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REVIEW AND SYNTHESIS

Do species' traits predict recent shifts at expanding range edges?

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Abstract

Although some organisms have moved to higher elevations and latitudes in response to recent climate change, there is little consensus regarding the capacity of different species to track rapid climate change via range shifts. Understanding species' abilities to shift ranges has important implications for assessing extinction risk and predicting future community structure. At an expanding front, colonization rates are determined jointly by rates of reproduction and dispersal. In addition, establishment of viable populations requires that individuals find suitable resources in novel habitats. Thus, species with greater dispersal ability, reproductive rate and ecological generalization should be more likely to expand into new regions under climate change. Here, we assess current evidence for the relationship between leading-edge range shifts and species' traits. We found expected relationships for several datasets, including diet breadth in North American Passeriformes and egg-laying habitat in British Odonata. However, models generally had low explanatory power. Thus, even statistically and biologically meaningful relationships are unlikely to be of predictive utility for conservation and management. Trait-based range shift forecasts face several challenges, including quantifying relevant natural history variation across large numbers of species and coupling these data with extrinsic factors such as habitat fragmentation and availability.

Keywords

Dispersal, global climate change, life history, range expansion.

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INTRODUCTION

One of the greatest challenges facing ecologists today is to understand the biological effects of, and responses to, climate change. Biological responses include movement to track preferred conditions, resulting in range shifts (Hickling *et al.* 2006; Parmesan 2006), plastic or acclimatory responses to altered conditions within existing populations (Nussey *et al.* 2005; Durant *et al.* 2007) and evolutionary adaptation to novel conditions (Visser 2008; Gardner *et al.* 2009). These responses are not mutually exclusive, and ultimately, biodiversity loss will be determined by the net demographic impacts of climate change that result from these possible responses. Range shifts are perhaps the best documented biological response to date, but there is very little consensus regarding the extent to which different organisms will be able to establish populations in newly suitable habitat, particularly given the rapid rate of climate change (Loarie *et al.* 2009). Understanding the capacity of species to expand into newly suitable habitat and shift geographic ranges in the face of climate change is important because it informs both species-specific extinction probabilities (Thomas *et al.* 2004; Loarie *et al.* 2008) and future community structure (Lawler *et al.* 2009; Gilman *et al.* 2010). Thus, *a priori* knowledge of which species are likely to exhibit range shifts would be of great benefit to conservation biologists and resource managers.

To assess the potential impact of climate change on species' distributions, many studies relate present-day geographic distributions to climatic variables and then project future distributions under various climate change scenarios (Peterson *et al.* 2002; Thomas *et al.* 2004; Hijmans & Graham 2006; Wiens *et al.* 2009). Such niche modelling approaches assume that range changes are determined solely by the availability of climatically suitable habitat, without additional limitations imposed by dispersal or life history. However, studies examining observed changes in the range boundaries of plants and animals in the face of climate change have consistently found that movement responses within a community are idiosyncratic; while many species shift range boundaries in the direction predicted, a significant fraction (e.g. *c.* 40%, La Sorte & Thompson 2007) either show counterintuitive movement patterns or very little shift in their range (Lenoir *et al.* 2010; Crimmins *et al.* 2011). These observations suggest that traits such as habitat preferences or life history characteristics, that are not often explicitly included in niche models, might affect each individual species' realized response to climate change (Broenniman *et al.* 2006; Schweiger *et al.* 2008; Buckley *et al.* 2010). Yet, we lack a systematic framework for how species' traits will affect range shifts.

In theory, species' capacities to track climate change via range shifts should depend on their abilities to colonize new areas and establish

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viable populations after arrival. The rate at which these processes occur will determine how rapidly species spread into newly available habitat. Invasion models offer some insight into what determines this rate of expansion. Specifically, simple diffusion models show that the rate of spread is determined jointly by a species' dispersal distance and rate of reproduction (Clark 1998). Although it is intuitive that greater dispersal ability should increase the rate of spread, dispersal distance is notoriously difficult to quantify because rare long-distance dispersal events can have a disproportionate effect on the overall rate of spread (Clark 1998; Higgins *et al.* 2003), and because behavioural interactions may affect movement probabilities in complex ways (McCauley 2010). Despite these difficulties, dispersal syndromes and morphometric measurements have proven to be useful indices of dispersal ability in some groups. For example, larval mode (planktonic vs. non-planktonic) is often used as a proxy for dispersal potential in marine invertebrates (Grantham *et al.* 2003), and wing morphology has been similarly used in insects (Simmons & Thomas 2004) and birds (Dawideit *et al.* 2009). The second determinant of spread, rate of reproduction, is a function of the age- or stage-specific survivorship and fecundity schedule. All else being equal, life history characteristics such as early reproduction, frequent reproduction and high fecundity should increase colonization opportunity by increasing the net reproductive rate and hence propagule pressure.

In real habitats, rates of increase and population persistence will be determined not only by intrinsic growth potentials but also by resource availability. For example, individuals must be able to find appropriate food, shelter and mates in a new area. Ecological generalization might increase the likelihood that individuals will find suitable resources and interactions in a new location (Hill *et al.* 2001; Warren *et al.* 2001; Pöyry *et al.* 2009). Conversely, species with specialized niche requirements or highly co-evolved interactions might encounter greater difficulty establishing populations in new habitats (Gilman *et al.* 2010). Another problem in establishing a viable population is presented by Allee effects (Stephens *et al.* 1999), which reduce population growth at small population sizes (Odum & Allee 1954). Thus, species that avoid Allee effects through self-fertilization, clonal reproduction or other mechanisms might be more likely to establish in novel areas (Pannell & Barrett 1998).

Many of the traits discussed above, such as dispersal ability or reproductive behaviour, require detailed knowledge of organismal natural history. Furthermore, to be useful for forecasting variation in responses to climate change, such knowledge must be generally available across the taxonomic group or geographic region of interest. Unfortunately, such details are lacking for most species. Given this situation, one approach is to rely on more commonly available surrogates for relevant life history characteristics. For example, data on body size and geographic range size are readily available for most species and show positive correlations with many characteristics, including dispersal ability, trophic level, competitive ability and environmental tolerance (Brown *et al.* 1995; Gaston 2003). Thus, range and body sizes might be useful proxies for many traits expected to show a positive association with colonization and establishment success (Roy *et al.* 2002; Tingley *et al.* 2010).

Despite theoretical support for the effects of species' traits on variation in colonization and establishment probabilities (Clark 1998), it remains unclear whether innate organismal differences will yield predictable differences in the rate and extent of range shifts in response to climate change. External factors such as habitat fragmentation or the relative quantity of specific habitats may instead constrain migration potential and have an overriding effect on the magnitude of observed range shifts (Hill *et al.* 1999; Honnay *et al.* 2002; Ibanez *et al.* 2006; Heikkinen *et al.* 2010). This possibility has many parallels in the invasion and extinction literatures, where biologists have asked if species' traits can predict which species become invasive or are vulnerable to extinction, or if instead each case is contingent upon unique historical and geographical circumstances (Rejmánek 1996; McKinney 1997; Williamson 1999; Kolar & Lodge 2001; Purvis *et al.* 2005). Furthermore, though life history differences may yield predictable differences in the extent of range shifts at equilibrium, it is possible that such differences will not be observed during the transient, non-equilibrium stages of active displacement (Clark 1998).

Here, we assess current evidence for the expectation that species' traits explain differences in recently observed range shifts. There is a large and growing body of evidence that many organisms have shifted poleward in latitude or upward in elevation in response to recent warming trends (Hickling *et al.* 2006; Parmesan 2006). Thus far, most researchers have focused primarily on documenting and quantifying that shifts have occurred, and hence have focused on the net direction and average rate or magnitude of observed shifts for a particular group of taxa. Yet within each group, there is often substantial variation in the amount of observed displacement. In a handful of cases, this variation has been shown to be partially explained by species' traits such as dispersal ability (Pöyry *et al.* 2009) or generation time (Perry *et al.* 2005). Given the emergence of several new datasets documenting range shifts for large numbers of species, it is now possible to conduct a quantitative assessment of the role of traits in explaining differences among species in observed range shifts. We focus on shifts at northern or upper elevation range margins ('leading edges') because of the clear predictions provided by invasion theory and the greater number of available datasets. We compiled traits and analysed variation in observed shifts at the leading edges of species' ranges for four published datasets, North American birds (La Sorte & Thompson 2007), British Odonata (Hickling *et al.* 2005), Swiss alpine plants (Holzinger *et al.* 2008), and western North American mammals (Moritz *et al.* 2008), to test the overarching hypothesis that differences in the rates of recent leading-edge range shifts are driven by differences in traits related to dispersal, life history and ecological generalization. We tested five specific predictions. We predicted that the magnitude or rate of range shift would be positively related to three factors: (1) dispersal potential, including dispersal modes and behavior, (2) intrinsic rate of increase, measured by underlying life history components such as generation time and offspring number and (3) ecological generalization, assayed by metrics such as diet breadth and mating system. Additionally, we predicted that general indices of body size and range size would be positively correlated with range shifts, as these often correlate with dispersal potential, life history, and ecological generalization. Finally, because species undergoing recent range shifts may not be at demographic equilibrium, we also predicted that traits related to colonization ability (i.e., dispersal potential and rates of increase) would be relatively more important for explaining current differences in range shifts than traits related to establishment probability (i.e., ecological generalization). For each group we found one or more traits that do explain some variation in recent range shifts, but none with clear influence across all groups. We synthesize these results with previous studies reporting taxon-specific relationships between range shifts and species' traits and discuss prospects for trait-based range shift forecasts.

