al. 2009). Habitat definitions in the sources consulted differed between Europe and the USA, so for comparability between the two continents, we defined our own broad habitat categories as *forest*, comprising 'forest'

(Europe) and 'forest and shrubland' (USA) habitats; *farmland*, comprising 'farmland' (Europe) and 'grassland' (USA) habitats, both of which included arable and grassland; *inland wetland*, comprising 'wetland' (Europe) and 'inland wetland' (USA) habitats, including rivers, lakes, marshes and other non-marine wetlands and *other*, comprising all habitats not considered forest, farmland or inland wetland.

Each species in each state was assigned to one of four migratory behaviour categories (MIG; Onlines Resource 1 and 3) classifying the behaviour of all or most individuals: *long-distance migrant*, *short-distance migrant*, *resident* and *mixed strategy* species (Gregory et al. 2009). For Europe, this was based on the text and maps in Cramp et al. (1977–1994) supplemented by available migration atlases (Speek and Speek 1984; Spina and Volponi 2008-2009; Wernham et al. 2002; Zink and Bairlein 1987-1995). For the USA, we based the classification on maps in Poole (2005). *Long-distance migrants* were defined as those usually making regular seasonal movements between their breeding range and either, for Europe, a non-breeding range outside the Palaearctic region (Snow and Perrins 1998), or, for the USA, a non-breeding range occurring south of latitude 25° N (the southern tip of Florida). We considered *short-distance migrants* to be those usually making regular migratory or dispersive movements within the Palaearctic region (Europe) or north of latitude 25° N (USA). *Residents* were those where most individuals were non-migratory, making only irregular movements within the Palaearctic region (Europe) or where breeding and non-breeding ranges overlapped by > 50% (USA). The *mixed strategy* category was only used in the USA in instances where information was insufficient to determine where birds from a state migrate to outside the breeding season, although the species was known to migrate to both short- and long-distance destinations in other states.

2.3 Climate suitability trends

Climate suitability trends (CST) for each species and state were derived from SDMs (Online Resource 5), which linked annual grid-cell specific probability of occurrence estimates for a given species to grid-cell specific contemporaneous climatic data. Steps involved in fitting SDMs and using them to derive CSTs followed the methods of Stephens et al. (2016), and are described in the following sections.

2.4 Species occurrence data for SDM fitting

For European birds, species occurrence data (the presence or absence of each species as a breeding bird) was obtained for Europe, Turkey, Cyprus and North Africa (Mediterranean to latitude 20° N). The latter three regions, representing the southern margin of the Western Palaearctic realm, were added to include the southern range margins of as many species as possible, which was expected to improve the performance of the SDMs (Barbet-Massin et al. 2010). For Europe, occurrence data was available for 50 × 50 km UTM squares from Hagemeijer and Blair (1997). Occurrence data for Turkey, Cyprus and North Africa was available for 0.5° × 0.5° latitude-longitude grid cells (approximately equal to 50 × 50 km UTM squares) from BirdLife International Natureserve (2013). For the USA, we used bird species occurrence data for 0.5° × 0.5° latitude-longitude grid cells spanning the whole of North America northwards from latitude 10° N from BirdLife International Natureserve (2013). Occurrence data on both continents was mostly derived from surveys conducted in the 1980s before the most rapid phase of recent climate change.

2.5 Observed climate data for SDM fitting

Monthly mean values for cloud cover, precipitation and temperature for the period 1961 to 1990 were obtained from www.worldclim.org (Hijmans et al. 2005) and CRUTS3.1 (Harris et al. 2014). Soil water capacity data were obtained from Prentice et al. (1992). Climate data were bilinearly interpolated onto the same grid structure as used for species occurrence data (50 km UTM grid for Europe; 0.5° grid for Turkey, Cyprus, North Africa and North America). Bioclimate variables shown elsewhere to be highly influential were derived from climate data following Prentice et al. (1992) and Gregory et al. (2009), and included annual temperature sum above 5 °C (GDD5), mean temperature of the coldest month (MTCO) and an estimate of the annual ratio of actual to potential evapotranspiration (APET). We restricted the number of bioclimate variables used to minimise the risk of overfitting and data-dredging, which can occur when large numbers of candidate explanatory variables are used in fitting SDMs (Pearce-Higgins and Green 2014). We chose these particular variables because they are known to influence the distribution of plant species and vegetation types and could therefore limit species' ranges directly through effects on species' physiology, or indirectly through effects on vegetation and habitats, or on prey, predators, competitors or diseases (Huntley et al. 2007; Pearce-Higgins and Green 2014).

