Expanding, shifting and shrinking: The impact of global warming on species’ elevational distributions

Benjamin G. Freeman1,2 | Julie A. Lee-Yaw1,3 | Jennifer M. Sunday1,2,4 | Anna L. Hargreaves1,5

1Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada
2Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada
3Department of Botany, University of British Columbia, Vancouver, British Columbia, Canada
4School of Marine and Environmental Affairs, University of Washington, Seattle
5Department of Biology, McGill University, Montreal, Quebec, Canada

Correspondence
Benjamin Freeman, Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada. 242 Beatty Biodiversity Centre, 6270 University Blvd, Vancouver BC V6T1Z4
Email: freeman@zoology.ubc.ca

Funding information
National Science Foundation, Grant/Award Number: 1523695; Banting Postdoctoral Fellowship, Grant/Award Number: #379958; Natural Sciences and Engineering Research Council, Grant/Award Number: PDF 487035-2016

Abstract
Aim: Species are responding to climate warming by shifting their distributions toward historically cooler regions, but the degree to which expansions at cool range limits are balanced by contractions at warm limits is unknown. We synthesized published data documenting shifts at species’ warm versus cool range limits along elevational gradients to (a) test classic ecological theory that predicts temperature more directly influences species’ cool range limits than their warm range limits, and (b) determine how warming-associated shifts have changed the extent and area of species’ elevational distributions.

Location: Global.

Time period: 1802–2012.

Major taxa studied: Vascular plants, endotherms, ectotherms.

Methods: We compiled a dataset of 975 species from 32 elevational gradients for which range shifts have been measured at both warm and cool range limits. We compared the magnitude and variance of shifts at species’ warm versus cool limits, and quantified how range shifts have impacted species’ elevational extents and areas.

Results: On average species have shifted upslope associated with temperature increases at both warm and cool limits (warm limit: 92 ± 455 m/C; cool limit: 131 ± 465 m/C; overall mean ± SD). There was no systematic difference in the magnitude or variance of shifts at warm versus cool limits and thus no indication that cool limits are more directly controlled by temperature. Species’ elevational extents and available area significantly decreased for mountaintop species.

Main conclusions: Our results do not support the long-standing hypothesis that cool limits are more sensitive or responsive to temperature. We find that, across the globe, mountaintop species’ ranges are significantly shrinking as they shift upslope, supporting predictions that high elevation species are especially vulnerable to temperature increases. Our synthesis highlights the extreme variation in species’ distributional responses to warming, which may indicate that biotic interactions play a more prominent role in setting range limits than previously thought.

Keywords
climate change, elevational gradient, mountaintop extinctions, range limits, range shifts, species distributions
INTRODUCTION

Climate change has caused species from diverse taxa around the world to shift their distributions to historically cooler climates (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011). However, species are not marching in lockstep toward the poles and up mountain slopes. Instead, there is extreme variation in the rate at which species are shifting their distributions associated with recent warming (Angert et al., 2011; Lenoir et al., 2010). This variation provides the raw material to investigate how temperature influences species’ ranges. Although previous syntheses have addressed variation in range shifts among species (Angert et al., 2011; MacLean & Beissinger, 2017; Sunday et al., 2015), variation in range shifts within species – how shifts differ between species’ warm (low elevation/latitude) and cool (high elevation/latitude) range edges – has been largely ignored (but see Chen, Hill, Shiu, et al., 2011 for an illustrative case study). There are two motivating factors – theoretical and practical – for focusing on shifts within species by comparing changes at warm versus cool range edges. First, this whole-range perspective offers a test of classic ecological theory that predicts temperature exerts a more direct impact on species’ cool range limits. Second, such a whole-range perspective is necessary to answer an important open question in conservation: as species’ ranges shift in space, do their distributions shrink, expand or remain stable in size?