MATERIALS AND METHODS

Range margin shift datasets

We identified four studies that (1) revisited historical census sites along latitudinal or elevational transects to quantify shifts in northern or upper elevation range boundaries over the last century, (2) provided a quantitative metric of shift and (3) enumerated all species in the dataset (i.e. rather than including only species that shifted significantly): North American birds (La Sorte & Thompson 2007; $n = 254$), European Odonata (Hickling *et al.* 2005; $n = 24$ for southerly species reaching a northern range limit within the study area), Swiss alpine plants (Holzinger *et al.* 2008; $n = 133$), and western North American mammals (Moritz *et al.* 2008; $n = 28$). Two of these datasets reported shifts poleward in latitude (Hickling *et al.* 2005; La Sorte & Thompson 2007) and two reported shifts up in elevation (Holzinger *et al.* 2008; Moritz *et al.* 2008). Range shifts were reported as rates of boundary displacement in kilometres per year (La Sorte & Thompson 2007) or metres per decade (Holzinger *et al.* 2008), or as magnitudes of boundary displacement in metres (Moritz *et al.* 2008) or kilometres (Hickling *et al.* 2005). Relationships between range shifts and some traits were reported in the original publications for plants and mammals (Holzinger *et al.* 2008; Moritz *et al.* 2008). Here, we add additional explanatory variables, consider phylogenetic relatedness, and reanalyse relationships following a consistent analytical framework for comparison across these four groups.

Species' traits

Table S1 summarizes our five predictions, the traits available for each of the four taxonomic groups, and the expected direction of relationship between each trait and range shift.

North American birds
Body mass (averaged over both sexes) and clutch size were obtained from The Birds of North America Online (Poole 2005). For simplicity, we used diet categories delineated by The Birder's Handbook (Erlich *et al.* 1988), and we created an ordinal index of diet breadth by counting the number of diet categories reported for each species (ranging from one to four, with omnivores coded as five). We also considered diet classes (e.g. insectivores or frugivores), but discarded it because it explained less variation than diet breadth (results not shown). In addition, because many water birds rely on open water for wintering, and the locations where open water is available have shifted considerably with climate change, we predicted that species that rely on open water will have shifted faster than those that do not. We used data from the Birds of North America Online (Poole 2005) to score each species based on open-water requirements. We considered any species that winters primarily or exclusively in freshwater habitats, as well as species that winter in both freshwater and marine habitats in which the northernmost portion of the wintering range is dominated by freshwater habitats, to require open water in wintering. We also obtained data on wingloading and flight behaviour from Viscor & Fuster (1987). When wingloading data were not available for a given species ($n = 162$ of 254 species), we substituted data from congeners where available ($n = 132$ of 162 species). Flight behaviour was ordered from potentially least to most dispersive (SF – short-flight, HF – high-frequency flapping, FF – forward and bounding flapping, UF – undulating flight with alternate active and passive periods, GS – mainly gliding and soaring; Viscor & Fuster 1987). Migratory status, a binary variable, was included from the original dataset (La Sorte & Thompson 2007). Range size was calculated using total range maps (e.g. wintering and breeding ranges) for each species downloaded from NatureServe (http://www.natureserve.org) on 15 November 2008. All range maps were projected using a World Sinusoidal Projection to minimize distortions in area in ArcGIS 9.3. The total range area for each species was then calculated to the nearest square metre using Hawth's Analysis Tools (Beyer 2004) within ArcGIS 9.3 (Esri, Redlands, CA). We used total range area because we hypothesized that larger ranges should increase environmental heterogeneity and hence ecological breadth. To account for heterogeneity in both rates of climate change and available land area beyond the range, we included as a covariate the position of a species' historical range limit (latitude of the northernmost pre-1975 locality record from the North American Christmas Bird Count of the National Audubon Society).

British Odonata
Trait data for the Odonata were obtained primarily from Askew (1988). These traits included male body mass, migration behaviour (a binary variable describing whether species are mass migrants or not), flight behaviour (perchers, which perch to survey feeding grounds and territories, vs. fliers, which hawk for prey and patrol territories without settling; Corbet 1963), the duration of the flight period in months, egg habitat (endophytic – clutches laid in plants, or exophytic – clutches laid on water or land; Hilsenhoff 2001) and larval habitat (temporary or perennial water). Egg habitat is potentially related to both ecological generalization and life history, because exophytic species tend to lay large clutches (i.e. 2000 or more; Corbet 1963), while endophytic species lay small clutches (Askew 1988). Larval habitat is also related to dispersal because species occupying more ephemeral water bodies tend to have greater dispersal ability (Hof *et al.* 2006). We also quantified adult habitat breadth based on the diversity of water body types (e.g. pond, lake and stream) and range of water flow regimes (stagnant, slow flowing or fast flowing) that the species utilizes. These two measures of habitat breadth were quantified independently as the number of water body types (from one to five) and the number of flow regimes (from one to three) regularly used by adults. Information on the number of generations per year (from one to three) was obtained from Corbet *et al.* (2006). As a metric of range size, we used the latitudinal span reported by Hof *et al.* (2006). Position of the northern range limit was as given in Hof *et al.* (2006).

Swiss alpine plants
We obtained plant trait data from three main sources. Seed mass data were obtained from the Royal Botanic Gardens Kew Seed Information Database, release 7.1 and Müller-Schneider (1986). When these two sources reported different numbers for a given species, we used the average. Seed dispersal mode was obtained from Müller-Schneider (1986). Primary dispersal modes of species in the dataset included gravity, animal and water. We converted these modes into a binary variable where zero represented limited gravity dispersal and one represented other dispersal modes with greater travel potential. Other plant traits were obtained from the LEDA Traitbase, a database of life history traits for the Northwest European flora (Kleyer *et al.* 2008). These traits included the duration of seed dispersal (calculated as the number of months between first and last reported seed shed), average height at seed shed and breeding system (ranked in order of decreasing

reliance on pollinators: obligately outcrossing, mixed mating and autogamously selfing). From the LEDA Traitbase we also calculated two indices of habitat generalization: the total number of floristic zones, and the total number of oceanic zones, encompassed by the species' range. We were not able to estimate range size for these plant species, as information on the total distribution of many of these species was unavailable. Position of the historical range limit was estimated as the elevation of the uppermost pre-1975 locality record, using locality records downloaded from the Global Biodiversity Information Facility (http://www.gbif.org).

Western North American small mammals

Mammal trait data were reported by Moritz *et al.* (2008). Variables included body mass (g), litter size, litters per year, longevity (years), and descriptions of diet and activity patterns. We converted diet into a binary index where insectivores, herbivores and carnivores were each coded as zero (because these groups each use a single food resource) and omnivores were coded as one. Daily and annual activity patterns also were converted into binary indices of behavioural plasticity (zero for obligately diurnal or nocturnal animals vs. one for facultatively diurnal; zero for obligate hibernators or non-hibernators vs. one for facultative hibernators). Range size was estimated from NatureServe range maps, as described above for birds. Position of the historical upper range limit was reported by Moritz *et al.* (2008).

Phylogenies

To control for phylogenetic relatedness in our analyses, we identified phylogenetic relationships among species within each taxonomic group. For birds, we used the phylogenetic hypothesis available on the Tree of Life website, which is based primarily on two recent molecular studies (Ericson *et al.* 2006; Hackett *et al.* 2008). For Odonata, phylogenetic relationships follow Bybee *et al.* (2008), with missing taxa placed according to Askew (1988). The mammal phylogeny is based on the supertree published by Bininda-Emonds *et al.* (2007). Three missing taxa were placed according to recent molecular phylogenetic studies (Piaggio & Spicer 2001; Herron *et al.* 2004; Miller & Engstrom 2008). For plants, we used the online tool Phylomatic (Webb & Donoghue 2005) to create a hypothesis of the relationships among species based on the conservative phylogeny of seed plants available at the Angiosperm Phylogeny Website (Stevens 2001 onwards). For all phylogenies, branch lengths were set to one.

