LETTER

Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure

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Abstract

Both tropical and temperate species are responding to global warming through range shifts, but our understanding of the consequences of these shifts for whole communities is limited. Here, we use current elevational range data for six taxonomic groups spanning 90° in latitude to examine the potential impacts of climate-driven range shifts on community change, or 'disassembly', across latitude. Elevational ranges are smaller at low latitudes for most groups and, as a consequence, tropical communities appear to be more sensitive to temperature increases compared with temperate communities. Under site-specific temperature projections, we generally found greater community disassembly in tropical compared with temperate communities, although this varied by dispersal assumptions. Mountain height can impact the amount of community disassembly, with greater change occurring on smaller mountains. Finally, projected community disassembly was higher for ectotherms than endotherms, although the variation among ectotherms was greater than the variation separating endotherms and ectotherms.

INTRODUCTION

Temperature is believed to play a major role in determining species' range limits (Grinnell 1917; Crozier & Dwyer 2006). Not surprisingly, climate warming has caused shifts in the distributions of terrestrial organisms towards higher latitudes and elevations (Walther *et al.* 2002; Parmesan & Yohe 2003; Wilson *et al.* 2005; Moritz *et al.* 2008). Although many studies have documented shifts in individual species' range limits, few studies have examined range shifts in a community context (Berg *et al.* 2010). Yet, the ability of organisms to shift their range is often constrained by interactions, such as competition, predation, and mutualism (Gilman *et al.* 2010). Range shifts of one species due to warming can decouple important species' interactions if other species within the community do not respond in a similar way (Walther *et al.* 2002; Schweiger *et al.* 2008). This decoupling could result in the loss or introduction of species' interactions, both of which could impact species' ability to persist (Schweiger *et al.* 2008).

The amount of warming associated with climate change generally follows a latitudinal trend, with greater increases in temperature predicted in temperate regions (IPCC 2007). Although this might suggest that the greatest impacts on communities will be seen in north temperate zones, many species' traits, including thermal physiology (Deutsch *et al.* 2008; Huey *et al.* 2009) and, potentially dispersal (Martin & Tewksbury 2008; Moore *et al.* 2008), are reduced at low latitudes, giving high-latitude species a greater capacity to respond to warming. Relative impacts across latitude are, thus, not easy to predict.

Mechanistic approaches that begin with physiological constraints can provide insights that remain hidden by approaches that rely on correlations between species' occurrence and climate variables (Buckley *et al.* 2010). This approach has been particularly well developed for organismal responses to temperature variation (Buckley

et al. 2010). We thus focus our work on potential community impacts emerging from differential movement of terrestrial organisms to temperature change.

Thermal tolerance, the range of temperatures over which an organism can function (Angilletta 2009), should be strongly influenced by the variation in environmental temperatures species experience (Janzen 1967; Gaston & Chown 1999; Ghalambor *et al.* 2006). Species that evolve in areas with little environmental temperature variation, such as the tropics, tend to be thermal specialists and have relatively narrow thermal tolerance. In contrast, species that evolve in areas with high environmental temperature variation, such as the temperate zones, are thermal generalists with broad thermal tolerance (Sunday *et al.* 2011). Thermal specialists should be especially vulnerable to climate change (Ghalambor *et al.* 2006).

Some species can handle climate warming by shifting their ranges to maintain their current thermal environment. However, different species probably have different dispersal capacities, such that species co-occurrences may shift as a result of climate change.

Thermal physiology may influence behavioural dispersal capacity, and thermal generalists should have greater dispersal capacity, all else equal (Janzen 1967). Consider both a thermal specialist and generalist that co-occur on a given mountain. If both disperse up (or down) exactly the same distance, the thermal specialist is more likely to encounter a thermal regime to which it is neither acclimated nor adapted. In effect, thermal specialists are likely to incur a greater fitness deficit from dispersal up or down mountains (Janzen 1967). Consequently, selection more likely favours limited dispersal of thermal specialists, and thus of tropical organisms (Ghalambor *et al.* 2006).

Evidence for restricted dispersal in tropical organisms is indirect, as no study has explicitly compared dispersal capacity of related

organisms across latitude (Ghalambor *et al.* 2006). Still, evidence for reduced dispersal in tropical organisms is mounting, coming from comparisons of genetic (Martin & McKay 2004) and phenotypic divergence across latitude (Martin & Tewksbury 2008) and an increasing number of studies pointing to greater dispersal limitation in tropical organisms (Develey & Stouffer 2001; Moore *et al.* 2008).

As the average magnitude of temperature change associated with warming is expected to be greatest in temperate regions, the optimal thermal regime of tropical species will not shift as far over the same period. If tropical species have dispersal capacity equal to temperate species, then they may be able to track their optimal thermal regime as well as or better than temperate species. If, however, tropical species have reduced dispersal, then they may not be able to track their optimal thermal regime as well as temperate species. Given greater species turnover with elevation in the tropics, reduced dispersal of tropical species could result in a greater 'disassembly' of tropical compared with temperate communities.

To understand the potential for climate-driven community change, or 'community disassembly', at different latitudes, we used data on the elevational ranges of species collected from 37 taxonomically focused mountain transects ranging from 45° N to 41° S. Mountain communities are an ideal place to study range shifts in response to temperature increase. Mountains provide a changing distribution of species and represent a thermal gradient that becomes progressively cooler with increasing elevation. The rate of temperature change along elevational gradients takes place over much shorter distances than the rate of change along latitudinal gradients. For this reason, species' range shifts along mountain gradients presents a window into the relative level of community disassembly we may expect with climate change, but in a spatially discrete and tractable system. Using empirical data from elevational transects of rodents, birds, herpetofauna, and dung beetles, we explore potential community responses to climate warming across latitude. We predicted that community disassembly would vary with latitude, with tropical communities showing greater change and sensitivity to increases in temperature.

