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RESEARCH PAPER

Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds

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ABSTRACT

Aim Species are expected to move uphill or poleward in response to climate change, yet their distributions show idiosyncratic responses; many species are moving in the predicted direction, but others are not shifting at all or are shifting downhill or towards the equator. Fundamental questions remain about the causes of interspecific variation in range responses and whether shifts along elevational and latitudinal gradients are correlated. We examined whether shifts in northern-latitude and upper-elevation boundaries of western North American songbirds over a 35-year period were correlated and whether species ecological and life-history traits explained interspecific variation in observed shifts.

Location North America.

Methods We used data from the North American Breeding Bird Survey to determine shifts in northern-latitude and upper-elevation boundaries of 40 North American songbird species between two time periods, 1977–81 and 2006–11. We used an analysis of covariance approach that controlled for species population trends and changes in survey effort to test whether: (1) songbirds shifted in elevation, latitude or both; (2) shifts in elevation and latitude were correlated; and (3) responses could be explained by species-level traits including life history, ecological generalization and dispersal capability.

Results The majority of species shifted uphill and poleward during this period, but there was no correlation between the distances that species range boundaries shifted in elevation and latitude. Species with smaller clutch sizes and narrower diet breadths exhibited greater northward shifts, while species with larger clutch sizes and narrower diet breadths exhibited greater uphill shifts.

Main conclusions Shifts in latitude and elevation were not correlated. However, a common set of species-level traits explained differential responses among species to climate change. Consideration of shifts in both elevation and latitude is needed to understand the full extent to which species are tracking changing climates.

Keywords
Ecological specialization, global climate change, life history, range shifts, species traits.

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INTRODUCTION

Species are expected to shift poleward and uphill in response to climate change (e.g. Peterson *et al.*, 2002; Virkkala *et al.*, 2008). However, while many species are indeed shifting in these predicted directions, others are not shifting at all or are shifting downhill or towards the equator (Hickling *et al.*, 2006; Moritz *et al.*, 2008; Chen *et al.*, 2011). Species whose shifts are lagging behind those of their climate envelopes (Devictor *et al.*, 2008; Forero-Medina *et al.*, 2011) may face an increased risk of

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extinction (Thomas *et al*., 2004). Differential range responses among species may also lead to the formation of no-analogue communities (Le Roux & McGeoch, 2008) and altered ecological interactions (Schweiger *et al*., 2008) that could negatively affect populations. These impacts demonstrate an urgent need to understand the full extent to which species are expanding their ranges and to determine which general patterns of site and species characteristics can be used to explain current shifts and to forecast future responses.

Most species live in areas with some topographical relief, and topographically complex areas such as mountainous regions make an important contribution to global biodiversity (Coblentz & Riitters, 2004; Orme *et al*., 2005). In theory, many species should therefore have the opportunity to track climate change through shifts in latitude, elevation or both. Studies have documented range shifts in elevation or latitude for many different organisms in response to recent climate change (e.g. Parmesan & Yohe, 2003), but none to our knowledge have considered elevational and latitudinal shifts simultaneously to examine whether such shifts are correlated. This is critical because studies that fail to consider shifts in both elevation and latitude may underestimate the extent of species responses and their capacities to respond to climate change.

Species differ greatly in the rates at which their range boundaries are shifting (Hickling *et al*., 2006), but the reasons for this variation are also not clear. Some species may not be shifting as much as others because they occupy areas where climate change has been less pronounced (Solomon *et al*., 2007; Loarie *et al*., 2009) or where climatically favourable habitats within their current range are still available (Hill *et al*., 1999). However, differential responses among sympatric species (Hickling *et al*., 2005; Chen, 2009) suggest that the degree to which species are shifting into new areas may be constrained by limitations imposed by their ecology and life history.

A species' capacity to track spatial shifts in its climatic optima will depend on its ability to disperse to and become established in areas with newly favourable conditions. Species that are mobile and can disperse great distances (e.g. migratory species) might be more successful in reaching newly suitable habitats (Schloss *et al*., 2012). Once within the new habitat, population persistence is likely to be driven by the degree of ecological generalization, such that generalists might be more successful in meeting their needs for food and shelter than specialists (Jeschke & Strayer, 2006). Species with faster life histories may also be better colonizers since their higher reproductive rates allow them to more rapidly reach larger population sizes that are less susceptible to environmental and demographic stochasticity (Angert *et al*., 2011; Buckley, 2012).

Ecological and life-history traits may be good predictors of species shifts in their northern-latitude and upper-elevation boundaries. However, few studies to date have examined their explanatory value, and results thus far are equivocal (Angert *et al*., 2011; Buckley, 2012). Whether a common set of traits can be used to predict shifts in both elevation and latitude is also unknown. Knowledge of these species-level traits may strengthen predictions for future species assemblages and aid resource managers in implementing protective measures that accommodate species responses to current and future climate change. Further work on the issue of whether species-level traits can be used to predict range responses to climate change is therefore warranted.