2.6 Fitting the SDMs

For each species, we fitted four types of SDM following Bagchi et al. (2013) to 1980s occurrence data and the 1961–1990 values of the three bioclimate variables. The four SDM types used were generalized linear models (GLMs, McCullagh and Nelder 1989), semiparametric generalized additive models (GAMs, Hastie and Tibshirani 1990), generalized boosted models (GBMs, Elith et al. 2008) and random forests (RFs, Cutler et al. 2007), all of which perform well when compared with other SDM-fitting techniques (Araujo et al. 2005; Elith and Leathwick 2009; Franklin 2009; Meynard and Quinn 2007; Wenger and Olden 2012).

We used a cross-validation approach to fit each type of SDM. The occurrence data used to fit each model was divided into ten similarly-sized blocks each with similar mean values for the three bioclimate variables, but spanning the full range of bioclimates. Blocks comprised spatially disaggregated sampling units consisting of whole or partial global ecoregions (www.worldwildlife.org/science/data). SDMs were fitted to data from nine blocks, excluding each block in turn, with the fitted SDM from each of the ten iterations of this procedure being used, together with grid-cell-specific values of the 1961–1990 bioclimate data to calculate the probability of occupancy for each cell in the left-out block. These predicted probabilities of occupancy were then assembled for the entire area. Full details of model fitting methods, outcomes and measures of goodness-of-fit are presented in Stephens et al. (2016).

2.7 Calculating CST for 1980–2009

For a given species and area (Europe or the USA), the ten models fitted using each SDM approach (i.e. the cross-validation models fitted with each block omitted) were applied to annual bioclimate data from all focal states for each of the years 1980–2009. The climatic data used for this were as described for the SDM fitting, but annual values of the bioclimate variables were used, in combination with the SDMs, to calculate annual values of expected

probability of species occurrence for each grid cell. Predicted probabilities of occurrence were averaged across the ten models for each cell to give the probability of occurrence for that cell in that year from the given SDM method. Probability of occurrence for each cell was then averaged across the four SDM approaches to give an ensemble probability of occurrence for the given cell in the given year. We used an ensemble approach to minimise the influence of potential bias associated with any particular modelling approach (Araújo and New 2007; Araújo et al. 2011; Bagchi et al. 2013). For a given state and year, annual mean probability of occurrence was then averaged across all cells in the state.

For a given species in a given state, the CST was calculated as the slope of an ordinary least squares linear regression of logit annual mean ensemble probability of occurrence (as described above) regressed on calendar year. A positive CST slope indicates an increased probability of occurrence over time (species is predicted to benefit from climate change in that state); a negative slope indicates that the species is predicted to be disadvantaged by climate change. CST was calculated for the same time period over which species-state-specific population trends were calculated, i.e. from 1980 or the first year of population data (whichever was later) to 2009 or the year after which there was no further data (whichever was earlier, Online Resource 5).

2.8 Statistical analysis

The principal objective of our analysis was to examine the relationship between observed recent population trends (r) and trends in climate suitability (CST) at the species-state level for each continent. We had an a priori expectation that r was positively related to CST (Green et al. 2008), and wished to examine firstly whether the strength of this relationship differed between species-states for which climate suitability was expected to decrease (CST-) or increase (CST+), and secondly whether species- and state-specific ecological traits affected the strength of this relationship.

