Montane species and communities track rising temperatures better in the tropics

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Abstract

Many species are responding to recent climate change by shifting their distributions upslope to higher elevations, but the observed rates of shifts vary considerably among studies. Here we test the hypothesis that latitudinal position in part explains this variation, using two independent datasets—resurveys of species' elevational ranges, and repeatedly surveyed tree plots. We find that communities are shifting 18.6 m per decade upslope, but these upslope shifts are slightly faster in the tropics (25.1 m per decade on average) than the temperate zone (13.1 m per decade on average). Faster upslope shifts in the tropics are surprising because rates of warming are faster in the temperate zone. Consequently, tropical communities are tracking changing temperatures 2.5 times (resurvey dataset) and 10.0 times (tree plot dataset) more than their temperate counterparts. For the amount of warming expected to lead to a 100 m upslope shift, tropical communities have shifted upslope by an average of 81 m while temperate communities have shifted upslope by an average of only 32 m. Similarly, for the amount of warming expected to lead to a 1 °C increase in CTI, tropical tree plots have increased in CTI by an average of 0.44 °C while temperate tree plots have increased by an average of only 0.044 °C. This latitudinal gradient in responsiveness to recent warming suggests tropical montane biotas are disproportionately sensitive to ongoing global warming.

Introduction

One consequence of global warming is the upslope shift, or "migration", of many montane species' ranges to higher, cooler elevations (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Parmesan & Yohe, 2003). However, there is significant variation in the degree to which montane species are effectively tracking temperature increases via distributional shifts to higher elevations. For example, while moths in Borneo are rapidly shifting their ranges upslope at rates that approximately match local warming rates (Chen et al., 2009; Wu et al., 2019), the upslope shifts in the ranges of plants in the European Alps lag far behind the pace of warming (Rumpf *et al.* 2018), and some birds in northeastern North America are shifting their ranges *downslope* despite recent warming (Zuckerberg *et al.* 2009; DeLuca & King 2017).

Here we address the question "why are some species and communities effectively tracking changes in local temperatures along mountain slopes while others are not?" Specifically, we test the hypothesis that variation in temperature tracking is explained, at least in part, by the species' latitude. Tropical species are hypothesized to be disproportionately sensitive to rising temperatures, even though the absolute magnitude of recent warming is lower in the tropics than in higher latitudes. The explanation for greater sensitivity of tropical species is that they tend to live closer to their optimal temperatures and exhibit narrower thermal tolerances than their temperate counterparts (Deutsch *et al.* 2008; Laurance *et al.* 2011; Sunday *et al.* 2012; Perez *et al.* 2016). Several studies have reported cases where tropical montane species are moving rapidly upslope associated with recent warming (reviewed by Freeman & Class Freeman, 2014; Sheldon,

2019). It is unknown, however, whether these scattered reports are general across taxa and continents.

We used two independent datasets to test the hypothesis that temperature tracking in montane taxa is related to latitudinal position. First, we compiled a dataset of resurveys that have reported elevational shifts for communities and species associated with recent warming (Fig. 1a, Table S1, Datasets S1 and S2). By “communities” we mean a set of species within a particular taxonomic group that lives within a particular montane region (e.g., a bird community or a bee community). Second, we analyzed inventory data from repeatedly surveyed forest plots located in montane areas across the Americas and that have experienced significant warming over the past several decades (Fig. 1b). These two datasets have complementary strengths for inferring latitudinal patterns in recent temperature tracking. Resurveys have the advantage of explicitly measuring changes in elevational distributions for individual species, with data available for many taxonomic groups, but have the disadvantage that studies use different methods to study different taxa. In contrast, forest inventories use standardized methods and provide comprehensive information about the composition of tree communities at given locations.

We calculated “temperature tracking” scores for resurvey and forest inventory datasets. For resurveys, we analyzed data for both communities and individual species. We calculated temperature tracking scores as the ratio of the observed elevational shift vs. the expected elevational shift, where the expected elevational shift is based on estimates of local warming between sampling events and measured or estimated adiabatic lapse rates. For forest inventory data, we calculated community temperature indices (CTI) as the weighted mean of species’ temperature optima based on the species

composition of plots at each sampling event. We then calculated temperature tracking as the annualized change in CTI (i.e., the "thermophilization rate") divided by the observed rate of change in mean annual temperature from 1979 to 2013. In both cases, temperature tracking scores of ~1 indicate that observed changes closely match those expected based on concurrent warming (i.e., strong temperature tracking), and scores >1 indicate that species are shifting their ranges faster than expected. Conversely, temperature tracking scores that are positive but closer to 0 indicate little or no change in the ranges of species or the composition of tree plots despite rising temperatures. Negative scores indicate changes in species ranges or composition that are in the "wrong" direction (e.g., downslope shifts despite warming temperatures).

