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META-ANALYSIS

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Climate-driven range shifts of montane species vary with elevation

Margaret A. Mamantov[1] | Daniel K. Gibson-Reinemer[2,3] | Ethan B. Linck[1] | Kimberly S. Sheldon[1]

[1]Department of Ecology & Evolutionary Biology, University of Tennessee, Knoxville, TN, USA

[2]Department of Biology, Adams State University, Alamosa, CO, USA

[3]Illinois Natural History Survey, Illinois River Biological Station, Havana, IL, USA

Correspondence
Kimberly S. Sheldon, Department of Ecology & Evolutionary Biology, University of Tennessee, Knoxville, TN 37996-1610, USA.
Email: ksheldon@utk.edu

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Abstract

Aim: In response to warming, species are shifting their ranges towards higher elevations. These elevational range shifts have been documented in a variety of taxonomic groups across latitude. However, the rate and direction of species range shifts in response to warming vary, potentially as a consequence of variation in species traits across elevation. Specifically, diurnal and seasonal climates are often more variable at higher elevations, which results in high-elevation species that have broader thermal physiologies relative to low-elevation species. High-elevation species that are thermal generalists might not need to move as far to track their thermal niche as low-elevation thermal specialists. We investigated whether rates of range shifts varied systematically with increasing elevation across taxa and regions.

Location: Sixteen montane regions world-wide.

Time period: 1850–2013.

Taxon: Nine hundred and eighty-seven species of plants and animals.

Methods: We gathered published data on elevational range shifts from 20 transect studies comparing historical and recent distributions and examined how rates of range shifts changed across elevation. Specifically, we performed a meta-analysis to calculate the pooled effect of elevation on species range shifts.

Results: We found that rates of range shifts show a negative relationship with elevation such that low-elevation species have moved upslope farther than high-elevation species on the same transect. This finding was primarily a result of shifts in the upper range limits. We also found that 28% of species shifted downslope against predictions, but elevation did not show a relationship with downslope range shifts.

Main conclusions: Idiosyncratic range shifts will significantly alter montane ecological communities, which are home to some of the greatest biodiversity on Earth. Our results demonstrate that species range shifts vary with elevation and might be a consequence of differences in species traits that also vary along montane gradients.

KEYWORDS

climate change, climatic variability hypothesis, elevational gradient, montane regions, range shifts, thermal physiology

1 | INTRODUCTION

The climate of montane regions is projected to warm three times faster than the global average (Nogués-Bravo et al., 2007). In response to this warming, species are expected to shift their ranges toward higher elevations (Chen et al., 2011), and these elevational range shifts have already been documented in a wide variety of taxonomic groups across latitude (Hickling et al., 2006; Konvicka et al., 2003; Lenoir et al., 2008; Lenoir & Svenning, 2015; Parmesan, 2006; Parmesan & Yohe, 2003; Pecl et al., 2017; Sheldon, 2019). However, the rate at which individual species have shifted their elevational ranges in response to warming varies; some species have moved upslope by tens of metres each year, other species have remained in place, and some species have moved downslope, counter to predictions (Brusca et al., 2013; Harris et al., 2012; Lenoir et al., 2010). Montane regions harbour some of the greatest biodiversity on Earth (Grenyer et al., 2006), and idiosyncratic range shifts will significantly alter these ecological communities, affecting ecosystem services and threatening human health (Körner, 2004; Pecl et al., 2017). Understanding the drivers that explain fine-scale variation in species range shifts is thus of great importance.

Observed range shifts of terrestrial species in response to climate warming have been greater in areas with a larger magnitude of temperature change (Chen et al., 2011). Evidence indicates that the rate of climate warming has generally been greater at high compared with low elevations (Beniston et al., 1997; Diaz & Bradley, 1997; Pepin et al., 2015). This suggests that high-elevation species might have shifted their ranges further upslope in response to contemporary warming compared with low-elevation species over the same period.

However, in addition to the magnitude of temperature change, range shifts are likely to be driven by the ability of species to handle temperature change, which might be greater at higher elevations. Specifically, the climatic variability hypothesis posits that the thermal tolerance of an organism should match the climatic variability it experiences (Bozinovic et al., 2011; Dobzhansky, 1950). Diurnal and seasonal temperatures tend to be more variable at higher elevations (Gaston & Chown, 1999; Sømme & Block, 1991), and thus high-elevation species should have broader thermal tolerance (i.e., ability to tolerate a wider range of temperatures) compared with their low-elevation counterparts (Janzen, 1967; Sheldon et al., 2018). Indeed, a pattern of increasing breadth of thermal tolerance with increasing elevation has been observed in both terrestrial (Brattstrom, 1968; Gaston & Chown, 1999; Lüddecke & Sánchez, 2002; Navas, 2006; Sheldon et al., 2015) and aquatic ectotherms (Shah et al., 2017), although exceptions exist (Shah et al., 2017). In plants, heat tolerance declines with elevation, but less than would be expected by adiabatic lapse rates (Feeley et al., 2020), and more freeze-tolerant genotypes are found at higher elevations (Körner, 2003; Vitasse et al., 2014). High-elevation plants might, therefore, have a broader thermal tolerance than low-elevation species, although tests of both heat and cold tolerance in plants across elevation are generally lacking. In birds, but not mammals, species tend to have broader thermal tolerance in areas with greater climatic variability (Khaliq et al., 2014). Thus, for many taxa, high-elevation species might be thermal generalists that do not need to move as far to track their thermal niche. Consequently, as climate has warmed, low-elevation thermal specialists might have shifted their ranges more than high-elevation thermal generalists to keep up with their narrower thermal niches (Rumpf et al., 2018).