2.9 Population trend vs. CST relationships for species-states expected to be positively or negatively impacted by climate change

To test whether responses to climate change differ between species-state combinations in which populations were expected to benefit from recent observed climate change (i.e. all species with a positive CST [CST+, Online Resources 1–4]) and those expected to be adversely affected (i.e. all species with a negative CST [CST-, Online Resources 1–4]), we compared the slope of the regression of r on CST for these two species-state groups separately through piecewise regression, assuming that the slope of the relationship would change at CST = 0. Linear mixed models (LMMs) were fitted using the lme4 package in R (Bates and Maechler 2009; R Core Team 2013) for Europe and the USA separately, incorporating the crossed random effects of species and state, thus accounting for the non-independence of trends among states within species, and among species within states. We also included random effects of the interactions between species and CST and between state and CST, to account for the non-independence of the relationship between r and CST among populations of a species and between states, and a nested random effect of 'order/family/species' to account for potential phylogenetic non-independence. Our data would not support the fitting of random coefficient terms. For all models, diagnostic plots were used to check that assumptions had been met.

A piecewise test was incorporated into models by including both CST and also the dummy variable CST*, where CST* = 0 if CST < 0 (CST- species-states) and CST* = CST if CST ≥ 0 (CST+ species-states; Hardy 1993). The regression coefficient for CST* represents the estimated difference in slope between the CST- (CST < 0) and CST+ (CST ≥ 0) sections of the CST range. We took the *t* value for the effect of CST* as a test of whether regression slopes differed for CST- and CST+ species and used two-tailed significance tests because the difference in slope could plausibly have been in either direction.

2.10 Population trend vs. CST relationships for species with different ecological traits

To examine the effects of ecological traits on the relationship of *r* with CST, we fitted LMMs, with the same random effects structure as above. We did this separately for Europe and the USA because two of the traits (HAB and MIG) had broadly similar, but not precisely equivalent, definitions on the two continents. We had no a priori expectations about the importance of the trait variables, so our model set of interest included all 27 possible models which included the main effect of CST and the main effects of Lmass, HAB and MIG, as well as their two-way interactions with CST (Online Resources 6 and 7). Including two-way interaction terms in this way allowed us to test the effects of trait variables on the slope of the *r* vs. CST relationship, which was the aim of this analysis. To avoid retention of overly complex models, selection followed the recommendations of Richards et al. (2011) whereby all models with ΔAICc < 6 were classed as a set of top models, excluding models that were more complex versions of those with a lower AICc.

3 Results

3.1 Comparing the *r* vs. CST relationship for species-states expected to be positively or negatively impacted by climate change

A significant positive relationship between population trend and CST was found for both species-state groups on both continents (Table 1; Fig. 1). There was no significant difference in the slope of the relationship between population trend and CST between species-states with expected negative (CST−) and positive (CST+) effects of recent climate change (Table 1; Fig. 1). Hence, there was no statistical support for a weaker

Table 1 Comparison of regression slopes (model coefficients *b*, standard errors SE, and 95% confidence intervals 95% CIs) between population trend and climate suitability trend (CST) for species-state populations on the two continents. The regression coefficient CST* represents the estimated difference in slope between populations expected to be adversely (CST-) or positively affected (CST+) by recent observed climate change. Italicised text indicates results significant at the 0.05 level

Continent		*b*	SE	95% CIs	*t*	*P*
Europe ($n = 1686$)						
	CST	*0.243*	*0.103*	*0.041–0.445*	*2.354*	*0.019*
	CST*	− 0.240	0.185	− 0.602–0.122	− 1.298	0.195
USA ($n = 6760$)						
	CST	*0.186*	*0.069*	*0.050–0.322*	*2.688*	*0.007*
	CST*	0.083	0.116	− 0.143–0.310	0.721	0.471