Statistical analyses

We used linear models (lm) to test for associations between species' traits (predictor variables) and observed range shifts (response variable) within each of the four datasets. We excluded wingloading from the bird dataset and position of the historical range limit from the Odonata dataset to avoid multicollinearity; all remaining correlations among predictor variables were <0.7 (Table S2). Residuals from lm were generally uniformly distributed and were not improved by transformations. All continuous variables were scaled to mean of zero and standard deviations of one for comparison across traits. We identified the best subset of models using the Akaike Information Criterion, adjusted for small sample sizes (AIC_c). We report all models with AIC_c differences ($\Delta_\text{i} = \text{AIC}_\text{i} - \text{AIC}_\text{min}$) less than or equal to two ($\Delta_\text{i} \leq 2$). The maximum number of variables that could enter a model was kept to approximately one-tenth of the number of data lines (e.g. analyses of the 28-species mammal dataset could include at most three predictor variables). We could not obtain measurements of all traits for all species in the bird or plant datasets, so model selection for these groups was based on reduced datasets without missing values (birds $n = 195$, plants $n = 39$). Results of univariate analyses, using the maximal dataset per trait, are given in Table S3. To account for model uncertainty, we performed model averaging of coefficients in all models with $\Delta\text{AIC}_\text{c} \leq 2$, including zeros as coefficients when variables did not enter a particular model (Burnham & Anderson 2002). Because traits of related taxa may be similar due to common ancestry and hence are not statistically independent, we repeated model selection and model averaging using a phylogenetic generalized least-squares model (pglm) framework (Freckleton *et al.* 2002). This method uses the phylogenetic variance/covariance matrix estimated from the phylogeny to adjust for correlated error structure. The parameter lambda (λ) measures the degree of phylogenetic autocorrelation (where a value of 0 implies no autocorrelation and a value of 1 implies maximum autocorrelation). Current implementations of pglm do not permit ordinal variables. For consistency with the pglm framework, we treated ordinal variables as continuous variables in lm analyses. However, lm analyses using ordinal variables yielded qualitatively similar results. All analyses were conducted in R version 2.9.2 (R Core DevelopmentTeam 2009) using the packages ape (Paradis *et al.* 2004) and MuMIn (http://r-forge.r-project.org/projects/mumin/). Code was provided by R. Freckleton and L. Buckley.

RESULTS

North American birds

The rate of shift at the northern range limit was poorly predicted by species' traits when all birds were considered together. Range size had a significant but weak negative effect on the rate of northern margin shift in all of the top non-phylogenetically corrected lm (Table 1, Fig. 1a). For every one standard deviation (7 568 169 km^2) increase in range size, the rate of range shift was predicted to decrease by 0.18 standard deviations (1.30 km year^{-1}). Migratory status, reliance on open water and diet breadth had marginally significant positive effects in many top-ranked lm, and these variables had high relative importance based on Akaike weight summations (w_ip) (Table 1). However, model R^2 were uniformly low (0.03–0.07; Table 1). In pglm models, lambda estimates were low (0.04–0.07). Range size again had a negative effect on range shifts while reliance on open water had a positive effect, and these two variables had high relative importance (Fig. 2a, Table 1).

Because the entire bird dataset contained many disparate species, we conducted parallel analyses for a large but more homogeneous subgroup, Passeriformes. Within this subgroup, the rate of range shift was predicted to increase by 0.32 standard deviations (2.47 km year^{-1}) with each standard deviation (1.06 items) increase in diet breadth (Fig. 1b). Diet breadth appeared in all top-ranked lm, resulting in high relative importance (Table 2). No other variables appeared consistently among top lm or had significant effects on the rate of northern margin shift. The predictive power of species' traits and model fit did not improve substantially within the Passeriformes subgroup (R^2 = 0.07–0.12; Table 2). In pglm, lambda estimates were zero and diet breadth remained the most important variable (Fig. 2b, Table 2).

Table 1 Results of model selection and model averaging for models relating recent shifts of the northern range margins of North American birds (La Sorte & Thompson 2007) to species' traits. Trait categories include dispersal potential (D), intrinsic rate of increase (R), ecological generalization (EG), general index (I), and historical range limit covariate (C). The variables included in each model are shown with the symbol •. Models are ranked in order of increasing AIC$_c$ differences (Δ_i). Akaike weights (w_i) indicate the relative likelihood of a model, given the particular set of best models being considered (Burnham & Anderson 2002). Model-averaged regression coefficients (β) are averages of β_i across all models with $\Delta_i \leq 2$, weighted by each model's Akaike weight w_i. Calculations for β include $\beta_i = 0$ when variables are not in a given model. β whose 95% confidence intervals do not encompass zero are given in bold. Relative variable importance (w_{ip}) is the sum of w_i across all models including that variable (Burnham & Anderson 2002). The column 'Pred.' lists whether model-averaged regression coefficients were numerically in the predicted direction ('y' = yes, 'n' = no, 'n/a' = not applicable). Traits are sorted in order of decreasing w_{ip} in linear models (lm). Lambda (λ) estimates the degree of phylogenetic autocorrelation in phylogenetic generalized linear models (pglm)

		lm																		
		Model rank																		
Category	Birds trait	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
I	Range size	•*	•**	•*	•*	•*	•*	•*	•*	•*	•*	•**	•**	•*	•*	•**	•**	•**	•**	•*
D	Migratory	•†	•†	•†	•†	•*	•†		•†			•†	•			•		•	•	•
EG	Open water	•†	•	•†				•	•	•†	•†	•†	•		•	•	•†		•†	
EG	Diet breadth	•		•†	•†	•			•†		•		•		•				•	•
C	Histor. limit							•					•	•†	•	•	•	•	•	•
I	Body size			•								•					•		•	
D	Flight rank				•				•											
R	Clutch size																			
	Δ_i	0	0.6	0.6	0.6	0.7	1.2	1.2	1.3	1.4	1.4	1.5	1.6	1.6	1.6	1.7	1.9	1.9	2.0	2.0
	w_i	0.10	0.07	0.07	0.07	0.07	0.05	0.05	0.05	0.05	0.05	0.05	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
	λ	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	R^2	0.06	0.04	0.06	0.05	0.04	0.03	0.04	0.06	0.03	0.04	0.05	0.06	0.03	0.05	0.05	0.05	0.04	0.07	0.05

		lm				pglm						
		Model average				Model rank			Model average			
Category	Birds trait	β	95% CI	w_{ip}	Pred.	1	2	3	β	95% CI	w_{ip}	Pred.
I	Range size	**−0.18**	**−0.34** to **−0.03**	**1.00**	**n**	•**	•**	•**	**−0.18**	**−0.34** to **−0.03**	**1.00**	**n**
D	Migratory	0.21	−0.18 to 0.60	0.83	y			•	0.12	−0.21 to 0.45	0.21	y
EG	Open water	0.23	−0.23 to 0.70	0.69	y	•*	•*	•**	0.33	−0.07 to 0.74	1.00	y
EG	Diet breadth	0.06	−0.09 to 0.21	0.57	y				–	–	–	–
C	Histor. limit	0.03	−0.08 to 0.15	0.37	n/a		•		0.03	−0.08 to 0.15	0.27	n/a
I	Body size	−0.02	−0.08 to 0.05	0.20	n				–	–	–	–
D	Flight rank	−0.01	−0.06 to 0.03	0.12	n				–	–	–	–
R	Clutch size	–	–	–	–				–	–	–	–
	Δ_i					0	1.3	1.8				
	w_i					0.52	0.27	0.21				
	λ					0.04	0.07	0.04				
	R^2					0.06	0.07	0.06				

†$0.05 \leq P < 0.10$, *$0.01 \leq P < 0.05$, **$P < 0.01$.

British odonata

Lm analyses of Odonata range shifts yielded low to moderate explanatory power ($R^2 = 0.10$–0.24; Table 3). Egg habitat, which is associated with clutch size, had a marginally significant positive effect in most top-ranked models and was the variable with highest relative importance (Table 3), but confidence intervals surrounding the model-averaged regression coefficient for egg habitat contained zero (Fig. 1c). In phylogenetically corrected analyses, egg habitat became a statistically significant predictor variable (Fig. 2c; Table 3). Specifically, exophytic species (large clutches laid on water or land) shifted 0.83 standard deviations (65.69 km) further north, on average, than endophytic species (small clutches laid in plants).

Swiss alpine plants

The top lm explained low amounts of variation in the magnitude of shifts in the upper elevation range margin ($R^2 = 0.05$–0.18; Table 4). Duration of the seed dispersal period was the most important lm predictor variable, and it was marginally significant in several top-ranked models (Fig. 1d). Longer dispersal periods were predicted to weakly increase rates of shift by 0.14 standard deviations (0.59 m decade^{-1}). The covariate, historical upper elevation range limit, had a marginally significant negative effect in several top-ranked models. Pglm analyses estimated lambdas to be low (0–0.08) and yielded similar R^2 (0.01–0.14) and variable selection (Table 4), although confidence intervals surrounding all pglm regression coefficients contained zero (Fig. 2d).