We examined shifts in northern-latitude and upper-elevation boundaries among songbird species breeding in western North America. Western North America is one of several regions projected to experience more intense levels of future warming relative to other areas throughout the globe (Diffenbaugh & Giorgi, 2012), but the region has already experienced substantial warming over the last 50 years (Booth *et al*., 2012). As such, we predicted that many bird species have already shifted their breeding ranges to higher elevations and/or more northerly latitudes. Using bird survey data collected over the last 35 years, we tested whether shifts in northern-latitude and upper-elevation boundaries were occurring independently or were correlated across species. We then examined whether traits associated with dispersal capability, ecological generalization and life-history strategy – specifically migratory behaviour, diet breadth, breeding range size and clutch size – explained species differences in boundary shifts. We also investigated whether a common set of species-level traits could be used to predict shifts in both elevation and latitude.

METHODS

Taxonomic and geographic scope

We examined shifts in upper-elevation and northern-latitude boundaries in songbirds using data from the Breeding Bird Survey (BBS; US Geological Survey Patuxent Wildlife Research Center, 2012). The BBS is a long-term (1966 onwards), large-scale monitoring programme that tracks the distribution and abundance of North American birds, primarily in the United States and southern Canada (Robbins *et al*., 1986). Routes are 40 km long, located along secondary roads and surveyed annually during the daytime and the height of the breeding season. Bird abundance is recorded during 50 3-minute point counts every 0.8 km along each route, and data on species abundances are summarized across 10 point counts conducted within each of five 8-km segments along each route (US Geological Survey Patuxent Wildlife Research Center, 2012).

We investigated boundary shifts between the two 5-year periods of 1977–81 and 2007–11. We did not consider data from the first decade during which the BBS was conducted because of the smaller number of routes surveyed. We focused on boundary shifts occurring in the topographically complex region stretching from the southern border of the United States northward to 54° N latitude where the density of routes starts to diminish in southern Canada, and from the Pacific coastline east to 97° W longitude (Appendix S1 in Supporting Information).

Species had to meet several criteria to be included in our analyses. First, we restricted our analyses to songbirds (order Passeriformes) since they comprise the majority of species in North America and are the group most reliably surveyed by the

BBS (US Geological Survey Patuxent Wildlife Research Center, 2012). Second, we were interested in the extent to which species can respond to climate change by expanding into and becoming established in new breeding areas under climate change, so we avoided including transients by restricting the analyses to records where a species was observed along a route segment for at least 3 years within one or both of the 5-year time periods. Third, a species' northernmost boundary had to be within the limits of the study area but south of 52° N during the first time period since this gave us an approximately 220-km buffer within which to detect northward shifts. Fourth, we considered only those species whose distributions included mountainous regions within the Pacific and Rocky Mountain systems, i.e. those which had the opportunity to shift in elevation, and those whose uppermost elevational extent during the first time period was lower than 3100 m since this gave us an approximately 240-m buffer within which to detect upward shifts.

Elevational and latitudinal distributions

We first determined the elevational and latitudinal distributions for each species. Latitude and elevation can vary considerably along the length of an entire 40-km route, so we based our analyses on bird data for the 8-km segments along each route to reduce within-route variation. Using a digital map of BBS route locations (US Geological Survey Patuxent Wildlife Research Center, 2002) within ArcMAP (ArcGIS 10.0, ESRI 2010), we identified the 8-km segments for which bird abundances are summarized and used a 30-arcsec digital elevation map of North America (US Geological Survey EROS Data Center, 1996) to determine both the elevation and latitude for the endpoints of each segment. Elevation and latitude for each segment were calculated as the mean of the two segment endpoints.

We then determined the upper-elevation and northern-latitude boundary for each species for each of the two sampling periods. Only those routes that were surveyed during both time periods were considered (Appendix S1). We also excluded records of a species' northernmost latitude or uppermost elevation if only one individual was observed at the survey point (Wilson *et al*., 2005). Additionally, we considered only the segment with the highest elevation and the segment with the northernmost latitude at which that each species was detected along each route and during each sampling period to avoid the inclusion of multiple measures per route per period in our analyses.

We identified the 10 northernmost latitudinal and 10 highest elevational extents for each species for each time period and then used the difference in means between these two time periods to quantify shifts in the distributional margins of each species. We chose this approach to evaluating boundary shifts for consistency and comparability with other studies of species distributional shifts in North America and Europe (Thomas & Lennon, 1999; Hitch & Leberg, 2007; Pöyry *et al*., 2008) and because it allowed us to examine shifts occurring across a broad portion of a species' northern-latitude and upper-elevation boundary but without including routes that were located too far into the core of a species' distribution.