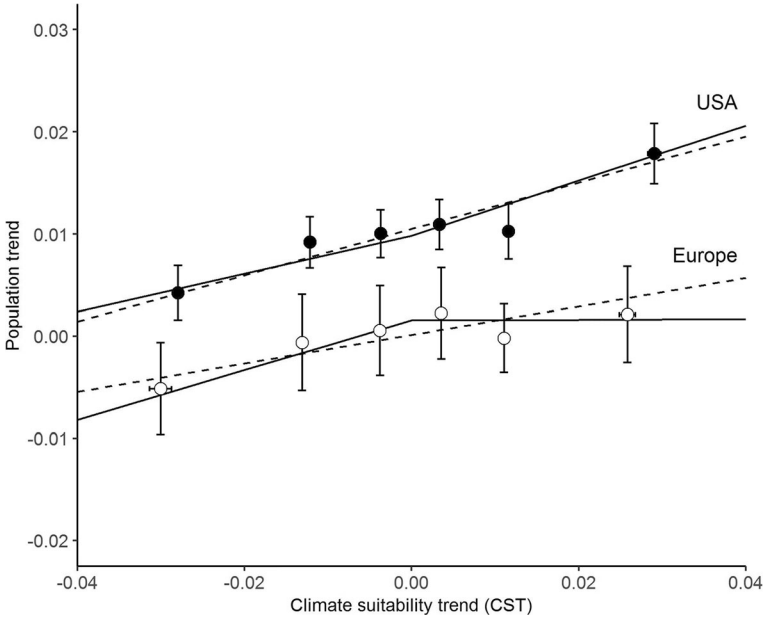

Fig. 1 The effect of climate suitability (CST) on bird population trends (r) for Europe and the USA. Dotted lines represent continent-specific regression models of r on CST from analyses presented by Stephens et al. (2016). Solid lines are those predicted by continent-specific piecewise regression models with a breakpoint at CST = 0 (see Table 1 for model coefficients). All models also included the random effects of species and state. Plotted points are mean values of population trend and CST (± 95% confidence intervals, which are very small for CST) for species-state combinations binned according to their CST value for each continent (species states sorted by descending CST value and grouped into three bins containing approximately equal numbers of CST- species-states and three bins containing approximately equal numbers of CST+ species-states: CST- = 284 and 1263 per bin, CST+ = 278 and 991 per bin for Europe and the USA respectively)

relationship between observed and expected changes for species expected to be affected negatively by recent change.

3.2 Effects of ecological traits on the *r* vs. CST relationship

For both continents, the top model of the relationship of population trend to CST incorporating ecological and life history traits included the two-way interactions between body mass and CST, and habitat association and CST (Table 2, Online Resources 6, 7 and 8). The main effect of migratory behaviour was also included in the top model for Europe, but not for the USA. Two models were eligible for inclusion in the top set for Europe, whilst four other models were also selected in the top set for the USA. For each continent, the top model set contained various combinations of the variables included in the top model.

The direction and magnitude of the effect of species' body mass on the slope of the regression of population trend on CST differed between continents (Fig. 2, Online Resource 8). For European species, the relationship between the r vs CST regression slope and body mass was negative, so the relationship of r to CST was strongly positive for species of low body mass and became less positive as body mass increased (Fig. 2a), as we hypothesised a priori. However, for birds in the USA, the relationship between the r vs CST regression slope and body mass was positive, so the relationship of r to CST was least positive for species of

Table 2 Top sets of linear mixed models of population trend in relation to climate suitability trend (CST) and ecological traits of species for Europe and the USA. Both top sets include only those models simpler than the top model with ΔAICc < 6. Models are shown in order of increasing AICc from the top model (shown in italics). Variables included in each model are denoted by codes: *HAB* broad habitat association, *Lmass* natural logarithm of body mass in grams. The log likelihood (logLik), number of fitted parameters (df) and Akaike weight (w) are shown for each model. Two-way interaction terms are coded by placing ':' between two variable codes. Results for the full set of models considered are presented in Tables S6 and S7