Western North American small mammals

Lm analyses of mammal upper elevation range shifts explained moderate amounts of variation ($R^2 = 0.22$–0.31; Table 5). The covariate, historical upper elevation range limit, appeared in all top-ranked lm and had the highest relative importance (Table 5; Fig. 1e). For each standard deviation (934.90 m) increase in historical

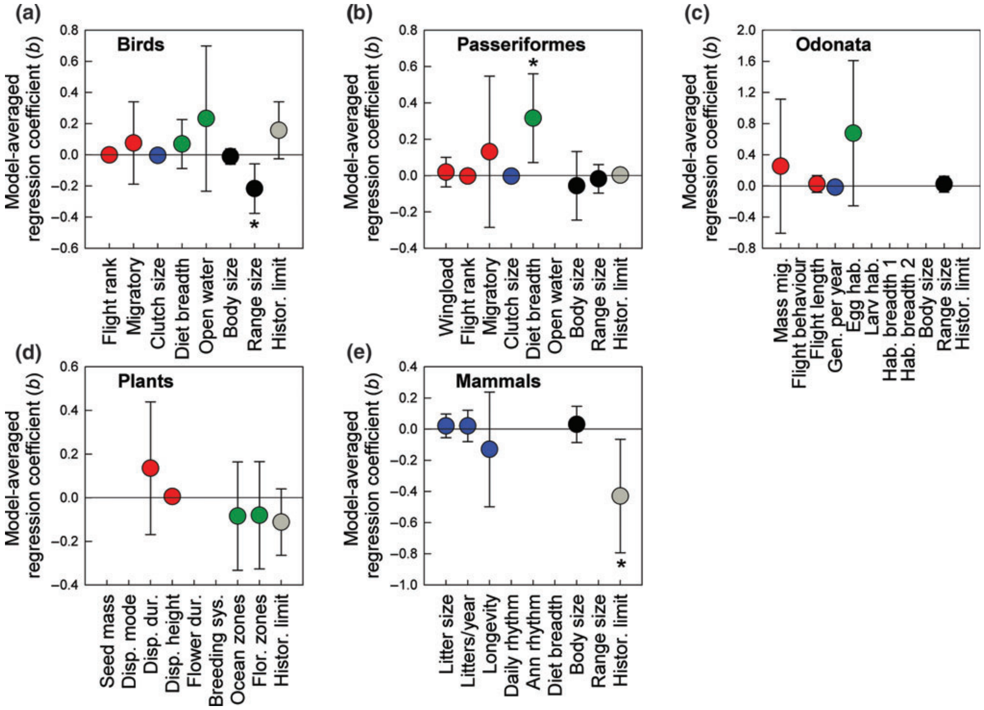

Figure 1 Model-averaged standardized regression coefficients (β) for linear models (lm) relating range shifts of (a) North American birds (La Sorte & Thompson 2007), (b) North American Passeriformes (La Sorte & Thompson 2007), (c) British Odonata (Hickling *et al.* 2005), (d) Swiss alpine plants (Holzinger *et al.* 2008) and (e) western North American small mammals (Moritz *et al.* 2008) to species' traits. Traits for which there is not a data point did not appear in any of the best models with AIC differences (Δ_i) ≤2. Trait categories are colour-coded as follows: red = dispersal potential, blue = intrinsic rate of increase, green = ecological generalization, black = general index, and grey = historical range limit covariate. Error bars depict 95% confidence intervals. Asterisks denote β with 95% confidence intervals not encompassing zero.

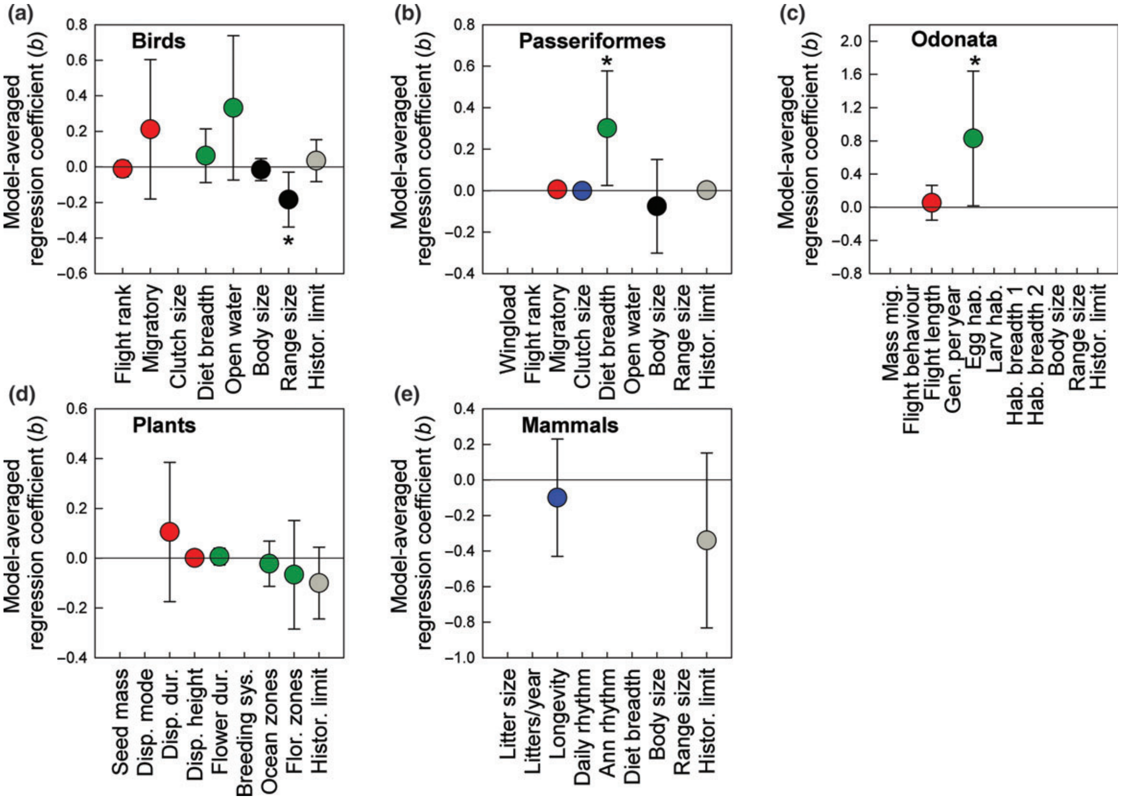

Figure 2 Model-averaged standardized regression coefficients (β) for phylogenetic generalized linear models (pglm) relating range shifts to species' traits. Figure layout and symbols as in Figure 1.

Table 2 Results of model selection and model averaging for models relating recent shifts of the northern range margins of North American Passeriformes (La Sorte & Thompson 2007) to species' traits. Table arrangement and variables are as explained in Table 1

		lm																
		Model rank													Model average			
Category	Passer trait	1	2	3	4	5	6	7	8	9	10	11	12	13	β	95% CI	w_{ip}	Pred
EG	Diet breadth	●**	●**	●**	●**	●**	●**	●**	●*	●**	●**	●*	●*	●*	**0.32**	**0.07** to **0.56**	**1.00**	**y**
D	Migratory			●	●		●	●			●				0.13	−0.29 to 0.55	0.38	y
I	Body size		●		●			●		●					−0.06	−0.24 to 0.13	0.32	n
D	Wingload					●				●	●				0.02	−0.06 to 0.10	0.18	y
I	Range size						●	●				●			−0.02	−0.10 to 0.06	0.18	n
R	Clutch size								●						−0.00	−0.02 to 0.02	0.06	n
C	Histor. limit													●	0.00	−0.01 to 0.02	0.05	n/a
D	Flight rank												●		−0.00	−0.02 to 0.02	0.05	n
EG	Open water														–	–	–	–
	Δ_i	0	0.2	0.4	0.8	1.0	1.4	1.7	1.8	1.8	1.8	1.9	1.9	2.0				
	w_i	0.14	0.12	0.11	0.09	0.08	0.07	0.06	0.06	0.05	0.05	0.05	0.05	0.05				
	λ	–	–	–	–	–	–	–	–	–	–	–	–	–				
	R^2	0.07	0.09	0.09	0.11	0.09	0.10	0.12	0.08	0.10	0.10	0.08	0.08	0.08				

		pglm								
		Model rank					Model average			
Category	Passer trait	1	2	3	4	5	β	95% CI	w_{ip}	Pred.
EG	Diet breadth	●**			●**		**0.30**	**0.03** to **0.58**	**0.51**	**y**
D	Migratory					●	0.01	−0.02 to 0.03	0.15	y
I	Body size				●		−0.08	−0.30 to 0.15	0.15	n
D	Wingload						–	–	–	–
I	Range size						–	–	–	–
R	Clutch size			●			−0.00	−0.01 to 0.01	0.16	n
C	Histor. limit		●				0.00	−0.01 to 0.01	0.18	n/a
D	Flight rank						–	–	–	–
EG	Open water						–	–	–	–
	Δ_i	0	1.4	1.6	1.8	1.8				
	w_i	0.36	0.18	0.16	0.15	0.15				
	λ	0	0	0	0	0				
	R^2	0.03	0.01	0.01	0.04	0.01				

*$0.01 \leq P < 0.05$, **$P < 0.01$.

upper range limit, the magnitude of upward shift was predicted to decrease by 0.43 standard deviations (119.30 m). No life history or ecological generalization traits were significantly related to the magnitude of upward shift, although longevity had moderate relative importance and was marginally significant in one top-ranked model (Table 5). Lambda estimates from pglm analyses were zero (Table 5), and again historical range limit was the only variable significantly related to the observed range shifts (Fig. 2e).

DISCUSSION

Within each of these four datasets, trait differences did explain variation in recent range shifts in a manner consistent with life history theory and invasion models, but the predictive capacity of these relationships was limited. For example, Passeriformes with greater diet breadth and alpine plants with longer seed dispersal periods tended to shift faster, while Odonata with endophytic egg-laying habitat and mammals with greater longevity tended to shift less. The pattern for Odonata may be driven by associated life history characteristics (smaller clutches) and/or ecological specialization (reliance on appropriate host plants). Because so few traits had significant effects, conclusions about the relative importance of different classes of traits (i.e. traits related to dispersal ability vs. those related to establishment probability) or about the effect of traits on different kinds of range shifts (i.e. altitude vs. latitude) are not possible. Although finding statistically significant relationships between some traits and recent leading-edge range shifts suggests that these traits do influence a species' ability to colonize newly available habitat, the low to moderate explanatory power of top-ranked models suggests limited utility in conservation applications. For example, the relationships that we detected are almost certainly too weak to aid managers attempting to designate species with the greatest vulnerability to climate change or to design reserves or corridors for species with different probabilities of range movement.