METHODS

Data collection and elevational range

We collected published transect data on elevational ranges of ectotherms (lizards, $n = 9$; snakes, $n = 8$; frogs, $n = 8$; dung beetles, $n = 9$) and endotherms (rodents, $n = 13$; birds, $n = 6$) from various latitudes (Appendix S1). We focused on transects because they provide extensive sampling along a single slope and are less likely to overestimate range size compared with regional scale studies (McCain 2009). For birds, we used species that breed at the transect locations as migrants may inflate range sizes.

As the quality of datasets is key to elucidating patterns of elevational range, we used transect studies where data had been collected in areas with little habitat disturbance, sampling effort was consistent across the gradient, and at least 50% of the mountain was sampled. In addition, we only included community surveys that sampled for all species of the group under consideration. Although we tried to control for differences among datasets, several factors could not be controlled, including variation in mountain height and distance between sampling points. To account for these differences, we included mountain height in statistical analyses and corrected elevational range to control for distance between sampling points (Appendix S2, Fig. S1).

Transect sampling provides presence and absence data for species in discrete locations, not true elevational range. Without controlling for differences in the distance between sampling locations, elevational range could be underestimated. As an example, consider a transect running from sea level to 1800 m with sampling points every 200 m. If we only used sampling locations where the species was present, a species with an actual elevational range from 300 to 1100 m (an 800 m range) would be trapped at sampling locations from 400 to 1000 m, and would be given an estimated elevation range of 600 m. Now consider the same transect with sampling locations every 400 m rather than every 200 m. The same species would be found at only two sampling locations, 400 and 800 m, and the estimated elevational range would be 400 m.

To control for distance between sampling locations on different transects, we determined elevational range by using the midpoint between the sampling locations where species were present and absent at both upper and lower range limits (Appendix S2, Fig. S1). In the previous example, estimated elevational range would be 800 m under both 200 and 400 m sampling intervals, even though the estimated upper and lower limits are different.

Climate change simulation

Model overview

We created a simulation model to explore the impact of climate warming on communities across latitude (Fig. 1). For our purposes, 'community' refers to all species from a single mountain transect. For each published transect study (Appendix S1), we simulated a mountain characterised by a thermal gradient with temperatures becoming progressively cooler with increasing elevation. We then imposed climate warming, which altered the range of habitable elevations. Finally, we explored several dispersal scenarios (see below), and the ensuing communities were observed for loss of species' range overlap, or co-occurrence, which could come about due to extinctions or differences in rates of dispersal. We used loss of co-occurrences and extinctions to indicate the potential for community disassembly.

Model simulation

For each dispersal scenario, we conducted a single model run with the exception of the random dispersal scenario (see below), which we ran 10 times. Each run was initiated by converting the elevational range of species on a mountain into a temperature 'envelope', describing the thermal conditions under which the species currently occurs. We converted species' elevational range limits to temperature values using site-specific estimates for elevational lapse rates (Fan & van den Dool 2008). Average temperatures for each transect site were based on global mean surface-air temperatures for the years 1961–1990 (New *et al.* 2002).

To estimate future shifts in the temperature envelope for each species, we used temperature projections from the Intergovernmental Panel on Climate Change (IPCC 2007) based on Special Report on Emissions Scenario A2. We chose to use the A2 scenario because it may be the most relevant under current greenhouse gas emissions (Raupach *et al.* 2007). As model simulations of current climates are offset from actual climates, we eliminated bias in projected warming following methods in Deutsch *et al.* (2008). We used changes in mean temperature at each location to estimate shifts in the climate envelope for each species, and used this shift to assess both the movement of
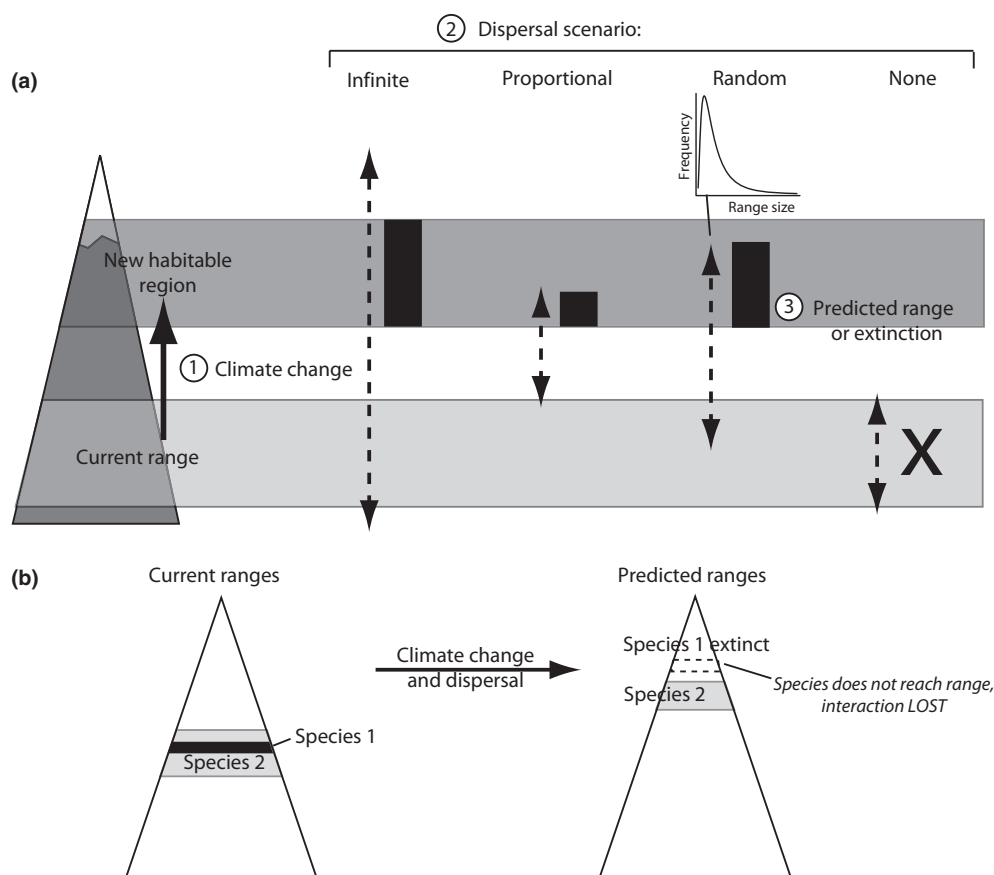
Figure 1 Model simulation. (a) The computational model simulates range shifts for a particular species using current elevational range (light grey shaded elevations) to determine potential habitat, or 'new habitable region' following site-specific temperature shifts associated with global warming (darker grey shaded elevations) (1). The species is then allowed different dispersal capacities from its current range – infinite, proportional, random or no dispersal – shown by the dashed arrows (2). The portion of the potential habitat that is within the dispersal distance of the species becomes the species' predicted range following global warming, shown by the black rectangle (3). (b) Following warming, some species will reach their potential range (Species 2), while some species will not reach their potential range and become extinct (Species 1). We estimated 'community disassembly' by tracking both the number of species' extinctions and the range overlaps that were lost (loss in co-occurrences).