Species-level traits

We obtained data on dispersal capability, life-history strategy and ecological generalization of western North American songbirds from the Birds of North America Online (Poole, 2005). We used migratory status (migrant versus resident) as an indicator of dispersal capability since natal and breeding dispersal distance is greater in migratory than non-migratory birds (Paradis *et al*., 2002). Estimates of reproductive rate were not possible given that generation time and the number of broods per year is not well studied in many species. Thus, clutch size was used as a measure of life-history strategy since it is correlated in birds with age at maturity, and offspring and adult survival (Ricklefs, 2000; Jetz *et al*., 2008). In those cases where multiple estimates of clutch size were available for a particular species we used the mean of those estimates as our measure of clutch size. Diet breadth was used as an index of ecological generalization. Data on diet breadth were gathered from both the *Birder's Handbook* (Ehrlich *et al*., 1988) and the Birds of North America Online (Poole, 2005) and were combined to create an index of the number of different food types consumed by each species. Food types were designated as being arthropods, seeds, fruit, nectar, vegetative plant parts such as leaves and carrion. Breeding range size, a positive indicator of habitat breadth in birds (Cofre *et al*., 2007), was also used as an index of ecological generalization. Breeding range size was calculated using breeding range maps for each species available from NatureServe (http://www.natureserve.org). Maps were projected using a World Sinusoidal projection and range size, in square kilometres, was estimated using the calculate geometry option in ArcMAP (ArcGIS 10.0, ESRI 2010).

Statistical analyses

We used analyses of covariance (ANCOVA) to test whether shifts in northern-latitude and upper-elevation boundaries across species were significantly different from zero. The intercept served as a measure of how far range margins shifted. We then used partial correlation analysis to determine whether shifts in upper-elevation and northern-latitude boundaries were correlated across species. Finally, we used ANCOVA to test whether shifts in latitude and elevation differed among species according to their migratory status, clutch size, diet breadth and breeding range size. Again, the intercept served as a measure of how far range margins shifted (Thomas & Lennon, 1999). Migratory status was modelled as a fixed categorical effect while clutch size and breeding range size were included as continuous predictors. The historic upper-elevation boundary of species during the period 1977–81 was included as a covariate in all analyses since it could limit species opportunities or our ability to detect uphill or northward shifts. Similarly, the northern boundary of species was included in the analyses of shifts in latitude since it could limit our opportunity to detect northerly shifts.

The expansion of species into new habitat or retraction from previously occupied habitats may be due simply to increases or decreases in their population sizes, respectively, and not because of any cause related to climate change. To account for species population trends in our analyses, we compiled BBS estimates of species trends between 1977 and 2010 (data for 2011 were not yet available) for the western BBS region (Sauer *et al.*, 2011) and included them as a covariate in our analyses. Trends for each species are based on the ratio of abundances derived from hierarchical model estimates of the annual abundance of each species during the first and last years of the study period (Link & Sauer, 2002).

Changes in survey effort across sampling periods were also included as a covariate because they may influence observed shifts beyond the effects of species population trends (Kujala *et al.*, 2013). The number of hours of effort per route per year was constant since routes are surveyed using 50 3-min point counts, but the number of years that a route was surveyed within each 5-year sampling period varied across routes. Thus, we included as a covariate the difference between the total combined number of years for which the 10 northernmost and 10 uppermost routes were surveyed across the two sampling periods (Kujala *et al.*, 2013). In particular, we included the difference in survey effort that occurred along routes occupied during the first sampling period for species whose boundaries retracted southward and downhill, and the difference in survey effort that occurred along routes occupied during the second sampling period for species whose boundaries expanded northward or uphill during the 35-year time period (Kujala *et al.*, 2013).

To identify which factors were the best predictors of shifts in latitude and elevation, we first evaluated the full model for each dependent variable and then used backward model selection, sequentially eliminating terms of explanatory variables with the lowest F-values until all terms in the model were significant. Results from the full and reduced models were qualitatively the same, so we report results only for the reduced models since this enabled us to calculate the total amount of variation (R^2) explained by the final set of predictors. Variance inflation factors and correlations between predictor variables were assessed to evaluate the potential for multicollinearity. Predictors had low variance inflation factors (all < 2.3) and were not highly correlated with one another (all $r < 0.52$; Appendix S2).

Variation in range margin shifts among species may be influenced by their evolutionary history, so we repeated the above analyses using Grafen's PHYREG macro for SAS (Grafen, 1989, 2006) to control for phylogenetic relatedness among species. We assembled a working phylogeny (Appendix S3) based on the Passeriformes supertree of Jønsson & Fjeldså (2006), supplemented with more recently published phylogenies for Tyrannidae (Tello *et al.*, 2009), Emberizidae (DaCosta *et al.*, 2009) and Icteridae (Jacobsen *et al.*, 2010). Since we did not have branch length estimates, we assumed equal lengths. We also used the branch lengths methods of Grafen (1989), whereby the ages of nodes are set equal to one less than the number of species arising from that node, but the results were the same. Results controlling for phylogeny were qualitatively identical to those using raw data, so we only report results from analyses based on raw data.