Synthesis with other range shift studies

Previous efforts with these and other datasets have detected somewhat stronger effects of dispersal, life history, and ecological generalization traits on recent range shifts (Perry *et al.* 2005; Holzinger *et al.* 2008; Lenoir *et al.* 2008; Moritz *et al.* 2008; Pöyry *et al.* 2009). This could result at least in part from a publication bias towards positive results. The datasets included in our quantitative review, however, were selected solely because they assessed range shifts for entire taxonomic groups and thus are unlikely to be biased with

Table 3 Results of model selection and model averaging for models relating recent shifts of the northern range margins of British Odonata (Hickling *et al.* 2005) to species' traits. Habitat breadth 1 = number of water body types, habitat breadth 2 = number of different water flow regimes. Table arrangement and variables are as explained in Table 1

		lm										pglm					
		Model rank						Model average				Model rank		Model average			
Category	Odonata trait	1	2	3	4	5	6	β	95% CI	w_{ip}	Pred.	1	2	β	95% CI	w_{ip}	Pred.
EG	Egg habitat	•†	•		•†	•†	•†	0.68	−0.26 to 1.61	0.89	y	•*	•*	**0.83**	**0.02** to **1.64**	**1.00**	**y**
D	Mass migrants		•	•				0.25	−0.61 to 1.11	0.31	y			–	–	–	–
I	Range size					•		0.02	−0.08 to 0.13	0.12	y			–	–	–	–
D	Flight length				•			0.02	−0.08 to 0.13	0.13	y		•	0.05	−0.16 to 0.26	0.28	y
R	Gen/year						•	−0.02	−0.10 to 0.07	0.11	y			–	–	–	–
D	Flight behaviour							–	–	–	–			–	–	–	–
EG	Larval habitat							–	–	–	–			–	–	–	–
EG	Hab. breadth 1							–	–	–	–			–	–	–	–
EG	Hab. breadth 2							–	–	–	–			–	–	–	–
I	Body size							–	–	–	–			–	–	–	–
C	Histor. limit							–	–	–	–			–	–	–	–
	Δ_i	0.0	1.2	1.6	1.6	1.7	1.9					0.0	1.6				
	w_i	0.33	0.16	0.15	0.13	0.12	0.11					0.72	0.28				
	λ	–	–	–	–	–	–					0.00	0.00				
	R^2	0.16	0.21	0.10	0.20	0.19	0.19					0.17	0.24				

†$0.05 \le P < 0.10$, *$0.01 \le P < 0.05$.

respect to trait effects. Prior studies also differed from ours in at least one of three ways: (1) where range shifts were measured, (2) how dispersal traits were quantified or (3) whether the range shift was considered a binomial variable (shifting vs. non-shifting species) or a continuous variable. Below we discuss each of these in turn.

Perry *et al.* (2005) studied latitudinal shifts of marine demersal fishes and found that species whose ranges shifted north tended to have smaller body sizes, faster maturation and smaller sizes at maturity than species whose ranges did not shift. Lenoir *et al.* (2008) studied elevational shifts of 171 forest plant species and found that species with narrower distributions (restricted to mountainous areas) and species with faster population turnover (herbaceous species compared to woody species) moved further upward over the study period. In both of these studies, range displacement was assessed at the distribution core [i.e. mean latitude (Perry *et al.* 2005) or maximum probability of presence (Lenoir *et al.* 2008)]. This is in contrast to our focus on shifts at northern or upper range margins, which we chose because of the clear predictions provided by invasion theory and the greater number of available datasets. Of the four datasets analysed here, one presented shifts of the range centre (La Sorte & Thompson 2007). Interestingly, we found greater explanatory power for species' traits, and different significant traits, when considering shifts in Passeriformes centre of abundance compared to shifts in the northern range margin (R^2 = 0.20–0.24 for centre of abundance vs. R^2 = 0.07–0.12 for northern boundary; Tables S4 and S5). Because shifts in the centre of abundance can occur without changes at the range margin (Kelly & Goulden 2008), it is not clear that the underlying processes controlling these different kinds of distribution changes are related. Changes in abundance within a species' former range are the net result of immigration, emigration and *in situ* changes in births and deaths within existing populations, perhaps resulting in a relatively greater role for deterministic effects driven by species' traits. In contrast, expansion of a northern or upper range limit depends on immigration by definition, and hence can only result from new colonization and establishment events. The relatively infrequent nature of these events, and high extinction risk during initial stages of colonization and establishment, may allow stochasticity to overwhelm deterministic signals of life history and other species' traits. Another potential explanation for the discrepancy between results for range centres vs. expanding range margins lies in dynamics at contracting margins; it is possible that species' traits are related to differences in rates of extinction at southern or lowland range margins, resulting in significant relationships between traits and net displacement of the range centre.

Some studies have detected an effect of life history traits even at expanding range margins (Holzinger *et al.* 2008; Moritz *et al.* 2008; Pöyry *et al.* 2009). For example, Pöyry *et al.* (2009) detected a positive relationship between range shifts and butterfly mobility among Finnish butterflies. Notably, their index of butterfly mobility was determined by expert ranking, which may incorporate subtleties about behaviour, philopatry, timing of dispersal and other important factors that contribute to realized dispersal. The failure of most of our dispersal indices to predict range shifts lends support to the notion that dispersal is difficult to quantify meaningfully via simple metrics. However, it is also possible the expert rankings inadvertently incorporate some knowledge of recent range shifts into assessments of mobility.

Rather than using a continuous estimate of the magnitude or rate of range shift as we did here, Holzinger *et al.* (2008) and Moritz *et al.* (2008) used binary comparisons of shifters vs. non-shifters. However, when we reanalysed our data via logistic regressions (for continuous predictors) or contingency tests (for categorical predictors), relationships were no stronger than reported here (Tables S3, S6–S10). For the alpine plant dataset (Holzinger *et al.* 2008), our inclusion of additional trait variables resulted in a smaller dataset (due to taxa with missing values), and we coded key variables such as seed dispersal syndrome differently, which may explain the difference between the original publication's results and our findings. Moritz *et al.* (2008) restricted analysis of traits associated with shifts vs. no-shifts to a subset of lowland species and then found that the probability of lowland species shifting upward was positively related to litter size and

Table 4 Results of model selection and model averaging for models relating recent shifts of the upper elevation range margins of Swiss alpine plants (Holzinger *et al.* 2008) to species' traits. Table arrangement and variables are as explained in Table 1

		lm															
		Model rank												Model average			
Category	Plants trait	1	2	3	4	5	6	7	8	9	10	11	12	β	95% CI	w_{ip}	Pred.
D	Seed shed dur.	•†	•†	•†	•†					•	•	•†		0.14	−0.17 to 0.44	0.61	y
C	Histor. limit	•†		•†	•	•						•*	•	−0.11	−0.42 to 0.19	0.53	n/a
EG	Ocean zones		•	•				•	•	•			•	−0.08	−0.33 to 0.16	0.45	n
EG	Floristic zones		•†		•		•	•						−0.08	−0.33 to 0.17	0.26	n
D	Seed shed height											•		0.01	−0.02 to 0.03	0.06	y
EG	Flowering dur.													–	–	–	–
D	Diaspore mass													–	–	–	–
D	Dispersal mode													–	–	–	–
EG	Breeding system													–	–	–	–
	$\mathbf{\Delta_i}$	0.0	0.7	0.9	0.9	1.0	1.0	1.3	1.5	1.7	1.8	1.9	2.0				
	$\mathbf{w_i}$	0.15	0.10	0.09	0.09	0.09	0.09	0.08	0.07	0.06	0.06	0.06	0.05				
	$\boldsymbol{\lambda}$	–	–	–	–	–	–	–	–	–	–	–	–				
	R^2	0.14	0.18	0.17	0.12	0.06	0.06	0.11	0.05	0.10	0.04	0.15	0.09				

		pglm											
		Model rank								Model average			
Category	Plants trait	1	2	3	4	5	6	7	8	β	95% CI	w_{ip}	Pred.
D	Seed shed dur.	•†			•		•			0.11	−0.18 to 0.39	0.41	y
C	Histor. limit	•†	•							−0.10	−0.39 to 0.19	0.36	n/a
EG	Ocean zones					•				−0.02	−0.11 to 0.07	0.12	n
EG	Floristic zones			•			•			−0.07	−0.28 to 0.15	0.23	n
D	Seed shed height								•	0.00	−0.03 to 0.01	0.07	y
EG	Flowering dur.							•		0.01	−0.03 to 0.04	0.08	y
D	Diaspore mass									–	–	–	–
D	Dispersal mode									–	–	–	–
EG	Breeding system									–	–	–	–
	$\mathbf{\Delta_i}$	0.0	0.0	0.5	0.5	0.9	1.3	1.7	2.0				
	$\mathbf{w_i}$	0.18	0.18	0.14	0.14	0.12	0.09	0.08	0.07				
	$\boldsymbol{\lambda}$	0	0	0	0.02	0.08	0	0.07	0.10				
	R^2	0.14	0.06	0.05	0.04	0.04	0.11	0.02	0.01				

†$0.05 \le P < 0.10$, *$0.01 \le P < 0.05$.

negatively related to longevity. Exclusion of high-altitude species is in keeping with our result that range shifts decreased to zero as historical upper range limits increased. For western North American small mammals, it appears that the failure to shift is largely explained by the fact that high-elevation species simply have nowhere higher in elevation to go, and only after accounting for this fact can the weaker effects of life history be detected. For alpine plants, a similar trend for high-elevation species to have shifted more slowly was also evident in several individual models (Table 4). In addition to constraints imposed by physical geography, in some cases it may be important to consider the relative quantities and arrangement of suitable habitat. For example, the availability of open water appeared to influence shifts in the wintering range of some birds, and these types of rapidly shifting habitats may have large influences on the dynamics of species dependent on these habitats (Nilsson *et al.* 2011).