the current temperature envelope up the mountain over the next 70–100 years and to estimate potential habitat for each species (Araujo *et al.* 2005).

The impact of warming on communities was then determined by coupling the potential habitat in 2100 with dispersal functions generated for each species (Fig. 1), and by assessing the degree of community change due to extinction and loss of co-occurrences.

As thermal tolerance is expected to influence both elevational range size (McCain 2009) and dispersal (Janzen 1967; Ghalambor *et al.* 2006), we modelled the impact of climate change on communities in which dispersal is constrained by thermal tolerance. To do this, we used the current elevational range of each species as an index of dispersal capacity with the assumption being that thermal tolerance is reflected in both elevational range and dispersal capacity (Ghalambor *et al.* 2006). Thus, under this scenario, a species with a narrower elevational range is a thermal specialist with reduced dispersal capacity, while a species with a broader elevational range is a thermal generalist with greater dispersal capacity. We explored several linear proportional functions linking elevational range to dispersal, but all functions produced similar results. Thus, we present results in which dispersal equalled elevational range (proportional scenario).

As elevational ranges may be limited by factors other than thermal tolerance (Jankowski *et al.* 2010), we also modelled the impact of

climate warming on communities when dispersal was random with respect to current elevational range (random scenario). This approach assumed that tropical species have dispersal capacity equal to that of temperate species. Dispersal for the random scenario was described by a lognormal distribution where the mean for each taxon was equivalent to the mean of the proportional scenario for that taxon. Thus, the mean dispersal for the proportional and random scenarios was equivalent for each taxon, allowing us to compare and contrast the impact of dispersal linked to elevational range (proportional) with dispersal not linked to elevational range (random).

Lastly, we composed baseline scenarios for communities in which dispersal was zero (no dispersal) and for communities in which dispersal was infinite, and thus species could always populate potential habitat within a mountain gradient.

For each ensemble model run (movement of all species in a taxon group on a mountain), we tracked the number of species that became extinct in each community. In our model, extinctions occurred when species could not reach their potential habitat due to insufficient dispersal or when the potential habitat essentially moved off the mountaintop (Fig. 1). We also examined loss of species' co-occurrences in each community following climate warming – a measure of community disassembly. Loss of co-occurrences was determined for each mountain by adding the total number of range

overlaps that were lost following warming and dividing this by the total number of possible range overlaps. A loss of range overlap is when two species that previously had overlapping ranges no longer do, which could occur when species were unable to disperse enough to reach their potential ranges or when mountaintop extinctions occurred (Colwell & Rangel 2010). Our approach did not simulate the emergence of new range overlaps for two reasons: we modelled potential upslope range shifts in a lock-step manner in response to warming (Colwell *et al.* 2008), and upslope dispersal was never more than the upslope shift of the thermal zones. As the number of extinctions or co-occurrences lost within communities could be influenced by the number of species in the community, we used the proportion of species going extinct or experiencing loss of co-occurrence, not the absolute number, for data analyses.

Finally, we grouped communities from tropical (< 23.5°) and temperate (> 23.5°) latitudes to understand the sensitivity of communities to shifts in both temperature and dispersal. First, we analysed how sensitive the co-occurrence response was to small shifts in temperature. For each trial, we used the proportional dispersal scenario to determine loss of co-occurrences at temperature shifts ranging from 0 to 5 °C.

Second, we explored two variants of random dispersal (Fig. 1), one where we varied the mean of the lognormal distribution (mean model), and one where we varied the standard deviation (variance model). For the mean model, we explored community disassembly arising from mean dispersal shifts of 1–7 °C. We used temperature as our unit of measurement for dispersal because previously, we translated species' ranges from metres into degrees Celsius using site-specific lapse rates (see above). Average site-specific lapse rates ranged from 0.5 to 0.65 °C per 100 m elevation. Therefore, depending on the mountain, mean dispersal of 1 °C translated into 154–200 m, while mean dispersal of 7 °C translated into 1077–1400 m. To explore sensitivity of community disassembly arising from variance in dispersal, we held mean dispersal constant (1, 3 or 5 °C) while shifting dispersal variance from a standard deviation of 0.8–4.0 °C. As all variance models showed the same trends regardless of the mean, we focus our results and discussion on the model where mean dispersal was 3 °C. We coded all model simulations in R (Appendix S3).

Statistical analyses

Our goals were to understand if latitude was a good predictor of both elevational range prior to climate warming and degree of community disassembly following climate warming. To determine how latitude relates to elevational range of each taxon, we used linear mixed-effects (LME) models in R (R version 2.11.1, R Development Core Team 2010). We included both latitude and mountain height as fixed effects because shorter mountains can constrain species' ranges (McCain 2009). We included transect site as a random effect to account for the non-independence of species at a site (Crawley 2007). Our null models included only an intercept and the random effect of site. To assess the explanatory power of latitude in relation to variation in elevational range, we fit linear models and report r^2 values.