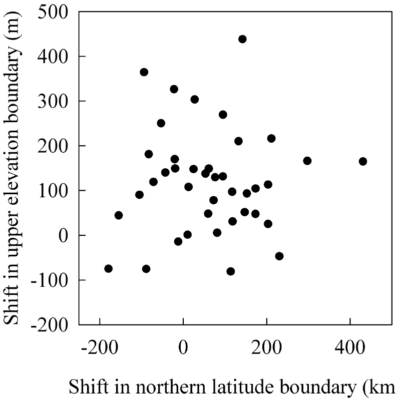

Figure 1 Correlation between shifts in upper-elevation and northern-latitude boundaries ($r = 0.15$, $n = 40$, $P = 0.38$) of 40 songbird species in western North America between the time periods 1977–81 and 2006–11.

RESULTS

Shifts in latitude and elevation were evaluated for 40 songbird species (Appendix S4) that were detected along a total of 559 routes throughout western North America (Appendix S1). Shifts in the northern-latitude boundary ranged from 179.1 km south to 431.89 km north and averaged 1.84 km year^{-1} northward across species. Overall, the northern boundary shifted northwards across all species over the 35-year period (estimate ± 1 SE: 35.27 ± 15.76 km, $t_{38} = 2.24$, $P = 0.03$) after controlling for changes in survey effort (8.6 ± 1.5, $t_{38} = 5.66$, $P < 0.001$).

Shifts in the upper-elevation boundary ranged from 81.1 m downhill to 438.0 m uphill across species and averaged 3.6 m year^{-1} upwards across species. Overall, the upper-elevation boundary shifted upward across all species over the 35-year period (65.8 ± 22.2 m, $t_{38} = 2.96$, $P < 0.01$) after controlling for changes in survey effort (8.6 ± 2.4, $t_{38} = 3.59$, $P < 0.001$). Shifts in elevation and latitude were not correlated ($r_{33} = 0.15$, $P = 0.38$; Fig. 1) after controlling for species historic range limits, population trends and survey effort.

Species ecological and life-history traits associated with dispersal ability, ecological generalization and life-history strategy differed in the amount of variation in latitudinal and elevational shifts they explained. There was no evidence that range size, migratory behaviour, historic northern boundary or population trend influenced shifts in latitude. However, clutch size, diet breadth, historic upper-elevation boundary and survey effort together explained 66% of the variation among species in their shifts in latitude. Species with smaller clutch sizes (−46.5 ± 15.8, $t_{35} = -2.94$, $P < 0.01$, partial-eta squared $\eta_p{}^2 = 0.20$; Fig. 2a), narrower diet breadths (−33.3 ± 11.9, $t_{35} = -2.79$, $P < 0.01$, $\eta_p{}^2 = 0.18$; Fig. 3a), and lower upper-elevation boundaries (−0.1 ± 0.02, $t_{35} = -2.18$, $P = 0.03$, $\eta_p{}^2 = 0.12$; Fig. 4) shifted

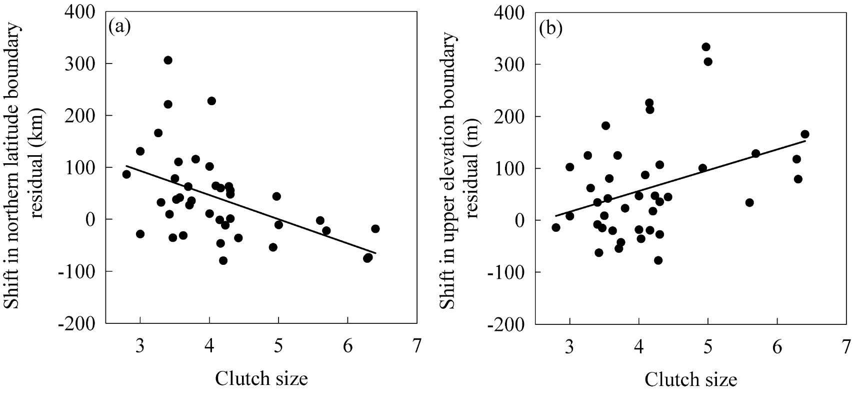

Figure 2 Effects of clutch size on shifts in northern-latitude ($n = 40$, $P < 0.01$, $\eta_p^2 = 0.20$) and upper-elevation ($n = 40$, $P = 0.02$, $\eta_p^2 = 0.14$) boundaries of 40 songbird species between the time periods 1977–81 and 2006–11. Plotted on the ordinate are the residuals after accounting for effects of the other predictors in the final model. Parameters were evaluated at survey effort = 0, mean historic upper elevation boundary = 1544 m and mean diet breadth = 2.4.