Unlike most of the previous studies discussed above (but see Pöyry *et al.* 2009 for an exception), we considered phylogenetic relatedness among species. Often, when phylogenetic associations are taken into account, fewer significant traits are found because the number of phylogenetically independent comparisons is lower than the number of taxa sampled. Further, the variables that are significant can also change (e.g. Purvis *et al.* 2005). In the present study, phylogenetic autocorrelation was low (lambda estimates generally zero or near-zero), and results from regular and phylogenetic lm were largely concordant.

The four taxonomic groups analysed here had very different sample sizes (n = 24 to 195), spatial scales (regional elevation gradients to continents), temporal scales (*c.* 3–10 decades), and temporal replication (a single resurvey up to multiple resurveys at decadal intervals), with different degrees of resolution. However, large datasets with high resolution such as that for North American birds did not necessarily yield clearer relationships in our analyses. By restricting our analyses to a taxonomic subgroup, the Passeriformes, we were able to detect somewhat stronger life history effects. However, due to issues of sample size, it was not possible to subdivide this or other groups further (e.g. to the family level). In addition to taxonomic heterogeneity that might make traits incomparable, another explanation for the lack of signal in even large datasets is that different species might have experienced different degrees of exposure to recent climate change (Williams *et al.* 2008). One assumption of our analyses is that species have had equal exposures to climate change and, without intrinsic limitations, every species should have shifted in the same direction and by the same amount. This assumption may not hold at large spatial

Table 5 Results of model selection and model averaging for models relating recent shifts of the upper elevation range margins of western North American small mammals (Moritz *et al.* 2008) to species' traits. Table arrangement and variables are as explained in Table 1

		lm									pglm					
		Model rank					Model average				Model rank		Model average			
Category	Mammals trait	1	2	3	4	5	β	95% CI	w_{ip}	Pred.	1	2	β	95% CI	w_{ip}	Pred.
C	Histor. limit	●*	●*	●*	●*	●*	**−0.43**	**−0.79 to −0.06**	**1.00**	n/a	●*		−0.34	−0.84 to 0.15	0.68	n/a
R	Longevity		●	●†			−0.13	−0.50 to 0.24	0.43	y		●	−0.10	−0.43 to 0.23	0.32	y
R	Litters/year				●		0.02	−0.08 to 0.12	0.14	y			–	–	–	–
I	Body size			●			0.03	−0.09 to 0.14	0.14	y			–	–	–	–
R	Litter size					●	0.02	−0.06 to 0.09	0.12	y			–	–	–	–
EG	Daily rhythm						–	–	–	–			–	–	–	–
EG	Annual rhythm						–	–	–	–			–	–	–	–
EG	Diet breadth						–	–	–	–			–	–	–	–
I	Range size						–	–	–	–			–	–	–	–
	$\mathbf{\Delta_i}$	0.0	0.1	1.6	1.6	1.9					0.0	1.5				
	$\mathbf{w_i}$	0.31	0.29	0.14	0.14	0.12					0.68	0.32				
	$\boldsymbol{\lambda}$	–	–	–	–	–					0.0	0.0				
	R^2	0.22	0.28	0.31	0.24	0.23					0.14	0.10				

†$0.05 \le P < 0.10$, *$0.01 \le P < 0.05$.

scales, where some species may occur in areas where climate has changed at a faster rate than other species. The assumption that all species should have shifted by the same amount also may not hold if species have different sensitivities to recent climate change (Gilman *et al.* 2006; Williams *et al.* 2008). For example, a given amount of warming may impose different degrees of physiological stress on co-occurring species, which can be true for even closely related species (Somero 2010). Further, concurrent changes in multiple climatic factors may drive species in different net directions (Tingley *et al.* 2009; Crimmins *et al.* 2011). A potential extension of our approach would be to use niche modelling to quantify predicted range shifts for each species (Tingley *et al.* 2009), and then relate species' traits to a relative range shift metric (e.g. the difference between observed and predicted shifts).

Comparisons to invasion and extinction studies

Analogous attempts to relate life history traits to range shifts of another sort are found in the invasion literature. Invasion biologists have long attempted to identify the attributes of species that explain their invasion success with the goal of using these characteristics to predict future invaders (Elton 1958; Baker 1965). Efforts to characterize invaders have been criticized for being taxon- and region-specific (Crawley 1987; Mack 1996; Moles *et al.* 2008). Nonetheless, a large number of studies have documented traits associated with invasion, and synthesis of this mature literature has begun to uncover robust patterns (Kolar & Lodge 2001; Cadotte *et al.* 2006; Pyšek & Richardson 2007; Vall-llosera & Sol 2009; van Kleunen *et al.* 2010). Cadotte *et al.* (2006) reported that invasion success in plants was associated with traits similar to those that we found to be largely unrelated to climate-induced range shifts, including short life cycle, high dispersal ability, and large native range size. van Kleunen *et al.* (2010) demonstrated consistent differences between native and invasive plant species when performance-related traits were measured in common garden experiments, suggesting that a focus on relatively simple traits, such as those that tend to be readily available in databases, may limit the success of efforts to detect plant traits associated with invasion and range expansion. In keeping with our results for Passeriformes, Vall-llosera & Sol (2009) examined bird invasions worldwide and determined that species with greater potential for ecological generalization (e.g. larger brains and broader habitat and diet niches) have had greater establishment success. However, even analyses that successfully detect relationships often have low explanatory power, as we also found. In a comparison of naturalized vs. non-naturalized Eurasian species in Argentina, Prinzing *et al.* (2002) found that univariate relationships explained no more than 9% of variation in invasion status, and all traits together explained only 21%. Accordingly, others have emphasized the importance of factors unrelated to species' traits, such as introduction histories and community invasibility (Simberloff 2009; Phillips *et al.* 2010). Analogous extrinsic factors, such as habitat fragmentation and human-mediated dispersal, might override intrinsic life history effects on rates of range shift. Likewise, species undergoing both invasions and range shifts are not dispersing into empty habitat, but must be able to successfully invade resident communities, and it might be particularly hard to predict the outcome of novel species interactions in non-equilibrium communities.

Species' life history characteristics and other traits also have been used to predict extinction risk in both modern and historical times (McKinney 1997; Purvis *et al.* 2005). As with range shifts and invasions, both intrinsic ecological characteristics (e.g. population size, body mass, age at first reproduction and dispersal distance) and stochastic factors (e.g. demographic, environmental and genetic stochasticity) interact to drive the net population response (Gilpin & Soulé 1986). In the extinction literature, traits are often categorized into levels of specialization, and many of the associated characters that are hypothesized to increase extinction risk are the same as those hypothesized to decrease the likelihood of successful range shifts or invasion. For example, characteristics that have been linked to extinction include habitat specialization, diet specialization, large body size, low fecundity, long life span, slow development and limited dispersal ability (McKinney 1997; Purvis *et al.* 2005; Collen *et al.* 2006; Walker & Preston 2006; Williams *et al.* 2009). The trait that is most commonly correlated with high extinction probability is geographic range size, especially when evolutionary history is controlled (Purvis *et al.* 2005; Collen *et al.* 2006; Walker & Preston 2006). However, our analyses failed to identify a strong or consistent effect of geographic range size on recent range shifts.

Conclusions and prospects for a predictive science of range shifts

There is now ample evidence for shifting ranges in response to recent climate change (Parmesan 2006), and it is equally clear that the response is individualistic (Tingley *et al.* 2009). Our ability to quantitatively predict the nature of that individualistic response, however, appears limited thus far. Intrinsic differences among species in life history, physiology, and other traits form a central part of the developing framework for vulnerability assessments (Williams *et al.* 2008). Although it seems intuitively appealing that traits should influence range shifts, results from our analyses do not lend strong support to this conventional wisdom and instead suggest that we require a better understanding of the process of range shifts to be able to develop a predictive framework. It is possible that species' traits have relatively minor effects on range shifts within these groups for reasons discussed above (e.g. the stochastic nature of colonization events, novel species interactions and extrinsic effects of habitat availability and fragmentation). It remains an open question whether we can gain greater explanatory power by incorporating landscape variables into hindcasting studies, and we suggest this as one area for future research. Also, studies examining niche tracking in multivariate climate space suggest that seemingly counterintuitive range shifts may be driven by the net effects of concordant changes in multiple climatic variables (Tingley *et al.* 2009; Crimmins *et al.* 2011). We propose that species' traits may become better predictors of variation in range shifts if realized movements are expressed relative to that predicted by climatic niche tracking, and we suggest this as another area for future research. Alternatively, our ability to meaningfully quantify dimensions of species' natural histories for large numbers of species may simply be too limited for detection of strong differences at these scales. Trait measurement within leading-edge populations may improve predictive power if populations exhibit local adaptation and genetic differentiation (Pelini *et al.* 2010). Although it may be possible to refine trait estimates for some groups, it is apparent that readily available and relatively coarse metrics alone will be insufficient for accurately forecasting range shifts. Still, there are reasons to be hopeful. Studies taking more mechanistic approaches modelling the details of individual species' biology have had significant success (Crozier & Dwyer 2006; Kearney & Porter 2009; Buckley *et al.* 2010). As the number of these studies increases, it may be possible to compare models to understand which traits are particularly informative within groups. In addition, the number and size of available movement datasets is expanding rapidly, and the availability of high-resolution climate and landscape data is also steadily increasing. These data, coupled with more accurate measures of relevant traits, may provide a more robust framework for predicting range shifts across species.