Climate underlies the range limits of diverse taxa (Wiens & Graham, 2005), but its relative importance in governing the warm versus cool ends of species’ distributions remains contentious. Ecologists have long proposed that climate more directly determines species’ cool range limits, while warm range limits are more influenced by biotic interactions (Darwin, 1859; Dobzhansky, 1950; Connell, 1961; MacArthur, 1972; hereafter termed the ‘Darwin–MacArthur’ hypothesis). Supporting this idea, data from ‘beyond the range edge’ transplant experiments suggest that biotic interactions limit fitness more often beyond warm range limits than beyond cool range limits (Hargreaves, Samis, & Eckert, 2014). In addition, terrestrial species’ cool limits more closely match their thermal tolerance limits (Sunday, Bates, & Dulvy, 2012) and are better predicted by climate (Normand et al., 2009), compared to warm range limits. In contrast, a recent synthesis (Cahill et al., 2014) found that abiotic factors commonly constrain warm range edges, suggesting that climate can play an equally important role at warm and cool limits.

Climate change constitutes an unplanned global experiment that enables us to test these alternative possibilities. While a complex array of abiotic, biotic and geographical variables influence species’ range limits, that species are typically shifting polewards and upslope in response to recent warming confirms that temperature is an important variable limiting species’ distributions. Here, we extend this premise to infer the role of temperature in recent shifts at species’ warm versus cool range limits in the context of the Darwin–MacArthur hypothesis, which is the only hypothesis that offers global, testable predictions about the relative speed and variance in shifts of cool versus warm limits. We draw together studies that have measured shifts across species’ entire elevational ranges associated with recent climate warming (Figure 1a) to test for differences in the rates of range shifts at species’ warm and cool range edges (building on recent reviews; e.g., Lenoir & Svenning, 2015; Wiens, 2016). In line with the Darwin–MacArthur hypothesis – which suggests climate more directly influences cool range limits – we predicted that shifts of species’ warm range edges would be smaller and more variable compared to shifts at cool range edges. Alternatively, comparable shifts at cool and warm limits would challenge this paradigm, or at least its usefulness for understanding short-term species responses to climate change.

The dynamics of range shifts at species’ warm versus cool limits determine whether the size of species’ elevational distributions expands, shrinks or remains stable as species’ ranges shift in space. If cool limits are indeed moving upslope faster than warm limits, as predicted by the Darwin–MacArthur hypothesis, we expect range extents to increase on average such that the overall area within species’ elevational extents also increases. In contrast, if shifts at warm and cool limits are comparable, the impact of climate change on species’ overall elevational extents and available area will be largely determined by initial range position. Lowland species bounded at their warm limit by the base of the mountain and mid-elevation ‘unconstrained’ species with both warm and cool range limits along the mountainside might be expected to maintain stable elevational extents as they shift upslope, but with a decline in the available area within their extents. Mountaintop species bounded at their cool limit by the physical mountaintop, on the other hand, cannot shift further upslope, and are thus expected to decline in both extent and available area. Because species’ range sizes are linked to their extinction risk (e.g., Manne, Brooks, & Pimm, 1999), understanding whether range shifts are altering the extent and area of species’ elevational distributions is a pressing question in global change biology. This question has not previously been addressed at a global scale. We address this data gap by examining changes in species’ elevational extents, and the area available within these extents, to provide a more complete understanding of how warming temperatures are changing species’ elevational ranges.

MATERIALS AND METHODS

2.1 Data collection

To investigate changes in species’ elevational ranges and extents, we used published datasets that reported species distributions along the same elevational gradient at two time points (we were unable to find studies with data from more than two time points). We considered all resurveys included in recent syntheses (Chen, Hill, Ohlemüller, et al., 2011; Lenoir & Svenning, 2015; Wiens, 2016), and followed citation webs to search for additional studies. We collected data from studies that: (a) included multiple species (single-species studies may suffer from publication bias: Parmesan & Yohe, 2003); (b) spanned at least 10 years from the initial survey to the resurvey; (c) reported changes in both warm and cool elevational limits for all species included in
the study (not just those shifting upwards); and (d) reported species’ elevational positions. This last criterion is critical because our study explicitly compares species’ responses at warm versus cool limits, and such comparisons are only fair when species’ range limits are not constrained by the limits of the survey itself. We illustrate this point with the following example. Imagine a species that formerly lived from mid elevations to the highest surveyed point along a mountainside but now only lives near the highest surveyed point. If this highest surveyed point falls well below the actual mountain summit, it would be misleading to compare the large upward shift at this species’ warm limit to the apparent stasis at its cool limit, as its cool ‘limit’ was simply the highest surveyed point. Thus, when we could not determine whether either range limit was already at the boundaries of the historic survey, we had to exclude the study from our analyses (e.g., Cannone & Pignatti, 2014; Rumpf et al., 2018).