To determine how latitude relates to the proportion of extinctions and co-occurrences lost in communities under dispersal scenarios of none, proportional and infinite, we used general linear models (GLM) in R (version 2.11.1, R Development Core Team 2010). For the dispersal scenario of random, we used LME models with the random

effect of site to account for the ten replicates from each site. In all models (GLM or LME), we included both latitude and mountain height as fixed effects because shorter mountains can influence extinctions following climate warming (La Sorte & Jetz 2010).

To examine the impact of shifts in dispersal mean and variance on community disassembly, we used GLMs that included an interaction between the fixed effects of dispersal distance and transect location (tropical or temperate).

All models examining the proportion of extinctions or loss of co-occurrences included a binomial error distribution and were fit using maximum likelihood estimation. We used Akaike Information Criterion (AIC) values to choose the best-fit model for each taxon (Burnham & Anderson 2004), and used the difference in AIC values between the best and second best model to indicate the strength of the relationship (ΔAIC). We performed model simplification for LMEs using likelihood ratio tests between models to test relative fit (*p*) (Crawley 2007).

Finally, we compared extinctions and loss of co-occurrences between all taxa to see if certain taxa suffered greater extinctions and loss of co-occurrences due to warming (R, multcomp package for simultaneous inference).

RESULTS

The relationship between elevational range and latitude was positive for all taxa (Fig. 2), but the strength of the relationship varied. Elevational range of birds, beetles and lizards showed strong positive relationships with latitude (i.e. birds, $r^2 = 0.70$, $P = 0.04$; beetles, $r^2 = 0.61$, $P = 0.01$; lizards, $r^2 = 0.70$, $P < 0.001$), while frogs showed only a weak relationship ($r^2 = 0.45$, $P < 0.07$). Rodent and snake ranges showed positive, but non-significant relationships with latitude (i.e. rodents, $r^2 = 0.12$, $P = 0.25$; snakes, $r^2 = 0.29$, $P = 0.17$). Latitude and mountain height best explained elevational range for frogs, rodents, and snakes (Table S1: frog, $P < 0.001$; rodent, $P = 0.03$; snake, $P = 0.01$). Latitude alone best explained elevational range for birds and lizards (Table S1: bird, $P = 0.01$; lizard, $P < 0.001$). As mountain height did not significantly improve model fit for beetles ($P = 0.76$), the most parsimonious model to explain elevational range of beetles included only latitude.

For all taxa, we found that tropical communities were more sensitive than temperate communities to a constant increase in temperature when dispersal was proportional to elevational range (Fig. 3). Following a shift of only 2 °C, loss of co-occurrences for all tropical herpetofauna reached or exceeded 40%, while the same shift in temperature resulted in 20% fewer losses for their temperate counterparts. With a temperature shift of 2 °C, birds, beetles and rodents showed similar loss of co-occurrences between tropical and temperate communities, although loss of co-occurrences in tropical communities was typically higher. A shift of 5 °C resulted in 50% of co-occurrences lost for tropical communities, an amount never reached by temperate communities of any taxon.

Following site-specific warming, we found significant differences in extinctions and loss of co-occurrences between several taxa (Fig. 4; Appendix S2, Fig. S2; Table S2). Many of these differences were driven by snakes, which showed significantly greater community disassembly.

The amount of community disassembly was highly dependent upon dispersal assumptions, with the greatest disassembly (indexed by extinctions and loss of co-occurrences) occurring in scenarios where we
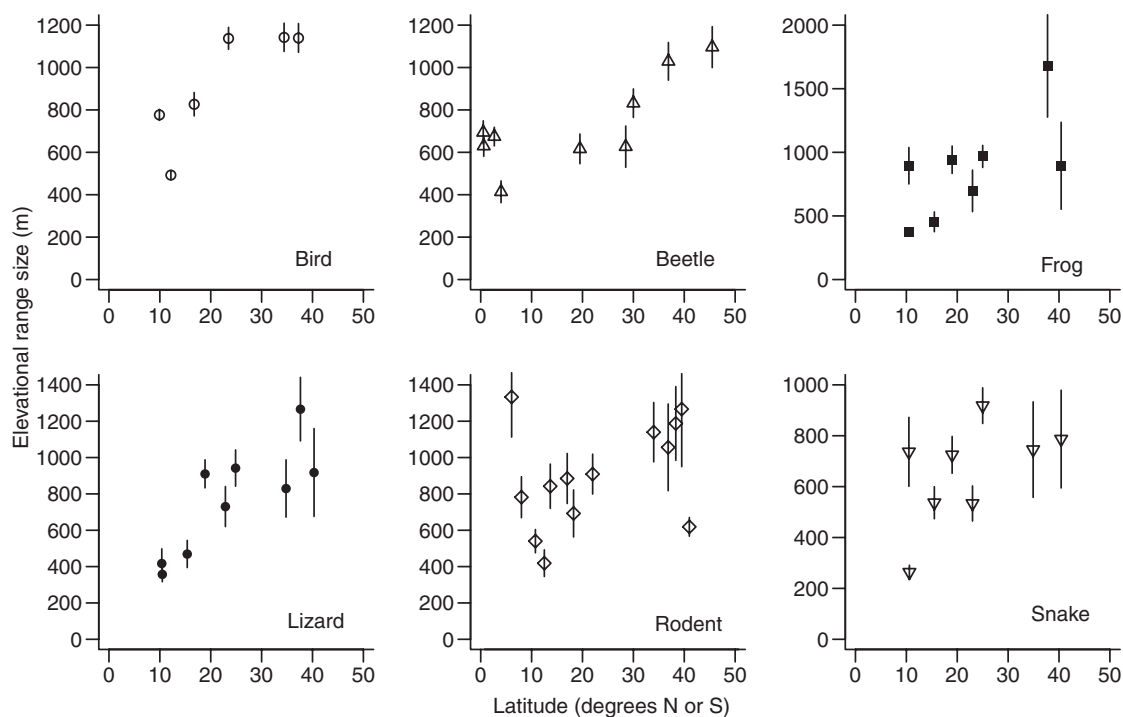
Figure 2 Elevational range size across latitude for all taxa. Each point represents elevational range size (mean ± SE) for all species in the taxonomic group at a single transect site. See Table S1 for best model fits.
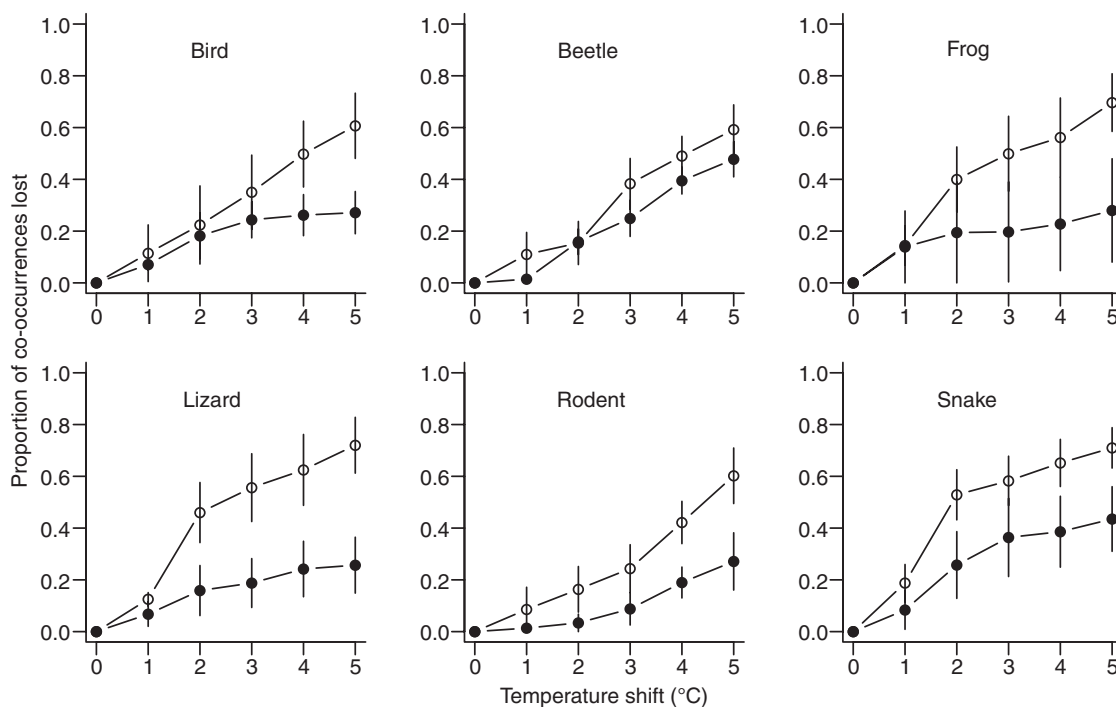