Our goal was to determine where upslope movements have been greatest (higher or lower elevations) in order to gain a better understanding of fine-scale variation in range shifts in montane regions. Given that species in environments with reduced temperature variation have been shown to track their thermal niche more closely along elevational gradients in response to warming (Freeman & Freeman, 2014), we made the a priori prediction that upslope range shifts have been greatest at lower elevations, where temperature variation is reduced and species tend to be thermal specialists (Gaston & Chown, 1999).

2 | METHODS

To examine species range shifts along montane gradients in response to warming, we collected data from the literature on elevational range limits from historical and recent surveys. Specifically, we carried out a Web of Science search in February 2020 using the terms "climate change, mountain*, range shifts, and elevation*" to find papers that published elevational range data from both a historical and a more recent survey. We also used recent meta-analyses (Freeman et al., 2018; Gibson-Reinemer et al., 2015; Rumpf et al., 2019) to identify additional papers containing relevant data.

To be included, published papers had to provide data on local temperature trends (specifically, the amount of warming between the historical and recent surveys) and changes in both the upper and lower limits of species distributions at two different time points. We limited our analyses to studies that were conducted in montane areas without significant anthropogenic habitat disturbance to minimize the confounding effect of habitat loss on range shifts (Guo et al., 2018). We removed species that were not present in both the historical and recent surveys (<1% were present in one study but not the other) because we would be unable to calculate range shifts for these species. In total, data from 987 species of plants, insects, birds, mammals, amphibians and reptiles located on 20 montane transects met these criteria (Table 1; Figure 1; Angelo & Daehler, 2013; Brusca et al., 2013; Chen, 2011; Felde et al., 2012; Forero-Medina, 2012; Forero-Medina et al., 2011; Freeman & Freeman, 2014; Koide et al., 2017; Menéndez et al., 2014; Moritz et al., 2008; Ploquin et al., 2014; Raxworthy et al., 2008; Rowe et al., 2015; Telwala et al., 2013; Tingley, 2011; Tingley et al., 2012).

We quantified the elevational range of a species as the distance (in metres) between the lower and upper elevational range limits for the species and used this to determine the elevational midpoint of the range (hereafter, range midpoint) for each species during both historical and recent surveys. We calculated the range shift (in

TABLE 1 Studies used in primary meta-analysis (Figure 3) of species range shifts along elevational gradients

Study area	Taxonomic group	Reference	Number of species	Study duration (years)	Warming (°C/decade)
Western USA, Lassen Volcanic National Park	Birds	Tingley (2011), Tingley et al. (2012)	74	98	0.08
Western USA, Yosemite National Park	Birds	Tingley (2011), Tingley et al. (2012)	49	87	0.09
Western USA, Sierra Nevada Mountains	Birds	Tingley (2011), Tingley et al. (2012)	43	81	0.1
Northern Spain, Cantabrian Mountains	Bumblebees	Ploquin et al. (2014)	17	21	0.45
Western USA, Yosemite National Park	Mammals	Moritz et al. (2008)	16	88	0.30
Eastern France, South-western Alps	Dung beetles	Menéndez et al. (2014)	15	19	0.32
Southern Spain, Sierra Nevada Mountains	Dung beetles	Menéndez et al. (2014)	8	24	0.46
Papua New Guinea, Mt. Karimui and Karkar Island	Birds	Freeman and Freeman (2014)	30	47	0.08
Borneo, Mt. Kinabalu	Moths	Chen (2011)	116	42	0.17
Peru, Cerros del Sira	Birds	Forero-Medina et al. (2011)	19	41	0.19
Madagascar, Tsaratanana Massif	Amphibians	Raxworthy et al. (2008)	19	10	0.45
Madagascar, Tsaratanana Massif	Reptiles	Raxworthy et al. (2008)	11	10	0.45
Hawaii, USA, Mauna Loa	Plants	Angelo and Daehler (2013)	14	42	0.7
Norway, Sikkilsdalen	Plants	Felde et al. (2012)	10	81	0.6
Hawaii, USA, Mauna Loa	Plants	Koide et al. (2017)	60	42	0.7
Western USA, Kings Canyon	Mammals	Rowe et al. (2015)	17	84	0.6
Western USA, Lassen Volcanic National Park	Mammals	Rowe et al. (2015)	23	84	0.6
Western USA, Sierra Nevada Mountains	Mammals	Rowe et al. (2015)	30	84	0.6
Sikkim, India, Eastern Himalayan Mountains	Plants	Telwala et al. (2013)	107	159	2.21
Western USA, Santa Catalina Mountains	Plants	Brusca et al. (2013)	20	48	1.06