A total of 23 published studies that reported data from 32 different elevational gradients met our criteria. For each distinct elevational gradient, we collected: (a) the maximum and minimum elevation surveyed by the historical and modern surveys; (b) the number of years between the historic and modern surveys; (c) the magnitude of change in mean annual temperature at the study site (as reported by the authors); (d) latitudinal zone (tropical: absolute latitude < 23.5, temperate: absolute latitude > 23.5); and (e) survey scheme (continuous surveys along the elevational gradient versus discontinuous, when sampling was completed at discrete localities, e.g., every 300 m of elevation).

For each species along each elevational gradient, we recorded:
(a) the elevation (metres above sea level: m a.s.l.) of the species’ warm and cool range limits in the historic and modern survey; (b) general taxonomic group (plant, invertebrate or vertebrate); and (c) basic thermoregulation strategy (plant, endotherm or ectotherm). When data were presented only in figures, we used WebPlotDigitizer (Rohatgi, 2017) to extract historic and modern range limits. There were 64 species from five elevational gradients found at only one

![Figure 1](image_url)

**Figure 1** (a) Map of studies (n = 32) included in our analysis, with size proportional to the number of species included in the study (ranging from 1 to 123 species). Colour represents the basic thermoregulatory strategy of the species included in the survey. (b) Shifts at warm versus cool range limits for species whose range limits were free to move upslope or downslope by any amount (‘unconstrained’ species; i.e., their range limits did not abut the mountaintop, base of the mountain, or the edge of the sampled extent). Variation in range shifts is high among species (open grey circles), and overall, the magnitude of species’ warm limit shifts was uncorrelated with the magnitude of their cool limit shifts (r = .02). Approximately equal number of species increased (48%, above the 1:1 line) versus decreased (43%, below the 1:1 line) in elevational extent (9% of species had stable elevational extents). Means within studies (black dots) show a central tendency of upslope shifts at range midpoints (points over white background), and the overall mean among studies (red point) was an upslope shift of 92 m/C at warm limits and 131 m/C at cool limits.
location in either the historic or modern survey. We did not include these rare, poorly sampled species in our analysis, but note that all results held when including these taxa and assigning them an elevational extent of 1 m to represent a small but non-zero range.

We binned all species into a category of elevational position based on their elevational ranges. The majority of species in our dataset are ‘unconstrained’ – both their historic and modern limits fell within the bounds of the historic and modern surveys. Unconstrained species thus exhibited range shifts that were not bounded by topography (e.g., the top of the mountain) or by survey limits. Our comparison of warm versus cool shifts included only unconstrained species. For a subset of surveys that reached to the base of the mountain or to the mountaintop, we classified species as lowland (species whose lower limit was within 50 m of the mountain base; Table S1) or mountaintop (species whose upper limit was within 50 m of the mountaintop; Table S1) based on their historical elevational position.

From the survey data for each species, we calculated: (a) the elevational midpoint of both the historic and modern range (mean of cool and warm limits); (b) elevational extent at the historic and modern time points (the difference between the maximum and minimum elevation occupied by a species in a given survey); (c) the rates of shift at each range limit (because studies differ in both duration and the magnitude of warming that has occurred in the study region, we calculated shift rates in metres per year divided by °C of warming per year, which simplifies to metres per °C of warming; Gibson-Reinemer & Rahel, 2015); (d) change in elevational extent (the difference between a species’ historic and modern extents, with negative values indicating contractions of elevational extent and positive values indicating expansions); and (e) change in available area within species historic and modern elevational range (change in the total two-dimensional land surface area within the species’ elevational extent in the survey region, see below).