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REFERENCES

Askew, R.R. (1988). *The Dragonflies of Europe*. Harley Books, Colchester.

Baker, H.G. (1965). Characteristics and modes of origin of weeds. In: *The Genetics of Colonizing Species* (eds Baker, H.G. & Stebbins, G.L.). Academic Press, New York, pp. 147–172.

Beyer, H.L. (2004). *Hawth*'s Analysis Tools for ArcGIS. [WWW document] Available at: http://www.spatialecology.com/htools. Last accessed 25 April 2008.

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R. *et al.* (2007). The delayed rise of present-day mammals. *Nature*, 446, 507–512.

Broenniman, O., Thuiller, W., Hughes, G., Midgley, G.F., Alkemade, J.M.R. & Guisan, A. (2006). Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Glob. Change Biol.*, 12, 1079–1093.

Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995). Spatial variation in abundance. *Ecology*, 76, 2028–2043.

Buckley, L.B., Urban, M.C., Angilletta, M.J., Crozier, L.G., Rissler, L.J. & Sears, M.W. (2010). Can mechanism inform species' distribution models? *Ecol. Lett.*, 13, 1041–1054.

Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York.

Bybee, S.M., Ogden, T.H., Branham, M.A. & Whiting, M.F. (2008). Molecules, morphology and fossils: a comprehensive approach to odonate phylogeny and the evolution of the odonate wing. *Cladistics*, 24, 477–514.

Cadotte, M.W., Murray, B.R. & Lovett-Doust, J. (2006). Ecological patterns and biological invasions: using regional species inventories in macroecology. *Biol. Invasions*, 8, 809–821.

Clark, J.S. (1998). Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *Am. Nat.*, 152, 204–224.

Collen, B., Bykova, E., Ling, S., Milner-Gulland, E.J. & Purvis, A. (2006). Extinction risk: a comparative analysis of central Asian vertebrates. *Biodivers. Conserv.*, 15, 1859–1871.

Corbet, P.S. (1963). *A Biology of Dragonflies*. Quadrangle Books, Chicago.

Corbet, P.S., Suhling, F. & Soendgerath, D. (2006). Voltinism of Odonata: a review. *Int. J. Odonatol.*, 9, 1–44.

Crawley, M.J. (1987). What makes a community invasible? In: *Colonization, Succession and Stability* (eds Gray, A.J., Crawley, M.J. & Edwards, P.J.). Blackwell, Oxford, pp. 429–453.

Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T. & Mynsberge, A.R. (2011). Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, 331, 324–327.

Crozier, L. & Dwyer, G. (2006). Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. *Am. Nat.*, 167, 853–866.

Dawideit, B.A., Phillimore, A.B., Laube, I., Leisler, B. & Bohning-Gaese, K. (2009). Ecomorphological predictors of natal dispersal distances in birds. *J. Anim. Ecol.*, 78, 388–395.

Durant, J.M., Hjermann, D.O., Ottersen, G. & Stenseth, N.C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Res.*, 33, 271–283.

Elton, C.S. (1958). *The Ecology of Invasions by Animals and Plants*. Methuen & Co., London.

Ericson, P.G.P., Zuccon, D., Ohlson, J.I., Johansson, U.S., Alvarenga, H. & Prum, R.O. (2006). Higher-level phylogeny and morphological evolution of tyrant flycatchers, cotingas, manakins, and their allies (Aves : Tyrannida). *Mol. Phylogenet. Evol.*, 40, 471–483.

Erlich, P.R., Dobkin, D.S. & Wheye, D. (1988). *The Birder*'s Handbook: A Field Guide to the Natural History of North American Birds. Simon & Shuster, New York.

Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002). Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.*, 160, 712–726.

Gardner, J.L., Heinsohn, R. & Joseph, L. (2009). Shifting latitudinal clines in avian body size correlate with global warming in Australian passerines. *Proc. R. Soc. Lond. B Biol.*, 276, 3845–3852.

Gaston, K.J. (2003). *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford.

Gilman, S.E., Wethey, D.S. & Helmuth, B. (2006). Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales. *Proc. Natl Acad. Sci. USA*, 103, 9560–9565.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010). A framework for community interactions under climate change. *Trends Ecol. Evol.*, 25, 325–331.

Gilpin, M. & Soulé, M. (1986). Minimum viable populations: processes of species extinction. In: *Conservation Biology: The Science of Scarcity and Diversity* (ed. Soulé, M.E.). Sinauer, Sunderland, pp. 19–34.

Grantham, B.A., Eckert, G.L. & Shanks, A.L. (2003). Dispersal potential of marine invertebrates in diverse habitats. *Ecol. Appl.*, 13, s108–s116.

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J. *et al.* (2008). A phylogenomic study of birds reveals their evolutionary history. *Science*, 320, 1763–1768.

Heikkinen, R.K., Luoto, M., Leikola, N., Pöyry, J., Settele, J., Kudrna, O. *et al.* (2010). Assessing the vulnerability of European butterflies to climate change using multiple criteria. *Biodivers. Conserv.*, 19, 695–723.

Herron, M.D., Castoe, T.A. & Parkinson, C.L. (2004). Sciurid phylogeny and the paraphyly of Holarctic ground squirrels (Spermophilus). *Mol. Phylogenet. Evol.*, 31, 1015–1030.

Hickling, R., Roy, D.B., Hill, J.K. & Thomas, C.D. (2005). A northward shift of range margins in British Odonata. *Glob. Change Biol.*, 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. *Glob. Change Biol.*, 12, 450–455.

Higgins, S.I., Nathan, R. & Cain, M.L. (2003). Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology*, 84, 1945–1956.

Hijmans, R.J. & Graham, C.H. (2006). The ability of climate envelope models to predict the effect of climate change on species distributions. *Glob. Change Biol.*, 12, 2272–2281.

Hill, J.K., Thomas, C.D. & Huntley, B. (1999). Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proc. R. Soc. Lond. B Biol.*, 266, 1197–1206.

Hill, J.K., Collingham, Y.C., Thomas, C.D., Blakeley, D.S., Fox, R., Moss, D. *et al.* (2001). Impacts of landscape structure on butterfly range expansion. *Ecol. Lett.*, 4, 313–321.

Hilsenhoff, W.L. (2001). Diversity and classification of insects and collembola. In: *Ecology and Classification of North American Freshwater Invertebrates* (eds Thorp, J.H. & Covich, A.P.). Academic Press, San Diego, pp. 661–732.

Hof, C., Brändle, M. & Brandl, R. (2006). Lentic odonates have larger and more northern ranges than lotic species. *J. Biogeogr.*, 33, 63–70.

Holzinger, B., Hülber, K., Camenisch, M. & Grabherr, G. (2008). Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates. *Plant Ecol.*, 195, 179–196.

Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B. & Hermy, M. (2002). Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecol. Lett.*, 5, 525–530.

Ibanez, I., Clark, J.S., Dietze, M.C., Feeley, K., Hersh, M., LaDeau, S. *et al.* (2006). Predicting biodiversity change: outside the climate envelope, beyond the species-area curve. *Ecology*, 87, 1896–1906.

Kearney, M. & Porter, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.*, 12, 334–350.

Kelly, A.E. & Goulden, M.L. (2008). Rapid shifts in plant distribution with recent climate change. *Proc. Natl Acad. Sci. USA*, 105, 11823–11826.

van Kleunen, M., Weber, E. & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Lett.*, 13, 235–245.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M. *et al.* (2008). The LEDA Traitbase: a database of life-history traits of Northwest European flora. *J. Ecol.*, 96, 1266–1274.

Kolar, C.S. & Lodge, D.M. (2001). Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.*, 16, 199–204.

La Sorte, F.A. & Thompson, F.R. (2007). Poleward shifts in winter ranges of North American birds. *Ecology*, 88, 1803–1812.

Lawler, J.J., Shafer, S.L., White, D., Kareiva, P., Maurer, E.P., Blaustein, A.R. *et al.* (2009). Projected climate-induced faunal change in the Western Hemisphere. *Ecology*, 90, 588–597.

Lenoir, J., Gegout, J.C., Marquet, P.A., de Ruffray, P. & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320, 1768–1771.

Lenoir, J., Gegout, J.C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N.E. *et al.* (2010). Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, 33, 295–303.

Loarie, S.R., Carter, B.E., Hayhoe, K., McMahon, S., Moe, R., Knight, C.A. *et al.* (2008). Climate change and the future of California's endemic flora. *PLoS ONE*, 3, e2502.

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.

Mack, R.N. (1996). Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biol. Conserv.*, 78, 107–121.