Continent	Variables retained	logLik	df	AICc	ΔAICc	w
Europe	*CST + Lmass + HAB + MIG + CST:Lmass + CST:HAB*	*3043.0*	*20*	*− 6045.5*	*0.0*	*0.47*
	CST + Lmass + HAB + CST:Lmass + CST:HAB	3040.7	18	− 6045.1	0.4	0.38
USA	*CST + Lmass + HAB + CST:Lmass + CST:HAB*	*10,861.4*	*18*	*− 21,686.8*	*0.0*	*0.19*
	CST + Lmass + CST:Lmass	10,855.4	12	− 21,686.7	0.1	0.18
	CST + Lmass + HAB + CST:Lmass	10,860.1	17	− 21,686.1	0.6	0.14
	CST + Lmass	10,853.6	11	− 21,685.2	1.6	0.08

low body mass and became more positive as body mass increased (Fig. 2b), counter to our expectation. This contrary effect appears to be driven by the strength of the response of the largest birds on this continent (Fig. 2). When only species of a comparable mass range (10–100 g, spanning the interquartile range of body mass for European species and excluding the heaviest species in the USA, Fig. 2) were included in analysis on both continents, the interaction between *r* vs CST regression slope and body mass was no longer upheld as important in the top model for the USA, although its effect in Europe remained unchanged (Online Resource 9).

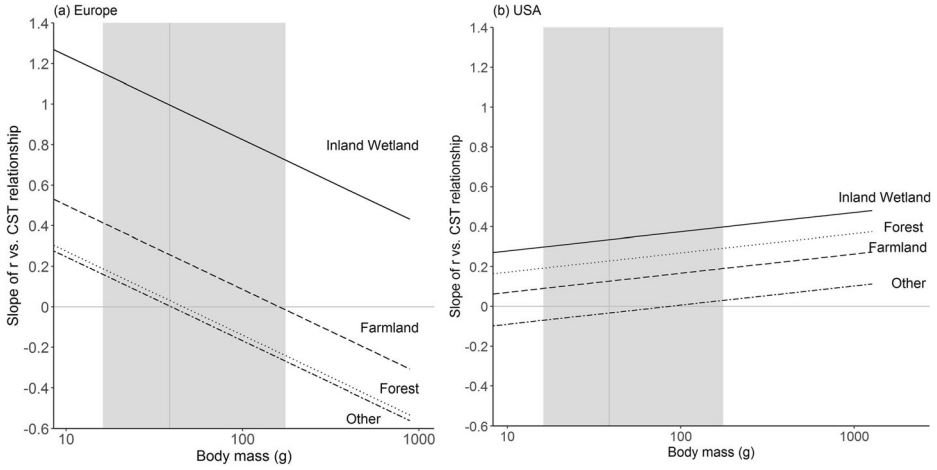

Fig. 2 Regression slopes of the relationship between bird population trends (*r*) and climate suitability trend (CST) derived from the top model for (**a**) Europe and (**b**) the USA. The top models for the two continents both included the main effects of CST, log body mass (Lmass) and habitat and the two-way interactions of CST with each of Lmass and habitat (Table 2, Online Resource 8). Each line shows the modelled slope of the *r* vs. CST regression in relation to body mass for a single habitat type, with the horizontal extent of the line corresponding to the central 90% of body mass values for the species studied on each continent. The shaded area shows the interquartile range of body mass and the vertical line its median value. For Europe, the lines for *forest* and *other* almost coincide, so for clearer differentiation between these habitats, the line for *forest* has been jittered upwards by 0.02 (the direction indicated by the model). Line segments lying above the horizontal grey line represent positive modelled relationships between *r* and CST

On both continents, species associated with *inland wetland* had the most positive relationship of *r* to CST. Species associated with *other* habitats had the least positive relationship, and relationships for *farmland* and *forest* species were of intermediate strength (Fig. 2, Online Resource 8). The slope of the *r* vs CST regression was positive across the whole of the observed range of body mass for species associated with *inland wetland* in Europe and for species associated with *inland wetland*, *farmland* and *forest* in the USA. It was also positive across most of the observed range of body mass for species associated with *farmland*, *forest* and *other* habitats in Europe but not for species associated with *other* habitat in the USA.