Our final dataset included 975 species from 32 distinct elevational gradients (Figure 1a, Table S1, Supporting Information Data S1). Most species were in our unconstrained category (623 species from 25 gradients), with smaller numbers of lowland (222 species from 12 gradients) and mountaintop (130 species from 22 gradients) species. Temperate regions were better represented than tropical regions, with 724 temperate-zone species from 24 gradients compared to 251 tropical species from eight gradients. Just over half the species in our dataset were endotherms (birds or mammals; 488 species; 13 gradients); the remaining species were plants (341 species; eight gradients) or ectotherms (amphibians, fishes, insects or reptiles; 146 species; 11 gradients).

2.2 | Analyses

2.2.1 | Are species moving upslope at both warm and cool limits?

Previous analyses have shown that most studied species have shifted upslope in response to recent temperature increases (Chen, Hill, Ohlemüller, et al., 2011; Lenoir, Gegout, Marquet, Ruffray, & Brisse, 2008; Parmesan & Yohe, 2003), but have not specifically investigated whether upslope shifts have been more common than downslope shifts at species’ warm versus cool limits. We addressed this question by fitting generalized linear mixed effects models (GLMMs; family = ‘binomial’) with sampling type (continuous versus discontinuous) as a fixed effect covariate and species and gradient as random factors using the ’lme4’ package (Bates, Maechler, Bolker, & Walker, 2014). We fit distinct models for warm limits and cool limits with the sign of the shift (positive = 1 versus negative = 0) as the response variable. All analyses were done in R (R Development Core Team, 2017).

2.2.2 | Are warm and cool limits changing at similar rates and with similar variance?

We tested whether shift rates at warm and cool limits in unconstrained species have different means or variances. We first fit a GLMM (family = ‘gaussian’) to predict the difference in shift rate between cold and warm limits (shift at cold limit – shift at warm limit) with latitudinal zone (temperate versus tropical), basic thermoregulation strategy (plant, ectotherm or endotherm), sampling type and the interaction between latitudinal zone and basic thermoregulation strategy as fixed effects, and gradient and species identity as random effects. This model tests whether the rate of shift was greater at cool or warm limits. We tested the significance of fixed effects by using the ’lmeansLT’ function in the ‘lmerTEST’ package (Kuznetsova, Brockhoff, & Christensen, 2017) to calculate 95% confidence intervals for change in elevational extent for the specific categories of each fixed effect.

Next, we tested for equality of variance between shifts at warm versus cool limits and investigated the correlation between shifts at warm versus cool limits. We fit two GLMMs (family = ‘gaussian’) with rates of shift as the response variable, type of limit (warm versus cool) as a fixed effect, and gradient and species identity as random factors. The only difference between these two models is that we specified that the variance in the second model was allowed to systematically differ between warm versus cool limits, and compared model fit using a likelihood ratio test. To test the correlation between shifts at warm versus cool limits, we fit a GLMM (family = ‘gaussian’) with shift at warm limit as the response variable, shift at cool limit as a fixed effect, and gradient and species identity as random factors. We additionally calculated the correlation between shifts at warm versus cool limits for the entire dataset (the easily interpreted Pearson’s r), but note that this simple correlation does not take into account the structure of our dataset. Last, to further investigate patterns in the individual studies that comprise our dataset, we calculated Levene’s test for homogeneity of variance and Pearson correlations for the 15 individual studies in our dataset that provided data for 10 or more species.

2.2.3 | Have species’ elevational extents changed?

We determined how elevational specialization and other factors have impacted changes in species’ elevational extents by fitting a
GLMM (family = ‘gaussian’) with elevational category, latitudinal zone, basic thermoregulation strategy, sampling scheme, the interaction term between elevational category and latitudinal zone and the interaction term between elevational category and basic thermoregulation strategy as fixed effects, and gradient and species as random effects. We did not include a latitudinal zone × basic thermoregulation strategy interaction because our primary interest was in whether results differed between different elevational categories. Again, we tested the significance of fixed effects using the ‘lsmeansLT’ function in the ‘lmerTEST’ package (Kuznetsova et al., 2017) to calculate 95% confidence intervals for change in elevational extent for the specific categories of each fixed effect.