metres per degree Celsius) for each species using both the change in range midpoint and the change in temperature between the historical and recent surveys reported in each study. We used metres per degree Celsius rather than the magnitude of range shift in order to standardize across studies. Given that each transect study was independent, species ranges and warming were not always measured in the same way. This did not affect our results because the analyses we performed (see below) compared range shifts within mountain transects, not among mountain transects. Thus, as long as factors were controlled across elevations in the same study, our

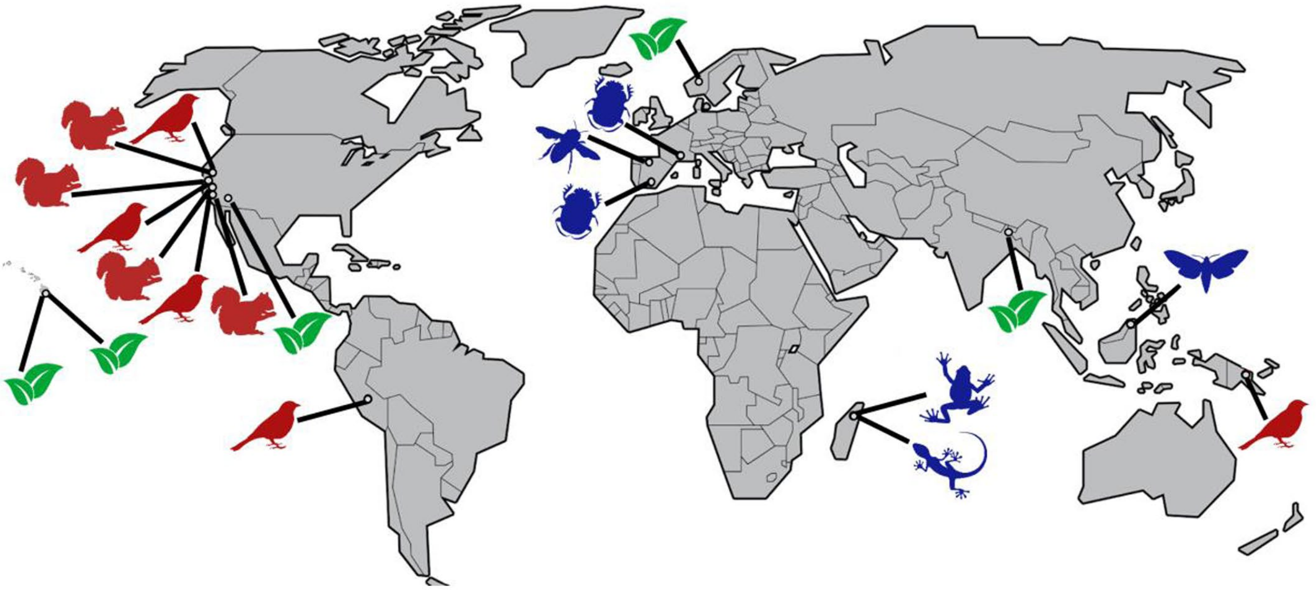

FIGURE 1 Map showing the study locations and taxa used in analyses. Symbols represent ectothermic (blue) and endothermic (red) animal taxa and plant taxa (green) sampled in transect studies, including dung beetles, bumblebees, moths, amphibians, reptiles, birds, mammals and plants. References for studies used in analyses are listed in Table 1.

results are valid. We used the range midpoint from the historical survey as a proxy for the elevation where the species occurred, and we predicted that rates of upslope shifts of the range midpoint should be negatively correlated with midpoint elevation of the species historical range (i.e., lower elevation species would have moved farther upslope).

To test our prediction, we examined range shifts along elevational gradients by subsetting the unaltered collection of aggregated data with three distinct sets of filtering criteria, each of which excluded certain species. These alternative datasets allowed us to determine whether our results were robust to biases related to our filtering of species. For our "primary" filtered dataset, we excluded any species with upper distributions that reached the maximum elevation of the transect during the historical survey so that we would be able to calculate the extent of upslope range shifts of species. Following the same logic, we also excluded species with lower distributions that reached the minimum elevation of the transect during the historical survey. After these exclusions, 698 species remained (Table 1). In our second filtered dataset, we excluded any species with upper or lower distributions that reached the maximum or minimum of the transect, respectively, during either the historical or the modern survey. In this dataset (610 species), species range shifts were entirely within the boundaries of their respective transects. Although these data could lead to the underestimation of upslope range shifts for higher-elevation species, they allowed us to measure the full extent of range shifts for species on a transect. Lastly, our third filtered dataset retained all species regardless of their maximum or minimum elevations relative to the transect during both the historical and the modern surveys (987 species). This dataset was intended to measure whether we continued to see the same patterns in range shifts when including all species regardless of whether or not their range intersected the limits of a transect.