We then tested the hypothesis that tropical montane species are tracking temperature increases better than temperate montane species. We analyzed the resurvey data at both the community-level (data = 146 estimates of temperature tracking from 83 communities, data provided in Dataset S1) and species-level (data = 5860 estimates of temperature tracking from 2871 species from 65 communities; species-level data was unavailable for 18 communities; see Fig. S1, data provided in Dataset S2). Our dataset of forest inventory plots contained 212 plots from temperate montane forests from the United States and 44 plots of tropical montane forests from Central and South America; (see Fig. S2, data provided in Dataset S3). Our primary analyses focus on temperature tracking, an index of relative response to climate change given local temperature increase. However, latitudinal variation in the absolute responses to climate change is also of interest, as greater warming at high latitudes could counter tighter temperature tracking in the tropics and lead to similar rates of upslope shift across latitude. We

therefore also assess the latitudinal patterns in upslope range shifts (resurvey dataset) and thermophilization rates (tree plot dataset). The combination of two independent datasets, with complementary strengths, and large sample sizes within each dataset, allow us to rigorously test the hypothesis that there is a latitudinal gradient in temperature tracking.

Materials and methods

Resurvey data

Our aim was to compile a comprehensive list of studies that have measured recent range shifts for species in mountainous regions in response to recent warming (within the past ~ 100 years). First, we conducted a Web of Science search on 11 July 2019 with the keywords “climate change” OR “global warming” AND “range shift” AND “mountain” OR “elevation” OR “altitude*”. This search returned 1827 hits. We retained studies that met the following three criteria: (1) they measured recent range shifts at species’ lower elevation limits, mean (or optimum) elevations, or upper elevational limits; (2) range shifts were reported for all species or the entire community, not just species with significant range shifts; and (3) range shifts were measured over a time period of >=10 years. Second, we located additional studies that met these three criteria by examining recent papers synthesizing the range shift literature (Chen et al., 2011; Freeman, Lee-Yaw, Sunday, & Hargreaves, 2018; Lenoir & Svenning, 2015; Rumpf, Hülber, Zimmermann, & Dullinger, 2019; Wiens, 2016). There were three cases for which multiple publications reported elevational range shifts for the same community using the

same underlying data (plants in France, and butterflies and birds in Great Britain). For these cases, we included only the study with a larger sample size of species.

For each study that met our criteria (see Table S1, full data provided in Dataset S1), we extracted the following key information: (1) taxon; (2) latitude of the study site; (3) duration over which range shifts were calculated (e.g., number of years elapsed between surveys); (4) spatial scale of study ("local" when studies were conducted along single elevational gradients or entirely within small montane regions; "regional" when the study was conducted within large political units such as the state of California or the country of Spain); (5) number of species studied; (6) range shifts at lower elevational limits, mean/optimum elevations, and upper elevational limits for the entire community (i.e., for a community of 30 species, the mean range shift of these 30 species); (7) range shifts at lower elevational limits, mean/optimum elevations, and upper elevational limits for individual species (note that not all studies reported species-specific range shifts); (8) temperature changes at the study site between surveys (because we were interested in responses to warming, we did not include two studies that reported cooling temperatures, both from the Appalachians in North America (Moskwik 2014)); and, if reported, (9) expected elevational range shifts based on local temperature changes and lapse rate. There were two studies that did not report local temperature changes (Moret *et al.* 2016; Kusrini *et al.* 2017). For these studies, we estimated local temperature changes using data from gridded data provided by the Climatic Research Unit (Harris *et al.* 2013). For studies that did not report local adiabatic lapse rates, we used lapse rates reported for the geographically nearest study within our dataset, following Chen et al. (2011). When data

were presented only in figures, we used WebPlotDigitizer to extract data from the published graphics (Rohatgi 2017).

All statistics were done in R version 3.6.2 (R Development Core Team 2020). We first analyzed categorical latitudinal differences in temperature tracking between the tropics and the temperate zone. We categorized communities and species as being "tropical" or "temperate" based on the location of the study, with tropical locations defined as < 23.4° absolute latitude. We then fit linear mixed-effects models using the "lme4" package (Bates *et al.* 2014). The response variable in both community-level and species-level models was the temperature tracking score, calculated as the ratio of the observed elevational shift to the expected elevational shift given estimates of local warming and adiabatic lapse rate. We included latitudinal zone (tropical vs. temperate) and four methodological covariates as fixed effects: (1) distributional variable measured (lower limit vs. mean elevation vs. upper limit); (2) spatial scale of study (local vs. regional); (3) number of species in the study (for the community-level model only); and (4) duration of the study. We included the community ID as a random effect, as multiple distributional variables were reported for many communities.