### 2.2.4 Has the area within species’ elevational distributions changed?

Changes in elevational extent do not necessarily correspond with changes in available area – for example, a species may maintain its elevational extent as it shifts upslope but, if the mountain is shaped like a pyramid with less land at higher elevations, decline in available area (Elsen & Tingley, 2015). We calculated changes in area within the elevational range occupied by species to test whether the potential area available to species within their elevational extents has changed over time. This analysis included only species for which authors reported the actual minimum and maximum elevations for each species for both historic and modern surveys (i.e., excluding studies that reported changes at warm and cool limits but not the raw limits themselves), and for which it was possible to delimit the study region (e.g., Chen et al., 2009; Freeman & Class Freeman, 2014; see Table S2 for further details). These criteria were met for 409 species from 16 elevational gradients (335 unconstrained, 54 mountaintop and 20 lowland species). We then used shapefiles defining each study region to subset the Shuttle Radar Topography Mission 1 Arc-Second Global digital elevation model (30 m resolution; available from the USGS Earth Explorer https://earthexplorer.usgs.gov; see Table S2 for details), and merged, cropped and reprojected to an equal area projection the resulting digital elevation model tiles using the ‘raster’ package in R (Hijmans, 2017). For each species, we then calculated: (a) area within the historic elevational extent; (b) area within the modern elevational extent; and (c) change in available area (units in m²; R scripts are available at https://github.com/jullee). We note that our methodology calculates changes in available area within a species’ elevational extent; it was not possible to measure whether species actually inhabit all available area or not. We first were interested in the degree to which categorical changes in elevational extent are a useful proxy for categorical changes in available area. We then investigated whether change in available area differed between lowland, unconstrained and mountaintop species by fitting a GLMM (family = ‘binomial’) with categorical change in available area (increase versus decrease; we excluded cases with no change in area from this analysis) as the response variable, elevational category (lowland, unconstrained or mountaintop) and sampling scheme as fixed effects, and gradient and species as random effects.

### 3 RESULTS

Across the globe, Species are moving upslope along elevational gradients at both warm and cool range limits (Table 1). However, we found no evidence that temperature exerts a stronger influence on shifts at cool versus warm range limits. There was no significant difference in shift rates at cool limits versus warm limits when considering all unconstrained species (estimated upslope shifts from a mixed model were 131 and 91 m/C, respectively, almost identical to the upslope shifts calculated from the raw data; 131 and 92 m/C), or when considering different latitudinal zones or thermoregulatory strategies (see Tables S3 and S4). While species tended to shift upslope at both warm and cool range limits, the magnitude of shift at one limit was not correlated with the magnitude of the shift at the other limit (Figure 1b; estimate of the shift at cool limits from a mixed model with warm limit shift as the response variable = −0.0021; 95% confidence interval (CI) CI = −0.079 to 0.077; Pearson’s correlation test on raw data; r = .027, t_{619} = 0.66, p = .51). Furthermore, although shift rates at both limits were highly variable (Figure 1b), shifts at warm limits were not more variable than shifts at cool limits, as might be expected if warm limits are less directly influenced by temperature. The standard deviations of the overall raw data were 455 and 465 m for warm and cool limits, respectively, and a model where cool and warm limits have different variances was not a better fit than a model with a single variance structure (likelihood ratio test; p = .23). Results were similar when we considered each study individually (Table S5).