To determine the magnitude and direction of species range shifts across elevation, we used a meta-analysis approach that took into account variation among transects and then pooled individual effect sizes for all transects to obtain an overall effect size. To do this, we first plotted the change in range midpoints (in metres per degree Celsius) as a function of the elevational midpoint of a species' range during the historical survey for all species on a transect (20 transects in total). We then fitted a linear regression to calculate the slope (β) and the standard error of the slope for each transect independently with the "lm()" function in R (v.3.6.3; R Development Core Team, 2020). Next, we performed a meta-analysis using a random effects model to calculate the pooled effect size, or the overall effect of the elevation of the historical range midpoint on shifts in range midpoint across all transects. The assumption of this model was that the true effect size varied across transects, which was important because the studies varied in geographical location, taxa, and the number of years between the historical and recent surveys (Borenstein et al., 2009). To calculate the pooled effect size from the value of β across all transects, we used the "metagen()" function in the R package "meta" and applied the Sidik–Jonkman method to estimate heterogeneity (R v.3.6.3; R Development Core Team, 2020). In this calculation, the contribution of a given study to the pooled effect size was weighted by the sample size and the degree of variation in the data of the study, such that a transect with many species and little variation in range shifts across species had a stronger influence on the value of the statistic than a transect with few species and a high level of variation in range shifts.

Given that we found a negative relationship between the elevation of historical range midpoint and shifts in range midpoint for all three datasets (see Results), we performed additional analyses to test whether this was attributable to greater upslope range shifts at lower elevations (as we predicted a priori) or three other hypotheses: (1) more frequent downslope range shifts at high elevations; (2) systematic contractions or expansions across elevation; or (3) asynchronous shifts in the upper or lower range limits of species across elevation. To test hypothesis 1, we further subset our primary dataset into only those species with range midpoints that shifted upslope or only those species with range midpoints that shifted downslope, and we examined the effect of elevation of historical range midpoint on upslope and downslope movements independently. To test hypothesis 2, we used our primary dataset and examined the relationship between elevation of historical range midpoint and change in range size. To test hypothesis 3, we used our primary dataset and examined the relationship between elevation of historical range midpoint and shifts in both lower and upper range limits independently. For all three hypotheses, we again used linear regression and random effects meta-analyses to calculate the pooled effect size of elevation on response variables.

Finally, to test whether results from our primary filtered dataset could be an artefact of our filtering procedure, we ran a simulation that randomly assigned elevational range shifts drawn from the data to species along the transect under a null model of no relationship between elevational range and range shift direction or magnitude (for model details, see Range Shift Simulation in Supporting Information). For the simulation, we used a nonparametric approach to resample range shifts randomly from empirically observed range shift values. We processed the randomly generated ranges in an identical manner to our primary dataset (i.e., by removing simulated species with original upper or lower range limits that reached the maximum or minimum transect elevation, respectively, during the historical survey). For most mountain transects, we found that the relationship between elevation and range shift was zero after randomly assigning range shifts to species (see Simulation Figure 1 in Supporting Information). Three mountain transects demonstrated slightly negative relationships between species elevational ranges and range shifts. However, these negative relationships from randomly generated range shifts were smaller than those calculated empirically, and they did not change the interpretation of the data. Overall, this indicated that the empirical findings for the primary dataset were robust to analytical choices (see Range Shift Simulation in Supporting Information).

3 | RESULTS

In our primary dataset (in which we excluded species with ranges that reached the top or bottom of each of the 20 transects during the historical survey), 61% of the 698 species moved upslope (measured as change in range midpoint), 28% moved downslope, and the remaining 11% did not shift their ranges (Figure 2). We found that for seven of the 20 transects, range shifts showed a significant negative relationship with elevation (Figure 2; $r^2 = .05–.56$). Represented among these transects were two bird studies and one study each of plants, dung beetles, moths, reptiles and mammals (Figure 2). Another nine transects had negative but non-significant relationships with elevation (Figure 2; $r^2 = 0–.27$). The remaining four transects had positive but non-significant relationships with elevation (Figure 2; $r^2 = .0002–.0043$). In the dataset in which we excluded any species with range limits that reached the top or bottom of the transect during either the historical or the recent survey, nine transects showed a significant negative relationship between range shifts and elevation, eight transects had negative but non-significant relationships with elevation, and three transects had positive but non-significant relationships with elevation (Supporting Information Figure S1). Lastly, in the dataset in which we did not exclude any species, 11 transects showed a significant negative relationship between range shifts and elevation, eight transects had negative but non-significant relationships with elevation, and one transect had a positive but non-significant relationship with elevation (Supporting Information Figure S2).