Figure 3 Sensitivity of high- and low-latitude communities of each taxon to temperature shifts. The proportion of co-occurrences lost (mean ± SE) for tropical and temperate communities when dispersal is proportional to elevational range is shown under temperature shifts of 0–5 °C. For each taxon, tropical sites (< 23.5° latitude) are shown with open circles and temperate sites (> 23.5° latitude) are shown with closed circles.

assumed no dispersal. We saw the lowest disassembly where dispersal was infinite and intermediate levels where dispersal was either random with respect to elevational range or proportional to thermal tolerance, indexed by elevational range (Fig. 5; Appendix S2, Fig. S3).

Based on our statistical models, loss of co-occurrences for all taxa under proportional dispersal was best explained by latitude or latitude plus mountain height (Table S3), while extinctions were best explained by latitude or mountain height (Table S4). When dispersal
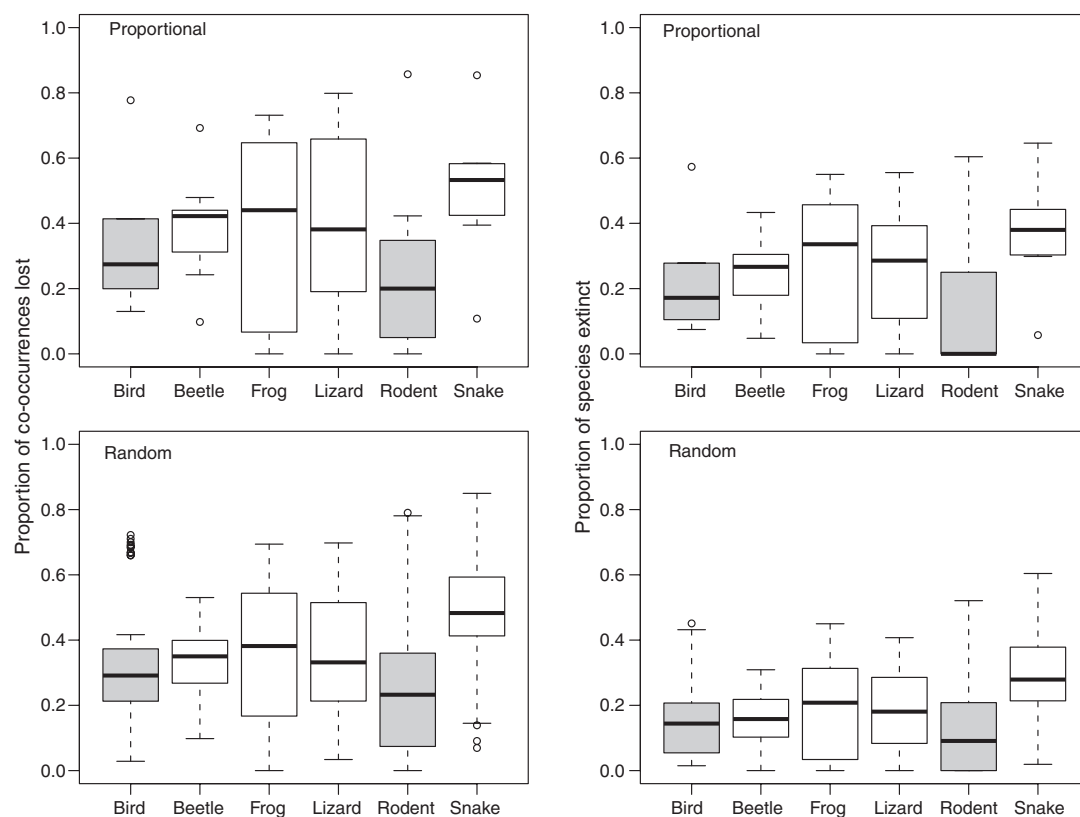
Figure 4 Impacts of global warming by taxon for all dispersal scenarios. Boxplots show the proportion of co-occurrences lost (left) and proportion of extinctions (right) for each taxon under dispersal scenarios of proportional and