4 Discussion

Our analyses of over 500 bird species confirm the overall positive relationship between population trend and climate suitability on our two focal continents in support of Stephens et al. (2016) and others (Green et al. 2008; Gregory et al. 2009). Importantly, we found no statistically supported difference in the strength of the relationship between population trend and climate suitability change between those species expected to benefit from climate change and those expected to be adversely impacted, failing to support previous reports that the positive effects of climate change have been more pronounced than its negative effects. Across our sample of 525 species over the two continents, we therefore found no strong evidence of a greater tendency for delay in effects of climate change on species' populations projected to be negatively impacted compared to those projected to be positively impacted by climate, in contrast to suggestions from previous, often finer-scale studies (e.g. see Thomas et al. 2006). The positive relationship between population trend and climate suitability largely persisted regardless of species ecology, although the strength of relationship varied with ecological traits, further increasing the causal evidence of a consistent effect of climate change on bird populations over recent decades.

It has been suggested that the evidence for negative population responses to climate change may be less strong than for positive population responses (e.g. Parmesan et al. 1999; Parmesan and Yohe 2003; Root et al. 2003; Thomas and Lennon 1999). However, our evidence of a positive relationship between population trend and CST was, if anything, more compelling for species-states expected to be negatively impacted rather than those expected to benefit (Fig. 1). A similar study examining community composition found a similar effect of comparable contributions of both cold-dwelling (~CST-) and warm-dwelling (~CST+) species to regional climate-induced changes across a smaller geographic area (Tayleur et al. 2016). A possible explanation for why we found no evidence that species favoured by changing climate suitability have responded more strongly than species expected to be disadvantaged, may be that we compared range change predictions from models of distribution data with detailed abundance data in our analyses. Assessments of climate impact based on distribution data alone are more likely to be biased towards increases in range which are often more noticeable (Thomas and Abery 1995; Thomas et al. 2006), whilst abundance data from long-term population monitoring schemes, by being more sensitive to changes than range, are unlikely to share this bias. This therefore stresses the importance of long-term population monitoring schemes over simple spatial occupancy data for detecting large-scale species' responses to environmental changes. Our assumption of a linear relationship between population trends and climate suitability may have resulted in our analysis being less able to capture the nature of the relationship. Developing theory to guide understanding of the relationship between population trends and climate suitability would provide a useful area of future research.

The population trend vs. CST relationship was slightly less positive for CST+ species in Europe than the other groups tested, indicating that this group may be less able to take advantage of an increasingly suitable climate. This may reflect differences in the underlying trajectories of avian abundance between the two continents, with average trends in Europe predominantly negative since 1980 (EBCC 2014), whilst US bird populations have, on average, remained relatively stable (Sauer and Link 2011; Stephens et al. 2016). This is reflected in the lower mean values of population trend at a given value of CST in Europe compared to the USA evident in Fig. 1. These different patterns could be related to the proportion of rare species included in population monitoring data for the two continents. In Europe, rarer species have been faring better than more common species (Inger et al. 2015) but our European dataset is focussed on common birds (PECBMS 2012). Differences in land-use change on the two continents (Clavero et al. 2011; Kampichler et al. 2012), both in terms of current rates of change and levels of historical conversion, might also have a bearing on mean population trajectories.

Another explanation for why CST+ species may not be responding as positively in terms of population trend in Europe is if they are following the pattern of increasing climate suitability into an ecological trap due to changing land use and intensity patterns (Herrando et al. 2014). This could be the case if pressures other than climate change, such as agricultural intensification or land abandonment, were particularly prevalent in Europe compared to the USA (e.g. Lasanta et al. 2017).