### 3.1 Range shifts impact the size of species’ distributions

How shifts at species’ cool and warm range limits altered the size of their elevational distribution depended in part on their elevational position (Figure 2; also see Tables S6 and S7). Lowland species tended to increase in elevational extent – more lowland species increased in extent (54%) than decreased in extent (34%; 13% had stable extents) – because they generally shifted up at their cold limit (113 lowland species’ cool limits shifted up versus 68 that shifted down; 41 did not change) without contracting at their warm limit (only 20% of lowland species’ warm limits shifted upslope). However, the modelled average change in extent for lowland taxa was not significantly different

| Table 1 | The number of unconstrained species with upslope versus downslope, and no movement at their warm and cool limits. This analysis considers only species that were unconstrained by topography/survey effort and could thus move either up or down at both range limits |
|-----------------|-----------------|-----------------|
|                | Upslope versus downslope | No change |
| Cool limit     | 370 > 130***     | 123            |
| Warm limit     | 341 > 150***     | 132            |

***Results of generalized linear mixed model were significant at p < .001
from zero (estimate from the GLMM was an increase of 86 m; 95% CI = −88 to 260 m; Table S6); even though expansions predominated, responses were highly variable and data for lowland species were available from few studies. Most lowland species in our dataset are from the temperate zone, and there was a trend for lowland temperate zone species to expand in elevational extent (the 95% CI for the estimate from the GLMM for temperate zone lowland taxa was −16 to 246 m, narrowly overlapping zero). For unconstrained species, increases and decreases in elevational extent were roughly balanced (48% increased in extent, 43% decreased in extent and 9% had stable extents), and there was no central tendency towards a change in elevational extent (estimate from the GLMM was an increase of 24 m; 95% CI = −43 to 90 m; Figure 2, Table S6). In contrast, more mountaintop species (52%) decreased than increased (34%; 15% had stable extents) in extent, and the modelled average change in extent for mountaintop species was significantly negative (estimate from the GLMM was a decrease of 173 m; 95% CI = −292 to −55 m, Figure 2, Table S6). Latitudinal zone and thermoregulation strategy were not significantly associated with change in extent for lowland or unconstrained species (Tables S6 and S7; Figure 2), but decreases in extent for mountaintop species were particularly strong for tropical species and for plants (Table S6 and Figure 2).

We found that categorical changes in elevational extent were tightly correlated with changes in available area. Nearly all (94%) species that decreased in elevational extent also decreased in available area, while the large majority of species (84%) that increased in elevational extent also increased in available area (Table S8). Thus, at least for our dataset, range shifts (typically upslope) that result in changes to species’ elevational extent are an excellent proxy for determining whether a population increases or decreases in available area. Accordingly, our results for how elevational position was related to changes in available area matched those for changes in elevational extent. We found no indication that the area within the extents of unconstrained species (n = 335) has declined systematically as a consequence of upslope shifts. A similar number of unconstrained species lost versus gained area within their elevational extents (Table 2), and the 95% confidence interval for change in area for unconstrained species overlapped 0.5 (the binomial null expectation; Table S9). In contrast, most mountaintop species (32 out of 56) lost area (Table 2), and this result was significant within GLMMs (Table S9). Our sample size for changes in available area for lowland species was very small (n = 20); within this sample, there was no systematic change in available area (Table S9).

**Figure 2** Changes in elevational extent for mountaintop (a), unconstrained (b) and lowland (c) species. Changes in extent are given for all species, and are also broken down by latitudinal zone and thermoregulatory strategy. The horizontal line at zero in each panel shows no change, and smaller horizontal black lines show modelled mean change in extent for each group from a linear mixed model. Sample sizes give number of species and studies that contribute to each group, and asterisks denote categories whose 95% confidence intervals calculated using the ‘lmerTest’ package for change in elevational extents did not overlap zero. Note that y axis scale differs between panels.
Global warming can be considered a massive uncontrolled experiment testing the degree to which temperature mediates species’ range limits. In this study we went beyond the common approach of documenting the direction of species’ range shifts to investigate how warming-associated shifts impact species at their warm versus cool range limits. This approach is necessary to understand how shifts at species’ range limits influence their overall distributions. For species whose range limits are not artificially constrained by survey limits, there was no systematic tendency for shifts at one limit to exceed shifts at the other, nor were shifts at one limit more variable than the other. Accordingly, for these ‘unconstrained’ species, although there was great variation in the amount by which elevational extents changed across species, there was no trend for elevational distributions to increase or decrease in either elevational extent or available area. Thus, for unconstrained species, we found that upward shifts in species’ distributions have not resulted in consistent changes in their distributions.