Analyses from all three datasets indicated that range shifts showed a negative relationship with elevation (i.e., low-elevation species moved upslope farther than high-elevation species on the same transect). In the primary dataset (698 species), the pooled effect size of elevation on range shift (in metres per degree Celsius) was −0.1776 (Figure 3; 95% confidence interval (CI): −0.2680, −0.0871; $p = .0001$). This suggests that with 1 °C of warming, a 100 m increase in elevation of the historical range midpoint of a species leads to a 17.76 m decrease in the upslope shift of the range midpoint. The pooled effect size was similar across the remaining two datasets, indicating that regardless of species exclusion criteria, the effect of elevation on range shift was negative and statistically significant. For the dataset in which we excluded species whose ranges reached the top or bottom of the mountain during either the historical or the recent survey (610 species), the pooled effect size was −0.2799 (Supporting Information Figure S3; 95% CI: −0.4126, −0.1473; $p < .0001$). For the dataset in which we kept all species regardless of their maximum or minimum elevations relative to the transect (987 species), the pooled effect size was −0.2100 (Supporting Information, Figure S4; 95% CI: −0.2991, −0.1209; $p < .0001$).

To test alternative hypotheses for the negative relationship between elevation and shift in the range midpoint of species, we examined range dynamics using different subsets of our primary dataset. Initially, we looked at the relationships between elevation and all species that moved upslope or all species that moved downslope (hypothesis 1). We found a significant decrease in upslope range shifts with increasing elevation and no significant change in the magnitude of downslope range shifts across elevation. Among only those species with upslope range shifts (425 species), the pooled effect size of elevation on upslope movement was −0.1797 (Supporting Information Figure S5; 95% CI: −0.2606, −0.0987; $p < .0001$), indicating that with 1 °C of warming, a 100 m increase in elevation leads to a 17.97 m decrease in the upslope shift of the range midpoint of species. Among only those species