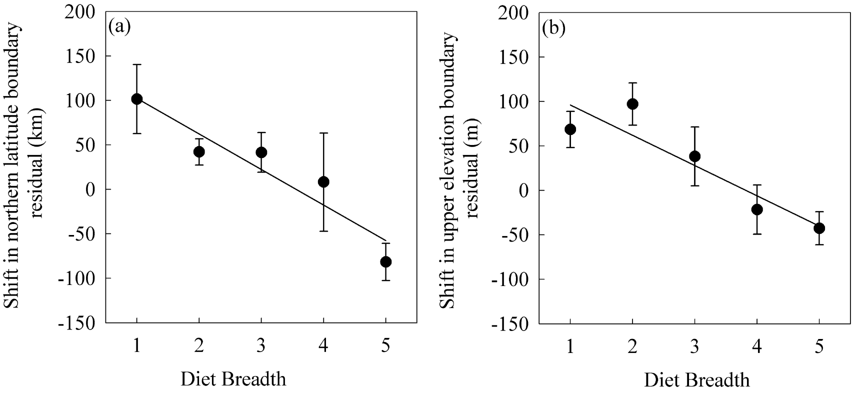

Figure 3 Effects of diet breadth on shifts in northern-latitude ($n = 40$, $P < 0.01$, $\eta_p^2 = 0.18$) and upper-elevation ($n = 40$, $P = 0.01$, $\eta_p^2 = 0.15$) boundaries of 40 songbird species between the time periods 1977–81 and 2006–11. Plotted on the ordinate are the residuals after accounting for effects of the other predictors in the final model. Parameters were evaluated at survey effort = 0, mean clutch size = 4.1 and mean historic upper-elevation boundary = 1544 m.

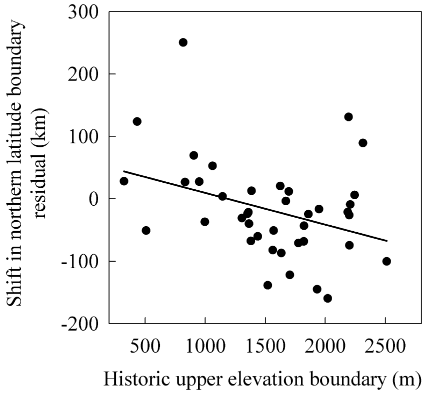

Figure 4 Effects of historic upper-elevation boundary on shifts in northern latitude ($n = 40$, $P = 0.03$, $\eta_p^2 = 0.12$) of 40 songbird species between the time periods 1977–81 and 2006–11. Plotted on the ordinate are the residuals after accounting for effects of the other predictors in the final model. Parameters were evaluated at survey effort = 0, mean clutch size = 4.1 and mean diet breadth = 2.4.

further north in latitude than species with larger clutches and wider diet breadths after controlling for survey effort (6.8 ± 1.4, $t_{35} = 4.75$, $P < 0.001$, $\eta_p^2 = 0.40$).

With respect to elevation, there was no evidence that range size, migratory behaviour, species population trend or historic upper-elevation boundary influenced shifts in elevation. However, clutch size, diet breadth and survey effort together explained 43% of the variation among species in their shifts in elevation. Species with larger clutch sizes (40.0 ± 16.7, $t_{36} = 2.39$, $P = 0.02$, $\eta_p^2 = 0.14$; Fig. 2b) and narrower diet breadths (−35.1 ± 14.1, $t_{36} = -2.49$, $P = 0.01$, $\eta_p^2 = 0.15$, Fig. 3b) shifted further up in elevation than species with smaller clutch sizes and wider diet breadths after controlling for changes in survey effort (9.1 ± 2.2, $t_{36} = 4.13$, $P < 0.001$, $\eta_p^2 = 0.32$).

DISCUSSION

The majority of bird species in this study exhibited uphill or northward shifts in their breeding range boundaries. This is not surprising given that bird distributions, like those of other organisms, are sensitive to temperature (Böhning-Gaese & Lemoine, 2004), and summer temperatures increased in this region over the duration of the study period (Booth *et al.*, 2012). Yet the rates at which species expanded their northern-latitude and upper-elevation boundaries were not correlated. Our observation that some species are shifting little in latitude but substantially in elevation, and vice versa, demonstrates that studies focusing on shifts in only one dimension may underestimate species capacities to cope with climate change. Similarly, focusing on shifts in only one direction may also underestimate species responses when shifts are occurring in both directions. Accounting for shifts in both latitude and elevation may therefore help to fine tune our assessments of the degree to which species are tracking shifts in their climate envelopes and their subsequent vulnerability to climate change.

Variation among species in the degree to which their northern-latitude and upper-elevation boundaries shifted over the 35-year period was correlated with a common set of ecological and life-history traits – diet breadth and clutch size. Diet breadth was negatively correlated with the degree to which species shifted in latitude and elevation, diet specialists expanding northward and uphill to a greater degree than diet generalists. Diet generalists are often predicted to expand their ranges more in response to climate change because they are better able to take advantage of new food types they might encounter (Buckley, 2012). However, our results indicate the opposite: that the distributions of diet specialists may actually be more sensitive to climate change. Similar to the results we report here, Swedish butterfly and moth species whose larvae exhibit greater specialization on plants in nitrogen-rich soils have shifted further in latitude than those species with a more general larval diet (Betzholtz *et al.*, 2013). Greater shifts among diet specialists may occur because they are more likely to track spatial shifts in their prey or host than diet generalists. However, diet breadth also had a positive, albeit weak, effect on latitudinal shifts in the wintering ranges of North American birds (Angert *et al.*, 2011), so the generality of our results is not yet clear.