The strength of the relationship between population trend and climate suitability varied in relation to the same ecological traits on both continents, with similar patterns found for species associated with different habitat types; associations with body mass, however, were more complex. It has been proposed that a warming climate favours smaller species (Atkinson 1994; Millien et al. 2006; Sheridan and Bickford 2011), and distribution shifts driven by climate change may be stronger in small-bodied species with more rapid reproduction and shorter generations (Devictor et al. 2012), so we expected that smaller species would respond more positively to warming climate and associated range changes. In accord with this hypothesis, we found that species with smaller body mass had a more positive population trend to CST relationship, but only in Europe.

In the USA, we found the opposite effect of body mass on the population trend to CST relationship, with larger species apparently having more positive population trend vs. CST relationships. This relationship was not supported when we considered equivalent mass ranges (10–100 g) of species on both continents however, suggesting that it is driven by strong responses to climate change among the very largest species in the USA. The reasons for this finding are unclear but could be explained by the inclusion of large bodied wetland species in our US dataset, which, as discussed below, appear to be more responsive to environmental change. Similar large bodied wetland species are absent from our European data set, potentially explaining the discrepancies in these results.

As hypothesised, species associated with different breeding habitats responded differently to changes in climate suitability, and these responses were largely consistent on both continents. Species associated with inland wetlands showed a consistently more positive relationship between r and CST than those associated with other habitat types. The biota of wetlands may be more responsive to environmental changes due to the already seasonal or stochastic

nature and spatial or temporal patchiness of wetland habitats relative to less labile ecosystems (e.g. forests), which can withstand environmental changes for many decades without exhibiting large-scale community changes (Erwin 2009; Lindner et al. 2010). Wetland breeding birds may also make longer-distance dispersal movements than those associated with dry habitats for the same reason (Paradis et al. 1998), so they may be better able to respond more rapidly to changing conditions. Strong and increasing protection of wetlands relative to other habitats, at least in Europe (Butchart et al. 2012), may also allow wetland bird populations to better track the direction of climate suitability without the trade-off of also adapting to habitat change and other threats (Gaüzère et al. 2016). These habitat changes and threats may also be more coherent with the impact of climatic changes (e.g. drainage and water abstraction similar to the drying effects of reduced rainfall and warmer temperatures; Erwin 2009), potentially explaining the enhanced the strength of the *r* and CST relationship for wetland species.

Surprisingly, migratory behaviour was not found to be important in affecting the strength of the relationship between population trend and CST on either continent. Long-distance migrants are less able to adapt their phenology than their resident and short-distance migrant counterparts. Phenological mismatch renders long-distance migrants vulnerable to the effects of worsening climate suitability across their breeding grounds, whilst also rendering them less able to benefit from improvements in climate suitability (Both et al. 2010; Franks et al. 2018; Mayor et al. 2017; Samplonius et al. 2018; Vickery et al. 2014). In addition, the effects of phenological mismatch vary between species, study systems and habitats (Both et al. 2010; Hurlbert and Liang 2012). With potentially contrasting responses by migratory species to changes in climate suitability, the effect of migratory behaviour on the *r* vs CST relationship may be weaker than expected.

Taken together, our results indicate that ecological traits and habitat associations substantially affect the strength of bird population responses to changing climate suitability, but that their impact may not always be consistent even between continents. Much emphasis is currently placed on examining the likely impacts of ecological traits on species' responses to climate change, with the aim of predicting global patterns of climate change adaption (e.g. Angert et al. 2011; Jiguet et al. 2007; Jiguet et al. 2010; Pearson et al. 2014). Our results suggest that generalizing the impacts of these traits from localised geographical studies, even those examining whole continents, to a universal scale may not be robust.

Thomas et al. (2006) highlighted the likely artefactual perception that range expansions and population increases as a result of climate change are more widespread than range retractions and population decreases. Here, we have shown that despite differences in species ecology, the relationship between population trend and climate suitability trend is persistently positive across an entire taxonomic group and two continents, with no evidence that species favoured by climate change have responded more strongly than those disadvantaged by it, thus providing clear evidence that climate change is causing widespread strong, quantifiable population increases and declines in equal measures.

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