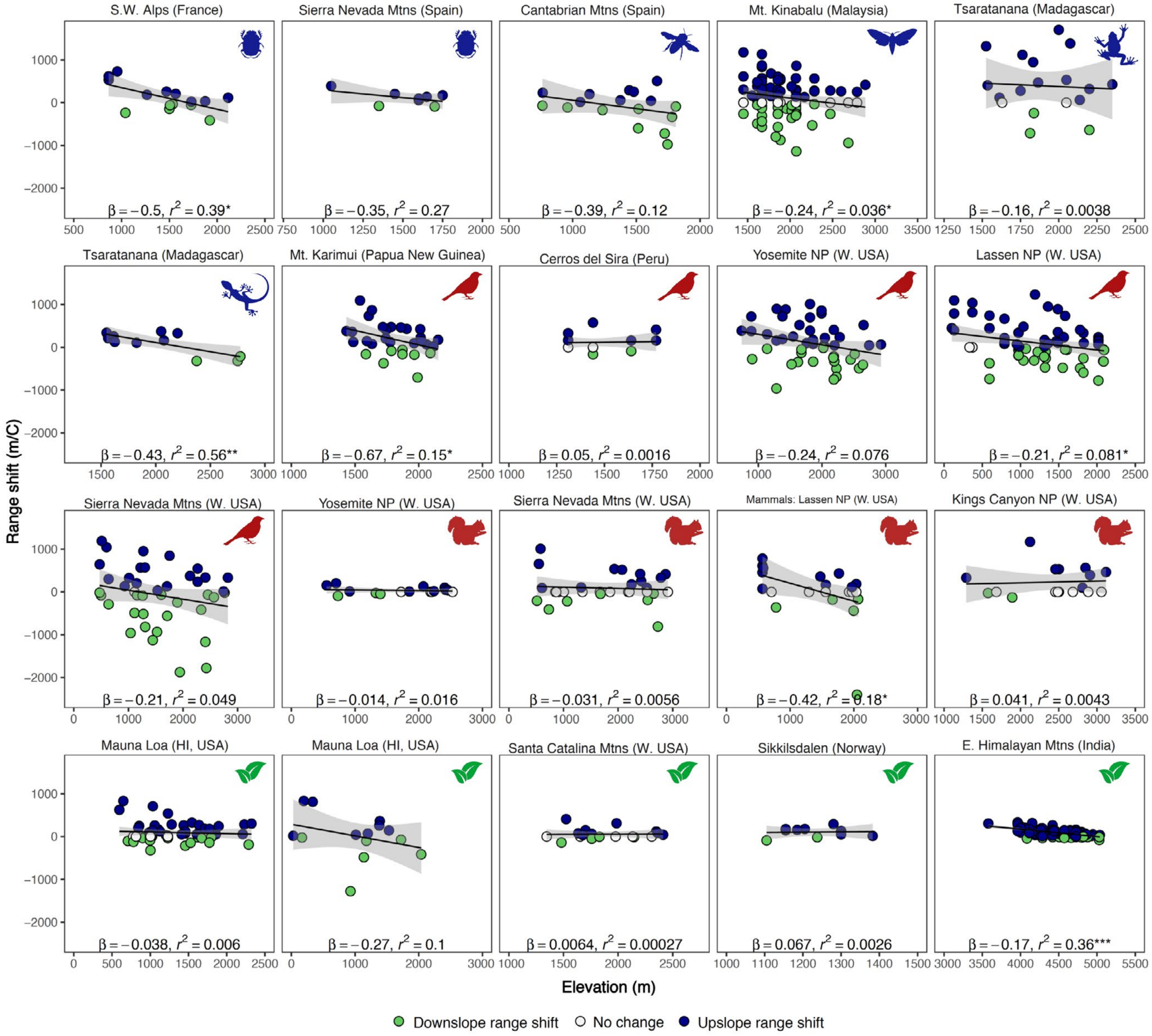

FIGURE 2 Rates of species range shifts decrease with increasing elevation. Range shifts (in metres per degree Celsius) were calculated as the total shift in midpoint of the elevational range of a species divided by the total change in temperature observed between historical and recent surveys. Elevation (in metres) is the midpoint of the species range from the historical survey. For each survey, elevation on the *x* axis ranges from the minimum to maximum elevation of the survey transect, whereas the range shift values on the *y* axis are the same for each panel. The midpoint of species ranges has moved upslope (dark blue), downslope (green) or stayed the same (white). Results are presented by taxonomic group and study location. Symbols represent ectothermic (blue) and endothermic (red) animal taxa and plant taxa (green) sampled in transect studies, including dung beetles, bumblebees, moths, amphibians, reptiles, birds, mammals and plants. Significant relationships between range shifts and elevation are indicated (**p* < .05; ***p* < .01; ****p* < .001).

with downslope range shifts (196 species), the pooled effect size of elevation on downslope range shift was −0.0052 (Supporting Information Figure S6; 95% CI: −0.0921, 0.0817; *p* = .91). Together, these results match our a priori prediction that the negative relationship between elevation and shift in range midpoint is attributable to changes in upslope range shifts with elevation, not downslope range shifts.

It was also possible that systematic changes in range sizes (i.e., range contractions or expansions) with elevation (hypothesis 2) could be driving the negative relationship between elevation and range shifts. From our primary dataset, 43% of species showed range contractions, 44% showed range expansions, and 13% showed no change in range size. When we examined changes in range sizes across elevation from the historical to the recent survey, we found that range sizes changed significantly less with increasing elevation (Supporting Information Figure S7; pooled effect size of elevation on changes in range size was −0.1825; 95% CI: −0.3502, −0.0149; *p* = .03). This pattern is explained by asynchrony in upper and lower