Clutch size, as a measure of life-history strategy, was also correlated with species range margin shifts, but in an opposing direction, being positively correlated with the degree of elevational shifts but negatively correlated with latitudinal shifts. Species with faster reproductive rates are often expected to expand their range margins at faster rates (Angert *et al.*, 2011; Buckley, 2012). However, a recent study of avian invasions throughout the world provides compelling evidence that species with slower life histories may be more successful at invading novel environments (Sol *et al.*, 2012), presumably because adaptations such as the prioritization of future over current reproduction and larger brain size make them less vulnerable to stochastic fluctuations and help buffer them against challenges imposed by new environments (Sol *et al.*, 2005, 2012). These findings might apply to the patterns we observed here if latitudinal shifts involved the invasion of more novel or stochastic environments relative to elevational shifts. For example, species shifting in latitude might encounter a higher diversity of new habitat types or greater variability due to habitat fragmentation, urbanization or climate extremes than those shifting up in elevation. However, we currently know very little about the extent to which range boundary shifts have thus far necessitated the invasion of new habitat types, or whether changes in climate or environmental variability differ between latitudinal and elevational gradients. While the influence of life-history strategy on climate change-driven range shifts requires further attention, our results suggest at the very least that the constraints underlying shifts in latitude and elevation are not equivalent and underscore the need for more fine-scaled analyses of the environmental challenges faced by populations expanding at their northernmost and upper-elevation range boundaries.

Finally, upper-elevation boundary had an important influence on the degree to which species shifted in latitude but not elevation; higher-elevation species shifted northward to a lesser degree than lower-elevation species. Slower northward shifts could be an artefact of the smaller number of high-elevation routes surveyed by the Breeding Bird Survey (Lawler & O'Connor, 2004) or may be due to the constraints that mountaintops place on expansion. High-elevation species are among those predicted to have the highest risk of climate change-induced extinction, given the limited availability of uphill terrain (Sekercioglu *et al.*, 2007). Species could compensate for these constraints by shifting poleward in latitude, but we show here that higher-elevation bird species are shifting less in latitude. This is surprising given that birds are highly mobile and that mountain ranges in western North American run in a north–south direction and therefore have the potential to accommodate northward shifts among high-elevation species. Taken together, these results support current predictions that high-elevation species will be among those that are more vulnerable to extinction if climate change continues at its present rate (Sekercioglu *et al.*, 2007).

Traits associated with ecological generalization and life-history strategy were important predictors of the magnitude of range shift. Yet they explained only around 50% of the variation among species. Additional variation among species may be explained by a number of causes that may or may not be related to climate change. For example, species may differ in how sensitive they are to different climatic factors, e.g. temperature versus precipitation (Tingley *et al.*, 2012), temporal aspects of climate change, e.g. long-term averages, more recent climate norms, or extremes (Beever *et al.*, 2010). The degree to which different aspects of climate have changed over the study period also varies spatially across western North America (Booth *et al.*, 2012) and may explain why some species are shifting more than others. Changes in land-use practices can also facilitate or constrain the expansion of range boundaries (Van der Putten, 2012). Ecological interactions (Van der Putten *et al.*, 2010), plastic responses that mitigate the effects of climate change *in situ* such as changes in phenology (Parmesan & Yohe, 2003), shifts in microhabitat use (Martin, 2001) as well as evolutionary adaptation (Parmesan, 2006), may also explain why the range margins of some species are shifting less, not at all or in directions opposite to general predictions.

Our study focused on shifts in latitude and elevation among 40 songbirds in western North America. We would have preferred to include a larger number of species in our analyses. However, nocturnal, crepuscular and aquatic species are not well sampled by the Breeding Bird Survey (US Geological Survey Patuxent Wildlife Research Center, 2012). Northern-latitude, high-elevation areas with a drier climate are also undersampled (Lawler & O'Connor, 2004). Despite these limitations, the species we considered were characterized by a broad range of ecological and life-history traits. For example, mean clutch size ranged from 2.8 to 6.4 eggs across species, and diet varied from specialists eating only seeds or insects to complete omnivores. Range size also spanned the limited distribution of endemics to the broad multicontinental distributions of more cosmopolitan species. Trait values of many western North American birds fall within these ranges, so it is our hope that our results might be used to better predict the effects of climate change on a larger number of species than considered here.