random. Endotherm taxa (birds and rodents) are shaded grey and ectotherms (beetles, frogs, lizards and snakes) are in white. See Table S2 for results of multiple comparisons between taxa for all dispersal scenarios.
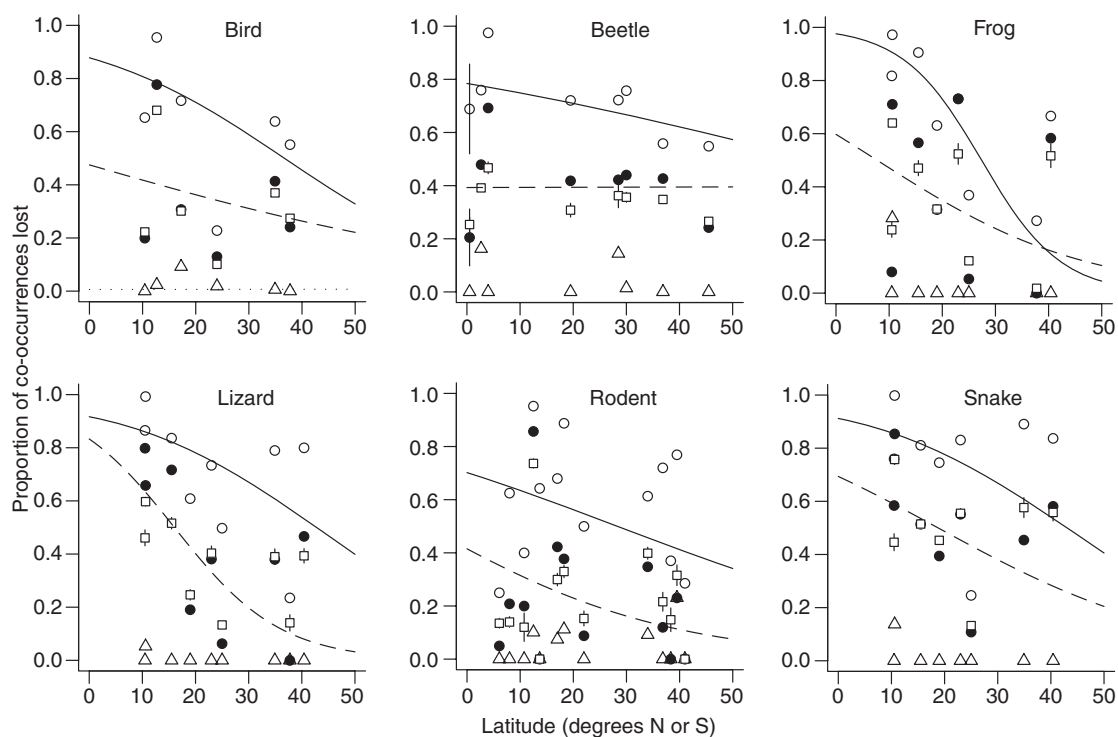

Figure 5 Proportion of co-occurrences lost (mean ± SE) across latitude under three different dispersal scenarios. Points represent transect sites under different dispersal scenarios while lines show the logit curves for the taxa and dispersal scenarios in which the latitude term was supported. Points and lines indicate where dispersal was none (open circles, solid black lines), proportional (filled circles, dashed lines), random (open squares) and infinite (open triangles, dotted lines). See Table S3 for best model fits.
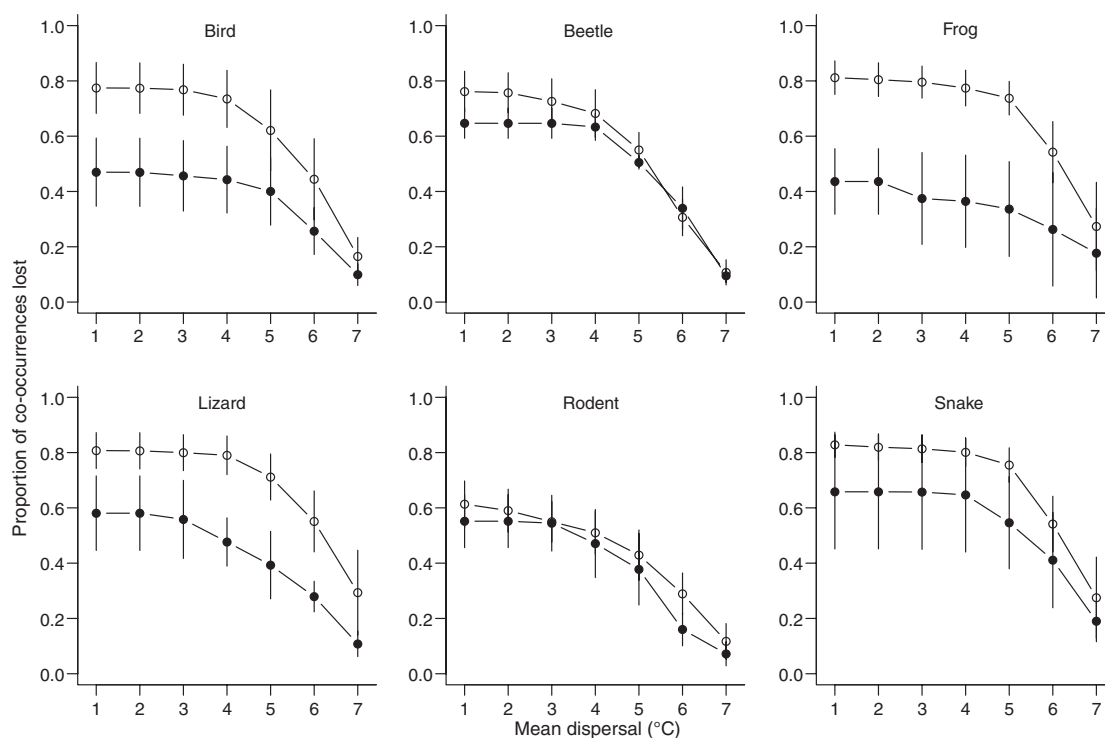
Figure 6 Sensitivity of high- and low-latitude communities of each taxon to shifts in mean dispersal. The proportion of co-occurrences lost (mean ± SE) for tropical and temperate communities is shown under mean warming regimes of 1–7 °C. For each taxon, tropical sites (< 23.5° latitude) are shown with open circles and temperate sites (> 23.5° latitude) are shown with filled circles. See Table S5 for best model fits.