McCauley, S.J. (2010). Body size and social dominance influence breeding dispersal in male *Pachydiplax longipennis* (Odonata). *Ecol. Entomol.*, 35, 377–385.

McKinney, M.L. (1997). Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annu. Rev. Ecol. Syst.*, 28, 495–516.

Miller, J.R. & Engstrom, M.D. (2008). The relationships of major lineages within peromyscine rodents: a molecular phylogenetic hypothesis and systematic reappraisal. *J. Mammal.*, 89, 1279–1295.

Moles, A.T., Gruber, M.A.M. & Bonser, S.P. (2008). A new framework for predicting invasive plant species. *J. Ecol.*, 96, 13–17.

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.

Müller-Schneider, P. (1986). *Verbreitungsbiologie der Blütenpflanzen Graubündens*. Geobotanisches Institut der ETH, Stiftung Rübel, Zürich.

Nilsson, A.L.K., Knudsen, E., Jerstad, K., Rostad, O.W., Walseng, B., Slagsvold, T. *et al.* (2011). Climate effects on population fluctuations of the white-throated dipper *Cinclus cinclus*. *J. Anim. Ecol.*, 80, 235–243.

Nussey, D.H., Postma, E., Gienapp, P. & Visser, M.E. (2005). Selection on heritable phenotypic plasticity in a wild bird population. *Science*, 310, 304–306.

Odum, H.T. & Allee, W.C. (1954). A note on the stable point of populations showing both intraspecific cooperation and disoperation. *Ecology*, 35, 95–97.

Pannell, J.R. & Barrett, S.C.H. (1998). Baker's law revisited: reproductive assurance in a metapopulation. *Evolution*, 52, 657–668.

Paradis, E., Claude, J. & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.*, 37, 367–669.

Pelini, S.L., Keppel, J.A., Kelley, A.E. & Hellmann, J.J. (2010). Adaptation to host plants may prevent rapid insect responses to climate change. *Glob. Change Biol.*, 16, 2923–2929.

Perry, A.L., Low, P.J., Ellis, J.R. & Reynolds, J.D. (2005). Climate change and distribution shifts in marine fishes. *Science*, 308, 1912–1915.

Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sanchez-Cordero, V., Soberon, J., Buddemeier, R.H. *et al.* (2002). Future projections for Mexican faunas under global climate change scenarios. *Nature*, 416, 626–629.

Phillips, M.L., Murray, B.R., Leishman, M.R. & Ingram, R. (2010). The naturalization to invasion transition: are there introduction-history correlates of invasiveness in exotic plants of Australia? *Austral Ecol.*, 35, 695–703.

Piaggio, A.J. & Spicer, G.S. (2001). Molecular phylogeny of the chipmunks inferred from mitochondrial cytochrome b and cytochrome oxidase II gene sequences. *Mol. Phylogenet. Evol.*, 20, 335–350.

Poole, A.E. (2005). The Birds of North America Online. [WWW document] Available at: http://bna.birds.cornell.edu/BNA/. Last accessed 15 July 2010.

Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. & Saarinen, K. (2009). Species traits explain recent range shifts of Finnish butterflies. *Glob. Change Biol.*, 15, 732–743.

Prinzing, A., Durka, W., Klotz, S. & Brandl, R. (2002). Which species become aliens? *Evol. Ecol. Res.*, 4, 385–405.

Purvis, A., Cardillo, M., Grenyer, R. & Collen, B. (2005). Correlates of extinction risk: phylogeny, biology, threat and scale. In: *Phylogeny and Conservation* (eds Purvis, A., Gittleman, J.L. & Brooks, T.). Cambridge University Press, Cambridge, pp. 295–316.

Pyšek, P. & Richardson, D.M. (2007). Traits associated with invasiveness in alien plants: where do we stand? In: *Biological Invasions* (ed. Nentwig, W.). Springer, New York, pp. 97–125.

R Core DevelopmentTeam (2009). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rejmánek, M. (1996). Species richness and resistance to invasions: woody species invaders of primary tropical forest. In: *Biodiversity and Ecosystem Processes in Tropical Forests* (eds Orians, G.D., Dirzo, R. & Cushman, J.H.). Springer-Verlag, New York, pp. 153–172.

Roy, K., Jablonski, D. & Valentine, J.W. (2002). Body size and invasion success in marine bivalves. *Ecol. Lett.*, 5, 163–167.

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

Simberloff, D. (2009). The role of propagule pressure in biological invasions. *Annu. Rev. Ecol. Evol. Syst.*, 40, 81–102.

Simmons, A.D. & Thomas, C.D. (2004). Changes in dispersal during species' range expansions. *Am. Nat.*, 164, 378–395.

Somero, G.N. (2010). The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *J. Exp. Biol.*, 213, 912–920.

Stephens, P.A., Sutherland, W.J. & Freckleton, R.P. (1999). What is the Allee effect? *Oikos*, 87, 185–190.

Stevens, P.F. (2001 onwards). Angiosperm Phylogeny. [WWW document] Available at: http://www.mobot.org/mobot/research/apweb/. Last accessed 1 April 2008.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C. *et al.* (2004). Extinction risk from climate change. *Nature*, 427, 145–148.

Tingley, M.W., Monahan, W.B., Beissinger, S.R. & Moritz, C. (2009). Birds track their Grinnellian niche through a century of climate change. *Proc. Natl Acad. Sci. USA*, 106, 19637–19643.

Tingley, R., Romagosa, C.M., Kraus, F., Bickford, D., Phillips, B.L. & Shine, R. (2010). The frog filter: amphibian introduction bias driven by taxonomy, body size and biogeography. *Glob. Ecol. Biogeogr.*, 19, 496–503.

Vall-llosera, M. & Sol, D. (2009). A global risk assessment for the success of bird introductions. *J. Appl. Ecol.*, 46, 787–795.

Viscor, G. & Fuster, J.F. (1987). Relationships between morphological parameters in birds with different flying habitats. *Comp. Biochem. Physiol.*, 87A, 231–249.

Visser, M.E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc. R. Soc. Lond. B Biol.*, 275, 649–659.

Walker, K.J. & Preston, C.D. (2006). Ecological predictors of extinction risk in the flora of lowland England, UK. *Biodivers. Conserv.*, 15, 1913–1942.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B. *et al.* (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, 414, 65–69.

Webb, C.O. & Donoghue, M.J. (2005). Phylomatic: tree assembly for applied phylogenetics. *Mol. Ecol. Notes*, 5, 181–183.

Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A. & Snyder, M.A. (2009). Niches, models, and climate change: assessing the assumptions and uncertainties. *Proc. Natl Acad. Sci. USA*, 106, 19729–19736.

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A. & Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.*, 6, 2621–2626.

Williams, S.E., Williams, Y.M., VanDerWal, J., Isaac, J.L., Shoo, L.P. & Johnson, C.N. (2009). Ecological specialization and population size in a biodiversity hotspot: how rare species avoid extinction. *Proc. Natl Acad. Sci. USA*, 106, 19737–19741.

Williamson, M. (1999). Invasions. *Ecography*, 22, 5–12.

SUPPORTING INFORMATION

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

Table S1 Five predictions stemming from the hypothesis that variation in recent leading-edge range shifts is driven by differences in species' traits. For each taxonomic group, we list traits used to test each prediction. Except for traits followed by "(-)", traits are coded so that positive regression coefficients are consistent with predictions.

Table S2 Pearson correlation coefficients for correlations among continuous predictor variables.

Table S3 Univariate relationships between traits and range shifts. For continuous response variables, we used linear regressions (continuous predictors) or *t*-tests (binary predictors, "bin"). For binary range shifts (shift vs. no-shift), we used logistic regressions or contingency tests. "Pred." lists whether effects were numerically in the predicted direction. Data are not mean-standardized.

Table S4 Results of model selection and model averaging for linear regressions of shifts in North American bird centers of abundance (La Sorte & Thompson 2007) versus species' traits. Table arrangement and variables are as explained in Table 1.

Table S5 Results of model selection and model averaging for linear regressions of shifts in North American Passeriformes centres of abundance (La Sorte & Thompson 2007) versus species' traits. Table arrangement and variables are as explained in Table 1.

Table S6 Results of model selection and model averaging for logistic regressions of recent shifts (shift vs. no-shift) for North American bird northern range margins (La Sorte & Thompson 2007) versus species' traits. Table arrangement and variables are as explained in Table 1.

Table S7 Results of model selection and model averaging for logistic regressions of recent shifts (shift vs. no-shift) of North American Passeriformes northern range margins (La Sorte & Thompson 2007) versus species' traits. Table arrangement and variables are as explained in Table 1.

Table S8 Results of model selection and model averaging for logistic regressions of recent shifts (shift vs. no-shift) of British Odonata northern range margins (Hickling *et al.* 2005) versus species' traits. Habitat breadth 1 = number of water body types, habitat breadth 2 = number of different water flow regimes. Table arrangement and variables are as explained in Table 1.

Table S9 Results of model selection and model averaging for logistic regressions of recent shifts (shift vs. no-shift) of Swiss alpine plant upper elevation range margins (Holzinger *et al.* 2008) versus species' traits. Table arrangement and variables are as explained in Table 1.

Table S10 Results of model selection and model averaging for logistic regressions of recent shifts (shift vs. no-shift) of western North American small mammal upper elevation range margins (Moritz *et al.* 2008) versus species' traits. Table arrangement and variables are as explained in Table 1.

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