Understanding how and why species are shifting their distributions is critical for our ability to forecast the ecological consequences of climate change and to maintain biodiversity in the face of larger global change. Species are responding to climate change in multiple ways that often appear to be idiosyncratic. However, examination of how these different responses are correlated across species – as we have done here for elevation and latitude – and whether these responses are explained by a common set of species-level traits will improve our understanding of their habitat requirements and vulnerability to extinction under climate change.

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REFERENCES

Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J. & Chunco, A.J. (2011) Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, **14**, 677–689.

Beever, E.A., Ray, C., Mote, P.W. & Wilkening, J.L. (2010) Testing alternative models of climate-mediated extirpations. *Ecological Applications*, **20**, 164–178.

Betzholtz, P.E., Pettersson, L.B., Ryrholm, N. & Franzen, M. (2013) With that diet, you will go far: trait-based analysis reveals a link between rapid range expansion and a nitrogen-favoured diet. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122305.

Böhning-Gaese, K. & Lemoine, N. (2004) Importance of climate change for the ranges, communities and conservation of birds. *Advances in Ecological Research*, **35**, 211–236.

Booth, E.L.J., Byrne, J.M. & Johnson, D.L. (2012) Climatic changes in western North America, 1950–2005. *International Journal of Climatology*, **32**, 2283–2300.

Buckley, L.B. (2012) Functional and phylogenetic approaches to forecasting species' responses to climate change. *Annual Review of Ecology, Evolution, and Systematics*, **43**, 205–226.

Chen, I. (2009) Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences USA*, **106**, 1479–1483.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.

Coblentz, D.D. & Riitters, K.H. (2004) Topographic controls on the regional-scale biodiversity of the south-western USA. *Journal of Biogeography*, **31**, 1125–1138.

Cofre, H.L., Böhning-Gaese, K. & Marquet, P.A. (2007) Rarity in Chilean forest birds: which ecological and life-history traits matter? *Diversity and Distributions*, **13**, 203–212.

DaCosta, J.M., Spellman, G.M., Escalante, P. & Klicka, J. (2009) A molecular systematic revision of two historically problematic songbird clades: *Aimophila* and *Pipilo*. *Journal of Avian Biology*, **40**, 206–216.

Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. (2008) Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2743–2748.

Diffenbaugh, N.S. & Giorgi, F. (2012) Climate change hotspots in the CMIP5 global climate model ensemble. *Climatic Change*, **114**, 813–822.

Ehrlich, P., Dobkin, D.S. & Wheye, D. (1988) *Birder's handbook: a field guide to the natural history of North American Birds*. Simon and Schuster Inc., New York.

Forero-Medina, G., Terborgh, J., Socolar, S.J. & Pimm, S.L. (2011) Elevational ranges of birds on a tropical montane gradient lag behind warming temperatures. *PLoS One*, **6**, e28535.

Grafen, A. (1989) The phylogenetic regression. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **326**, 119–157.

Grafen, A. (2006) *A user's guide to the SAS implementation of the phylogenetic regression*, v. 0.6. Available at: http://users.ox.ac.uk/grafen/phylo/.

Hickling, R., Roy, D.B., Hill, J.K. & Thomas, C.D. (2005) A northward shift of range margins in British Odonata. *Global Change Biology*, **11**, 502–506.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.

Hill, J.K., Thomas, C.D. & Huntley, B. (1999) Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 1197–1206.

Hitch, A.T. & Leberg, P.L. (2007) Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology*, **21**, 534–539.

Jacobsen, F., Friedman, N.R. & Omland, K.E. (2010) Congruence between nuclear and mitochondrial DNA: combination of multiple nuclear introns resolves a well-supported phylogeny of New World orioles (Icterus). *Molecular Phylogenetics and Evolution*, **56**, 419–427.

Jeschke, J.M. & Strayer, D.L. (2006) Determinants of vertebrate invasion success in Europe and North America. *Global Change Biology*, **12**, 1608–1619.

Jetz, W., Sekercioglu, C.H. & Bohning-Gaese, K. (2008) The worldwide variation in avian clutch size across species and space. *PLOS Biology*, **6**, 2650–2657.

Jønsson, K.A. & Fjeldså, J. (2006) A phylogenetic supertree of oscine passerine birds (Aves: Passeri). *Zoologica Scripta*, **35**, 149–186.

Kujala, H., Vepsäläinen, V., Zuckerberg, B. & Brommer, J.E. (2013) Range margin shifts of birds revisited–the role of spatiotemporally varying survey effort. *Global Change Biology*, **19**, 420–430.

Lawler, J.J. & O'Connor, R.J. (2004) How well do consistently monitored breeding bird survey routes represent the environments of the conterminous United States? *Condor*, **106**, 801–814.

Le Roux, P.C. & McGeoch, M.A. (2008) Rapid range expansion and community reorganization in response to warming. *Global Change Biology*, **14**, 2950–2962.

Link, W.A. & Sauer, J.R. (2002) A hierarchical analysis of population change with application to Cerulean Warblers. *Ecology*, **83**, 2832–2840.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052–1055.

Martin, T.E. (2001) Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? *Ecology*, **82**, 175–188.

Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C. & Beissinger, S.R. (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, **322**, 261–264.

Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.S., Rasmussen, P.C. & Ridgely, R.S. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature*, **436**, 1016–1019.

Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. (2002) Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, **67**, 518–536.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sánchez-Cordero, V., Soberón, J., Buddemeier, R.H. & Stockwell, D.R. (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature*, **416**, 626–629.

Poole, A. (2005) *The birds of North America online*. Cornell Laboratory of Ornithology, Ithaca, NY. Available at: http://bna.birds.cornell.edu/bna/ (last accessed 1 May 2013).

Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. & Saarinen, K. (2008) Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, **15**, 732–743.

Ricklefs, R.E. (2000) Density dependence, evolutionary optimization, and the diversification of avian life histories. *The Condor*, **102**, 9–22.

Robbins, C.S., Bystrak, D. & Geissler, P.H. (1986) *The Breeding Bird Survey: its first fifteen years, 1965–1979*. USDI Fish and Wildlife Service, Washington, DC.

Sauer, J.R., Hines, J.E., Fallon, J.E., Pardieck, K.L., Ziolkowski Jr, D.J. & Link, W.A. (2011) *The North American Breeding Bird Survey, results and analysis 1966–2010*. Version 12.07.2011. USGS Patuxent Wildlife Research Center, Laurel, MD.

Schloss, C.A., Nunez, T.A. & Lawler, J.J. (2012) Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences USA*, **109**, 8606–8611.

Schweiger, O., Settele, J., Kudrna, O., Klotz, S. & Kühn, I. (2008) Climate change can cause spatial mismatch of trophically interacting species. *Ecology*, **89**, 3472–3479.

Sekercioglu, C.H., Schneider, S.H., Fay, J.P. & Loarie, S.R. (2007) Climate change, elevational range shifts, and bird extinctions. *Conservation Biology*, **22**, 140–150.

Sol, D., Duncan, R.P., Blackburn, T.M., Cassey, P. & Lefebvre, L. (2005) Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences USA*, **102**, 5460–5465.

Sol, D., Maspons, J., Vall-Llosera, M., Bartomeus, I., Garcia-Pena, G.E., Pinol, J. & Freckleton, R. (2012) Unraveling the life history of successful invaders. *Science*, **337**, 580–583.

Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K., Tignor, M. & Miller, H. (eds) (2007) *The physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change*, pp. 235–337. Cambridge University Press, Cambridge.

Tello, J.G., Moyle, R.G., Marchese, D.J. & Cracraft, J. (2009) Phylogeny and phylogenetic classification of the tyrant flycatchers, cotingas, manakins, and their allies (Aves: Tyrannides). *Cladistics*, **25**, 429–467.

Thomas, C.D. & Lennon, J.J. (1999) Birds extend their ranges northwards. *Nature*, **399**, 213–213.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A. & Hannah, L. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.

Tingley, M.W., Koo, M.S., Moritz, C., Rush, A.C. & Beissinger, S.R. (2012) The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology*, **18**, 3279–3290.

US Geological Survey Patuxent Wildlife Research Center (2002) Breeding Bird Survey route locations for lower 48 States, Alaska and southern portion of Canada. National Atlas of the United States, Reston, VA.

US Geological Survey Patuxent Wildlife Research Center (2012) *North American Breeding Bird Survey ftp data set*. Available at: ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/datafiles/ (accessed August 2012).

US Geological Survey EROS Data Center (1996) *Global 30 arc-second elevation (GTOPO30)*. US Geological Survey, Sioux Falls, SD.

Van der Putten, W.H. (2012) Climate change, aboveground–belowground interactions, and species' range shifts. *Annual Review of Ecology, Evolution, and Systematics*, **43**, 365–383.

Van der Putten, W.H., Macel, M. & Visser, M.E. (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2025–2034.

Virkkala, R., Heikkinen, R.K., Leikola, N. & Luoto, M. (2008) Projected large-scale range reductions of northern-boreal land bird species due to climate change. *Biological Conservation*, **141**, 1343–1353.

Wilson, R.J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R. & Monserrat, V. (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, **8**, 1138–1146.

SUPPORTING INFORMATION

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

Appendix S1 Study area and 559 Breeding Bird Survey routes.

Appendix S2 Coefficients from bivariate correlations between predictor variables.

Appendix S3 Working phylogeny used to account for relatedness among species.

Appendix S4 Summaries of range shifts and species-level traits used in analyses.

BIOSKETCHES

Sonya Auer studies how organisms respond to environmental change through plasticity in the physiological, morphological and behavioural traits that underlie their more general life-history strategies. Her recent work focused on how climate change can have indirect effects on bird communities by altering of plant–herbivore interactions.

David King studies the effects of climate change and other anthropogenic stressors on bird populations with the goal of providing science-based recommendations for accommodating native biodiversity in the face of global change. His recent work has centred on understanding the threats that climate change poses to high-elevation bird species.