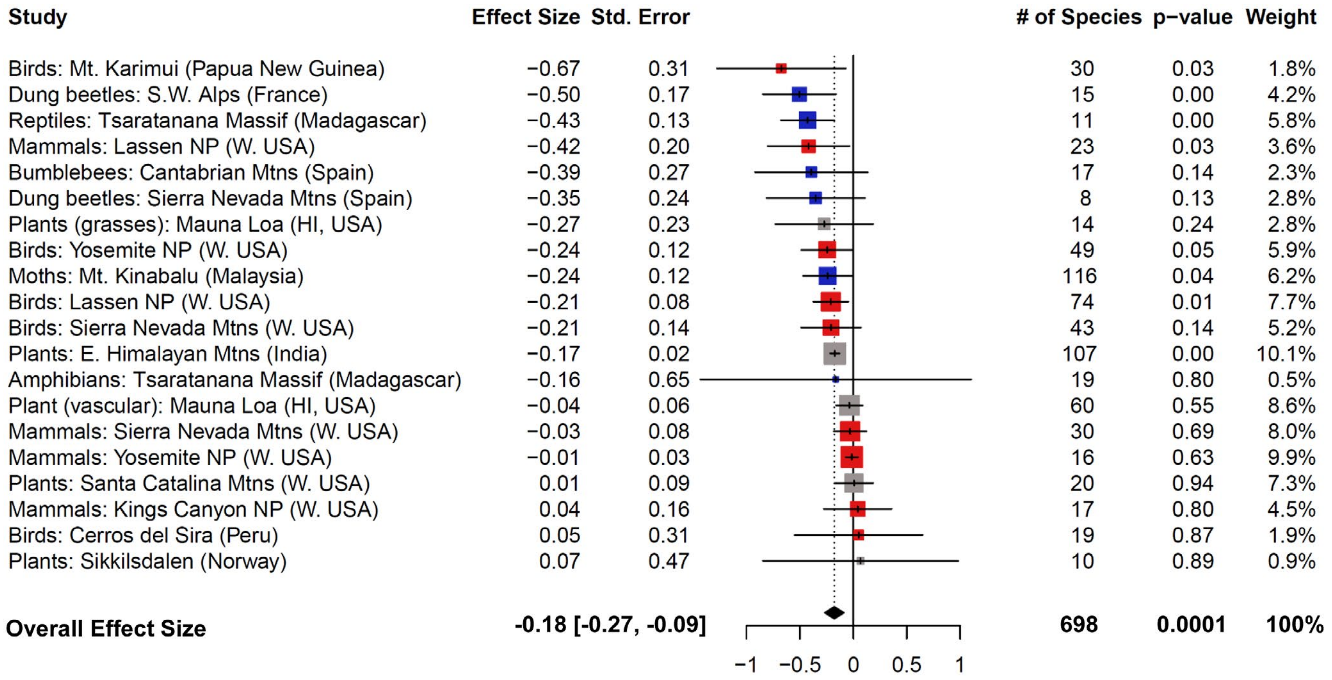

FIGURE 3 Meta-analysis indicates a negative overall effect size of elevation on range shift. Species range shifts (in metres per degree Celsius) thus decrease with increasing elevation. The effect size of each study was calculated as the slope of the regression line (β) between the midpoint elevation of the species range during the historical survey (in metres) and the shift in midpoint of the species range by change in temperature (in metres per degree Celsius). The *p*-value for each study indicates the significance of this relationship. For each study, the centre of the box represents the effect size, and the black bar shows the standard error of the effect size. The box colour represents transect studies of endotherms (red), ectotherms (blue) and plants (grey). The box size represents the study weight in the meta-analysis, which is based on the number of species and the standard error of the effect size of the transect study. The overall effect size and 95% confidence interval are listed in bold and represented by the diamond. The *p*-value of the overall effect size and the total number of species included in the meta-analysis are also in bold (right of plot).

range limits (hypothesis 3); we found that shifts of upper range limits showed significant negative relationships with elevation, whereas shifts in lower range limits showed no relationship with elevation. The pooled effect size of elevation on upper range limits was −0.2441 (95% CI: −0.3590, −0.1291; $p < .0001$; Supporting Information Figure S8), and the pooled effect size of elevation on lower range limits was −0.1097 (95% CI: −0.2427, 0.0246; $p = .11$; Supporting Information Figure S9). Thus, shifts in upper range limits in species moving upslope are driving the observed pattern in range shifts with elevation.

4 | DISCUSSION

Our analysis of 987 species range shifts across 20 montane transects indicates that low-elevation species have moved upslope farther than high-elevation species. Our results were robust to different assumptions, suggesting that this observation is not a product of which species were included in the analyses. The negative relationship between elevation and range shifts was primarily a result of variation in the upper range limits of species moving upslope. Our findings are consistent with a recent study (Rumpf et al., 2018) that found plant species in the Alps shifted upslope faster the lower in elevation they were situated historically on the mountain. However, contrary to our results, a meta-analysis (Rumpf et al., 2019) found that upper and lower range limits of montane plant species are shifting at similar rates in response to climate change.

The relationship between elevation and range shifts (Figure 2) might be driven, in part, by variation in the thermal physiology of species along montane gradients. Theory and empirical work suggest that high-elevation species have evolved broader thermal tolerances in response to greater diurnal and seasonal temperature fluctuation (Gaston & Chown, 1999; Ghalambor et al., 2006; Janzen, 1967; Sheldon et al., 2018; Stevens, 1992). This could allow high-elevation, thermal generalist species to tolerate more warming relative to low-elevation, thermal specialist counterparts and allow high-elevation species to stay in place longer. This mechanism could be responsible for the negative relationship we found between elevation and species range shifts in response to warming.

However, in addition to thermal physiology, variation in fecundity could also explain the patterns we observed. More fecund species have been shown to shift their ranges faster than less fecund species (Moritz et al., 2008). Given that the length of the reproductive season influences the number of generations (Altermatt, 2010; Roff, 1983; Stearns, 1992) and reproductive attempts per year (Badyaev, 1997; Bears et al., 2009), low-elevation species might have more opportunities to reproduce and disperse compared with high-elevation species. This mechanism could allow low-elevation species to shift their ranges farther over the same period compared with high-elevation species (Crozier & Dwyer, 2006). We cannot tease apart the roles of thermal physiology and fecundity in the observed patterns, and it is possible that both mechanisms play a role in the variation in range shifts of species along elevational gradients.

As elevation increases, geographical area, and thus habitat space, is thought to decrease (Colwell et al., 2008; Sekercioglu et al., 2008). If this is the case, high-elevation species might be limited in their ability to shift to cooler habitats, which could result in reduced range shifts with increasing elevation. However, a reduction in geographical area with elevation rests on the assumption that mountains are pyramid shaped. Through an analysis of 182 mountain ranges, Elsen and Tingley (2015) demonstrated that the majority of mountains do not conform to this pattern, and in many cases the geographical area was unaffected or even increased with elevation. Therefore, it is unlikely that lack of area at higher elevations is leading to the observed pattern of reduced range shifts at higher elevations.