was random, latitude did not explain extinctions or loss of co-occurrences for any taxon with the exception of lizard extinctions. When dispersal was infinite, mountain height best explained loss of co-occurrence for most taxa; however, mountain height explained extinctions for only one taxon, beetles. Finally, where we assumed no dispersal, extinctions and loss of co-occurrences were best explained by latitude or latitude plus mountain height (Tables S3, S4).

When varying the mean dispersal in the random model, we found that tropical communities generally showed a greater loss of co-occurrences than temperate communities for most dispersal values (Fig. 6; Table S5). Community disassembly decreased as mean dispersal increased in both tropical and temperate communities. At low mean dispersal, tropical communities showed a greater loss of co-occurrences, but this difference decreased at higher mean dispersal (Fig. 6). In comparison with shifts in mean dispersal, shifts in variance resulted in a similar pattern, with greater variance leading to reduced community disassembly (Appendix S2, Fig. S4). For both mean and dispersal models, loss of co-occurrences was best described by statistical models that included both dispersal and location (tropical or temperate), and often, the interaction between the two (Tables S5, S6).

DISCUSSION

The impact of global warming on communities will be complex (Gilman *et al.* 2010), likely varying among taxa and locations. Our study represents a first approximation of how shifts in temperature may alter tropical and temperate communities for a variety of taxa. Trends across latitude are dependent upon dispersal assumptions, but tropical communities suffer greater community disassembly compared with temperate communities when exposed to similar levels of

warming. When modelled as a function of site-specific warming, tropical communities change more under many, but not all, dispersal scenarios. In addition to community location (tropical or temperate), mountain height can influence community disassembly, with greater disassembly found on smaller mountains.

As extinctions in our model drive loss of co-occurrences, we use the term 'community disassembly' to discuss both these phenomena jointly. Community disassembly was the greatest in snakes and the lowest in rodents (Fig. 4; Appendix S2, Fig. S2; Table S2). All ectotherms had higher mean disassembly than endotherms, but the variation among ectotherms was greater than the variation between endotherms and ectotherms. The greater disassembly in ectotherms may be due to differences in physiological constraints. Endotherms can heat themselves metabolically and use evaporative cooling to maintain a stable body temperature. Ectotherms do not have the same physiological tools and must rely on behavioural modification of heat exchange to regulate body temperature (Angilletta 2009). Even with behavioural controls of heat exchange, the 'climate space', or temperature range over which an ectotherm can survive, is considerably smaller than a comparably sized endotherm (Angilletta 2009). In the simple framework of our model, the reduced climate space of ectotherms at an individual level and population level scales up to create communities that turn over more rapidly up mountains, making them more vulnerable than endotherms to climate warming. This rapid turnover up tropical mountains ultimately occurs because climate-driven differences in physiology across latitude are much greater than differences in lapse rates across latitude (Deutsch *et al.* 2008; Fan & van den Dool 2008).

After imposing temperature increases from 0 to 5 °C on tropical and temperate communities, we found that shifts greater than 2 °C

resulted in greater loss of co-occurrences for tropical communities under the proportional dispersal scenario (Fig. 3). Therefore, tropical communities should disassemble faster than temperate communities under even small temperature increases. When we factored in site-specific temperature projections, the latitudinal gradient in disassembly was highly dependent on dispersal assumptions (Fig. 5; Appendix S2, Fig. S3; Tables S3, S4).

As temperate sites may warm by 40% more than tropical sites, the potential habitat of tropical species should not shift as far upslope. As a result, when dispersal capacity was randomly assigned, we found no latitudinal trend in disassembly for any taxon with the exception of lizards. Our results are consistent with previous findings that the largest impacts of warming are not isolated to tropical mountains (La Sorte & Jetz 2010), but are also expected at high northern latitudes (Williams *et al.* 2007). In our model, lizards may be an exception because they showed the strongest latitudinal trend in elevational range among taxa, suggesting that tropical lizards may have a harder time reaching their potential habitat despite reduced warming in the tropics.

Although we did not find a latitudinal trend in community disassembly when dispersal was random, we might expect the same degree of disassembly to have greater impacts in tropical regions. Changes in species' ranges are often asymmetrical, with low-elevation species moving faster upslope than high-elevation species (Walther *et al.* 2002). As low elevations in the tropics harbour greater biodiversity, tropical communities could change more than temperate communities (Hillebrand 2004). In addition, because the lowland tropics can lack species adapted to higher temperatures (Huey *et al.* 2009), we might expect lowland biotic attrition and, thus, fewer species to replace those shifting upslope in response to warming (Colwell *et al.* 2008).