Equivalent responses at cool and warm limits do not support our predictions based on the Darwin–MacArthur hypothesis, which holds that species’ cool limits are more often set by climate while warm limits are more often imposed by negative interactions with other species. Contrary to the predictions developed in the Introduction, we found that warm range limits were neither slower nor more variable in responding to climate warming than were cool limits. Our results suggest instead that: (a) abiotic factors such as temperature play a more direct role in limiting species’ warm limits than previously predicted; (b) shifting biotic interactions push species’ warm limits upwards just as fast as colonization of newly climatically suitable habitat expands cool limits; and/or (c) biotic interactions are equally important at both types of range limits, and upward range shifts primarily reflect changes in the biotic, not abiotic, landscape in response to warming. Indeed, although MacArthur famously suggested that equatorward limits were driven disproportionately by competition, he also described in detail how biotic interactions appear to limit both warm and cool elevational limits of many tropical bird species (MacArthur, 1972).

As long suspected, mountaintop species have disproportionately declined in distribution size: they have significantly declined in both elevational extent and the potentially available area within their extents. This pattern has been previously noted in individual studies (e.g., high elevation taxa tend to decline in abundance and range size in European montane plants; Rumpf et al., 2018), but has not been addressed previously at the global scale. Our finding that mountaintop species are generally shrinking in range size across the globe supports widespread predictions that warming will cause upslope shifts that will eventually drive local extinctions in species restricted to mountaintops (La Sorte & Jetz, 2010; Sekercioglu, Schneider, Fay, & Loarie, 2008). However, although such warming-driven ‘mountaintop extirpations’ are widely predicted, empirical case examples are scarce. “Mountaintop extirpations” occur when species are limited by the physical location of the mountaintop, but species may also be constrained by habitat boundaries at high elevations. For example, the location of the tree line can act as a ‘mountaintop’ for a species that requires forested habitat; if tree lines in some regions are not shifting upslope despite recent temperature increases (e.g., Rehm & Feeley, 2015), we should expect that high elevation forest dwelling species in these regions will suffer due to tree line shifts lagging behind climate change (Bertrand et al., 2016).

In contrast to mountaintop species, the majority of lowland species in our study are expanding in elevational range size. Lowland species in our dataset were generally able to persist at low elevations near sea level, despite warming temperatures, while also expanding their cool limits upslope. Although most lowland species expanded in elevational range size, the mean change in elevational range size for lowland species was not significantly different from zero in GLMMs (although there is a trend for an increase in elevational range size for lowland temperate taxa). Our dataset contained only a small number of studies that included lowland taxa, limiting our ability to statistically assess this apparent pattern. Clearly, additional studies are needed to evaluate whether most lowland species have indeed expanded at their cool limits without concomitant contractions at their warm limits. Despite this caveat, we note that our preliminary findings are more consistent with the idea that species occurring in hot lowland areas may be able to tolerate warmer temperatures than currently exist (the ‘truncated niche’ hypothesis; Feeley & Silman, 2010) compared to the prediction that warming-associated range shifts will lead to decreases in species richness in lowland environments (the ‘lowland biotic attrition’ hypothesis; Colwell, Brehm, Cardelus, Gilman, & Longino, 2008). Additional research is urgently needed to determine which of these competing hypotheses better describes what is happening to real communities, particularly in the lowland tropics, which are both the hottest of Earth’s biodiversity hotspots and the most vulnerable to lowland biotic attrition.