Previous research has also indicated that microhabitat complexity, which could buffer species from climate warming, increases with elevation (Byrne et al., 2017; Elsen & Tingley, 2015; Rumpf et al., 2018; Scherrer & Körner, 2010, 2011). This suggests that species living at high elevation might not need to move as far to reach newly suitable habitats. The reduced distance to suitable habitats at high elevations could contribute to our observation that range shifts decrease with elevation but is unlikely to be the primary factor. Increase in microhabitat complexity is especially pronounced in alpine and nival elevational zones (Elsen & Tingley, 2015; Scherrer & Körner, 2010). However, for many of the studies we analysed, the transects do not reach these habitat zones, and species on those transects still showed a negative relationship between elevation and range shifts (Figure 2).

Our results are unlikely to be driven by elevational patterns in either habitat modification or warming. Previous work demonstrates that habitat modification at lower elevations can accelerate the upslope movement of species (Guo et al., 2018). However, this is an unlikely driver of our results because we used data from studies that reported minimal habitat modification or that were conducted in protected areas to reduce the confounding effect of habitat loss on range shifts. Likewise, variation in climate warming along montane gradients is unlikely to drive the patterns we observed. Climate warming has tended to be greater at higher rather than lower elevations (Barry, 2008; Ohmura, 2012; Pepin et al., 2015), suggesting that high-elevation species should be moving upslope faster. However, our results show the opposite pattern.

Although our meta-analysis indicates a negative relationship between elevation and range shifts, different transects and different species within transects show heterogeneity in both the direction and the magnitude of range shifts (Figure 2). The idiosyncratic nature of range shifts in response to climate change is common (e.g., Chen et al., 2011; Crimmins et al., 2011; Gibson-Reinemer & Rahel, 2015; Lenoir et al., 2010) and is likely to be the result of multiple factors, including abiotic changes that may or may not be related to climate change, species-specific traits and biotic interactions (Gibson-Reinemer & Rahel, 2015). As examples, natural changes in edaphic conditions are known to restrict the upslope movements of species in response to warming (Brown & Vellend, 2014; Frei et al., 2010). Additionally, loss of snow cover or changes in precipitation associated with climate change at high elevations have led to declines in population sizes, occasionally resulting in local extirpations and thus downslope movement (Crimmins et al., 2011; Lenoir et al., 2010). Variation in species range shifts might also be affected by differences in species traits. For instance, greater ecological specialization can lead to range declines (Angert et al., 2011; Mattila et al., 2011). In addition, because oxygen availability decreases with elevation, species with higher oxygen demands might show counterintuitive range shifts with climate warming (Jacobsen, 2020). Biotic interactions, including competition (Alexander et al., 2018; Urban et al., 2012) and facilitation (Ettinger & HilleRisLambers, 2017; HilleRisLambers et al., 2013), can greatly influence distributions and alter range shifts in response to climate change. Finally, changes in community composition and local extinctions might result in novel biotic interactions that affect species distributions (Alexander et al., 2015; Davis et al., 1998; Lenoir et al., 2010; Urban et al., 2013). These factors could affect the direction or magnitude of range shifts and thus might be responsible for the idiosyncratic responses observed among species on the same mountain. However, these factors do not show a relationship with elevation and are, therefore, unlikely to be driving the relationship between range shifts and elevation that we observed.

The majority of species ranges have shifted towards higher elevations, probably in response to climate warming, and these upslope shifts consistently show greater movement of species that were historically present at lower elevations (Figures 2 and 3; this meta-analysis; Rumpf et al., 2018). Asynchronous range shifts along montane gradients alter ecological communities (Gibson-Reinemer et al., 2015; Pecl et al., 2017). Given that ranges of low-elevation species have shifted more in response to climate warming compared with high-elevation species, ecological communities at low elevations have probably experienced more biotic reshuffling and greater community disassembly. This is particularly troubling because low elevations tend to have greater species diversity compared with high elevations. Understanding species range shifts, which vary along elevational gradients in montane regions, improves our ability to formulate predictions of future distributions of global biodiversity and changes to community composition.

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AUTHOR CONTRIBUTIONS

K.S.S. and D.K.G.-R. conceived the original idea. M.A.M. and K.S.S. designed the study. M.A.M. and D.K.G.-R. gathered data. M.A.M. performed analyses, with contributions from E.B.L. M.A.M. and K.S.S. wrote the manuscript. All authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

Data and R scripts are available in the Supporting Information.

ORCID

Margaret A. Mamantov https://orcid.org/0000-0002-3637-8748
Ethan B. Linck https://orcid.org/0000-0002-9055-6664
Kimberly S. Sheldon https://orcid.org/0000-0002-3215-2223

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BIOSKETCH

The authors share an interest in the impacts of climate change on species and ecological communities and have drawn on previous work, including modelling and use of historical and recent surveys, to understand how climate-driven range shifts will alter ecological communities across latitude.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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