When we assumed that dispersal was proportional to elevational range, tropical communities showed greater disassembly than temperate communities. Thus, despite greater predicted warming at temperate sites, the narrower elevational ranges of tropical species led to greater community disassembly in the tropics. Similarly, previous research has shown that extinction risk is higher in species with restricted ranges (Colwell & Rangel 2010; La Sorte & Jetz 2010). The latitudinal trend in community disassembly under proportional dispersal is also consistent with work on populations (Deutsch *et al.* 2008; Huey *et al.* 2009), in which the greater physiological sensitivity of tropical species appears to trump the gradient in warming.

In addition to latitude, mountain height can impact the degree of community disassembly following warming. Species on smaller mountains are more vulnerable to extinction because their habitat moves off the mountaintop sooner (La Sorte & Jetz 2010).

Importantly, several assumptions and simplifications are embedded in our model that could lead to overestimated risks of community disassembly. First, we made the simplifying assumption in our proportional dispersal model that current elevational ranges are reflective of species' fundamental niches (Thomas *et al.* 2004; Feeley & Silman 2010). Second, dispersal in our proportional model may be conservative. Higher dispersal would result in levels of community disassembly lower than those found in the proportional scenario. Third, we did not consider generation time. If dispersal per generation was proportional to elevational range, we expect short-generation time species to have greater dispersal and climate tracking than depicted here. Fourth, species could remain in their current range via evolution (Balanyá *et al.* 2006) and acclimation (Stillman 2003) of thermal tolerance (Colwell & Rangel 2010), neither of which was included

in our model. Finally, broad-scale temperature data used in our model do not allow for microhabitats that could act as refuge and ameliorate impacts of warming (Colwell *et al.* 2008).

In some respects, however, our model excluded factors that could increase community disassembly, particularly in the tropics. Physiological compensation may follow a latitudinal trend (Ghalambor *et al.* 2006). The ability to acclimate in response to warming may be reduced in areas with limited temperature variation (Stillman 2003). Evolutionary rates needed to track warming suggest that species would be under constant selection (Sinervo *et al.* 2010). Taken together, lower acclimation ability and constant selection could reduce population growth rates and hasten extinctions (Sinervo *et al.* 2010). This would be particularly detrimental in the tropics where population sizes are smaller and communities contain more geographically restricted, endemic populations (Grenyer *et al.* 2006). Next, our model shifted all species' ranges upslope in a lock-step manner. Yet, species show unique responses to climate change and may shift downslope following warming (Moritz *et al.* 2008; Chen *et al.* 2009), leading to novel range overlaps. In addition, past periods of warming have led to increases in diversity through speciation (Jaramillo *et al.* 2010). Historically, the remixing of species in response to climate change produced 'no-analog' communities that were compositionally different from current communities (Williams *et al.* 2007).

Community disassembly will not only involve species of the same taxonomic groups as modelled here, but shifts in community composition of different groups will affect one another through trophic interactions (snakes eat rodents, etc.). Asynchronous range shifts of different groups in response to warming could result in the loss of critical species' interactions and the introduction of novel interactions (Schweiger *et al.* 2008). As specialisation is greater (Dyer *et al.* 2007) and interactions appear more tightly coupled in the tropics (Schemske *et al.* 2009), the same degree of community disassembly across latitude may lead to larger impacts on tropical communities.

Although we used mean temperature to determine range limits, we recognise that other factors, such as precipitation, extreme events and competition, may determine species' distributions (Brown *et al.* 1996) and dispersal in response to warming (Knapp *et al.* 2008). Still, temperature has been shown to play a significant role in determining range limits of many species (Gaston & Chown 1999; Crozier & Dwyer 2006). The strongest signals of climate change include range shifts in response to mean temperature increases (Parmesan & Yohe 2003; Wilson *et al.* 2005), and studies have already documented upslope shifts and extinctions of montane species in both tropical (Raxworthy *et al.* 2008; Chen *et al.* 2009) and temperate (Beever *et al.* 2003; Moritz *et al.* 2008) regions.

Although tropical communities appear more sensitive to warming, the impacts are dependent upon community structure, and this fact, coupled with the greater warming in temperate regions, leads to complex responses to warming. Even in communities where elevational ranges are generally large, the loss of a few narrow ranged species can greatly alter community composition. Therefore, we must consider how communities are built when trying to determine the impacts of warming. Given a greater degree of specialisation (Dyer *et al.* 2007; Schemske *et al.* 2009), tropical species may suffer greater costs for the same amount of community disassembly. Regardless of location, however, the degree of disassembly can be large in montane communities with only slight increases in temperature if species fail to track thermal zones (Fig. 3). Most of the world's biodiversity is found along mountain ranges (Grenyer *et al.* 2006), yet, faced with climate

change, montane ecosystems are some of the most threatened on the planet (La Sorte & Jetz 2010). Thus, understanding the impacts of warming on montane communities is essential for conservation. Results from our analyses extend our knowledge of the potential for community change across a broad latitudinal gradient in a host of taxa. Future models would benefit from integrating information on other abiotic and biotic factors that affect both range size and dispersal. Ultimately, such models could be used as tools to direct conservation efforts.

AUTHORSHIP

KSS collected data, analysed output data and wrote the manuscript. SY performed modelling work. JJT contributed substantially to revisions. All authors designed the study.

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SUPPORTING INFORMATION

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

Appendix S1 List of transect studies used to test impacts of global warming on community disassembly, including study location, latitude (N or S), and reference.
Appendix S2 Additional figures.
Appendix S3 Code for model simulation in R.
Table S1 Results from linear mixed-effects models for factors affecting elevational range size of each taxon.
Table S2 Multiple comparisons of extinctions and loss of co-occurrences for taxa following projected range shifts under four dispersal scenarios (proportional, random, none and infinite).
Table S3 Results from general linear models (GLM) and linear mixed-effects models (LME) for factors affecting loss of co-occurrences for each taxon.
Table S4 Results from general linear models (GLM) and linear mixed-effects models (LME) for factors affecting extinction for each taxon.
Table S5 Results from general linear models (GLM) for the impact of mean dispersal on loss of co-occurrences for each taxon.
Table S6 Results from general linear models (GLM) for the impact of dispersal variance on loss of co-occurrences for each taxon.

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