Generalizing our findings requires caution on at least four fronts. First, these results apply to landscapes with relatively intact natural habitat. Elevational range shifts are likely to have quite different effects on potential occupancy in landscapes where deforestation or agricultural expansion has been prevalent (Friskhøft et al., 2016). Second, species’ distributional responses to warming may be nonlinear, experience lag-effects, or change over time due to evolution. Hence, future studies may reveal patterns obscured here due to the short time-scale of recent climate warming. Third, our analysis is necessarily restricted to published data, which suffer from several taxonomic and geographical biases (recently reviewed in Lenoir & Svenning, 2015). For example, data are particularly sparse from the tropical regions that are home to the majority of Earth’s biodiversity (e.g., Feeley, Stroud, & Perez, 2017).
In addition, there is not yet sufficient published data to analyse whether range shifts at warm versus cool limits at a global scale consistently differ between different taxonomic groups (e.g., birds versus mammals), or between species with trait differences that are likely important to the processes of dispersal and persistence that underlie range shifts (e.g., long-lived versus short-lived species). For example, we know from focused studies that species’ life span can impact the magnitude of their range shifts – for example, upslope shifts in optimum elevations in European plants are much stronger for non-woody species, which tend to be short-lived, than for woody species, which tend to be much longer-lived (Lenoir et al., 2008). Yet there is not currently enough data to assess the degree to which woody versus non-woody plants differ in shifts at their warm versus cool range limits at a global scale. Additional studies that describe species’ geographical responses to climate change are necessary to more fully investigate the patterns we document in this manuscript. Finally, the Darwin–MacArthur hypothesis is usually articulated to explain range limits along latitudinal rather than elevational gradients, and latitudinal ranges may show different patterns (e.g., because climatic factors such as seasonality typically change along latitudinal gradients but are minimized along elevational gradients).

Perhaps our most striking finding is the enormous variation in species’ distributional responses to warming (Figures 1b and 2). There are many reasons why species vary in how their ranges have recently shifted, and a large literature details how functional traits (e.g., dispersal ability; Sunday et al., 2015), different abiotic factors (e.g., precipitation; Tingley, Koo, Moritz, Rush, & Beissinger, 2012), landscape variables (e.g., habitat fragmentation; Bertrand et al., 2016) and phenological shifts (e.g., Socolar et al., 2017) may explain some of this variation. We add to this literature by showing that shifts in warm and cool range limits of the same species along the same mountain slope are tremendously variable. Taken together, these results are not consistent with a simplistic scenario where temperature is such a dominant factor limiting species’ distributions that whole communities shift upslope together. Instead, there is a great deal of idiosyncrasy in the proximate importance of temperature in governing both species’ cool and warm range limits. This variation implies that novel species interactions and ‘no-analogue’ communities are to be expected (Gibson-Reinemer, Sheldon, & Rahel, 2015; Urban, Tewsksbury, & Sheldon, 2012), even in landscapes with minimal land use alteration. We emphasize that climate change will indeed result in ecological change, and that understanding the response variation among taxa will likely require embracing the complex ways in which species interactions influence range limits and how these range limits respond to climate change.

ACKNOWLEDGMENTS

This research was supported by a National Science Foundation Postdoctoral Fellowship in Biology (Award No. 1523695) and a Banmg Postdoctoral Fellowship (#379958) to BGF, a Natural Sciences and Engineering Research Council PDF Award to JAL (PDF 487035-2016), and Biodiversity Postdoctoral Fellowships from the UBC Biodiversity Research Centre to ALH, JS and BGF. None of our funders had any influence on the content of the submitted manuscript, and none of our funders required approval of the final manuscript to be published. Comments from Jonathan Lenoir, Ralf Yorque and three anonymous referees greatly improved this manuscript.

DATA ACCESSIBILITY

The dataset we analyse in this manuscript is available as a Supporting Information file.

REFERENCES


BIOSKETCH

This project was the outcome of a post-doc reading group focused on range limits and climate change at the Biodiversity Research Centre at the University of British Columbia. Individually, we each study the ecological and evolutionary processes that generate the distributional patterns we observe in modern biotas, often with a particular focus on understanding the abiotic and biotic factors that explain species’ range limits.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Freeman BG, Lee-Yaw JA, Sunday JM, Hargreaves AL. Expanding, shifting and shrinking: The impact of global warming on species’ elevational distributions. Global Ecol Biogeogr. 2018;00:1–9. https://doi.org/10.1111/geb.12774