We then analyzed latitudinal differences in temperature tracking as a continuous function of position along the latitudinal gradient by replacing the factor "tropical/temperate" with absolute latitude in models. We did not include taxa as a predictor variable in the community or species-level models because taxonomic differences predict minimal observed variation in recent range shifts (Chen *et al.* 2011; Lenoir *et al.* 2019). Latitudinal sampling was also poor for most taxonomic groups. For the one exception—birds—we repeated analyses after restricting our dataset to only bird

studies (6 from tropics, 12 from temperate zone). To investigate whether our results were driven by the inclusion of communities with few species, we fit an additional model including data only from communities with ≥10 species (125 estimates of temperature tracking from 70 communities).

Last, to assess latitudinal variation in absolute response to recent warming, we repeated analyses with elevational shift (m/decade) as the response variable instead of temperature tracking.

Forest Inventory Data

We compiled our forest inventory plot dataset using Forest Inventory and Analysis (FIA) plots from the United States and previously published inventory plot data from Central and South America (Feeley *et al.* 2013; Fadrique *et al.* 2018). We filtered for FIA plots that were fully forested and have not received observable treatment, including cutting, site preparation, artificial regeneration, natural regeneration, and other silvicultural treatment (Smith 2002). We also filtered for FIA plots that have not experienced disturbances in at least five years. Because we were interested in changes in just mountain forests, we selected FIA plots that fell within mountainous areas using the global mountains raster map derived from the 250 m global Hammond landforms product (Karagulle *et al.* 2017). We included only FIA plots that had been surveyed at least twice. We collected the species identity of all individual adult trees (diameter at breast height > 12.7 cm, or 5 inches) for each survey of each FIA plot. We then calculated the community temperature index (CTI) of the plot as the average of optimal temperature of each species weighted by basal area, following the method of Fadrique et al. (Fadrique *et*

al. 2018). Specifically, we downloaded all georeferenced plant location records available through the BIEN database (version 4.1.1 accessed in November 2018 via BIEN package in R) for the New World (North America, Central America, and South America, but excluding the Caribbean islands). The BIEN database provides collated observation and collection data from multiple sources and provides a base level of data filtering and standardization. We used BIEN's default download preferences to exclude records of known introduced species and cultivated individuals. We further filtered the records to include only those that were georeferenced and that list the year of collection/observation as being between 1970 and 1980. We restricted records to just this 10-year window to minimize errors due to the possibility of species changing their ranges through time. For each species, we then extracted the estimated mean annual temperature (BIOCLIM1) at all retained collection coordinates from the CHELSA v1.2 raster of "current" (i.e., mean of 1979-2012) climate at 30 arc-second resolution and estimated the thermal optima (MAT_{opt}) of each species as the mean MAT of all collections. If species had fewer than 10 records, we estimated MAT_{opt} at the genus-level using combined records of all congeners. Genera with <10 records were excluded from subsequent analyses. We additionally ran analyses using only species-level climatic optima measurements. We next used the collection records to calculate the community temperature index (CTI) of each plot in each census as the mean MAT_{opt} for species in the plot weighted by their relative basal area.

We then calculated the thermophilization rate of each FIA plot as the linear trend of CTI over time, and combined this dataset with previously published thermophilization

rates for 10 sites in Costa Rica and 63 sites in the tropical Andes (Feeley *et al*. 2013; Fadrique *et al*. 2018).

For each plot, we calculated the rate of temperature change as the linear trend of mean annual temperature over time, using monthly mean temperature estimates from 1980 to 2013 from the CHELSA time-series dataset (Karger & Zimmermann 2019). As with the resurvey data, we calculated the thermal tracking score for each plot as the ratio of observed changes (rate of change in thermophilization rate) and expected changes (rate of change of mean annual temperature).

In order to focus on the response of organisms to the warming climate, we selected plots with significant warming trends (plots with $p < 0.05$ in a regression of mean temperature versus year). As FIA plots are generally smaller in size compared to the plots in Central and South America (168 m^2 for FIA plots compared to 1-hectare for most tropical plots), we aggregated FIA plots into 1 degree diameter hexagons that contain approximately 30 plots each, averaging the thermophilization rate and temperature tracking score weighted by total basal area. We removed hexagons with <5 plots from subsequent analysis. We examined the relationships between latitude and the temperature tracking score by fitting linear mixed-effects models using the "nlme" package in R (Pinheiro *et al.* 2017). We included both latitude (either the factor "tropical/temperate", or absolute latitude) and elevation as fixed effects. Due to the close proximity of hexagons/plots and spatial dependence in the residuals of non-spatial linear models, we modeled spatial random effects that follow Gaussian covariance functions, and then evaluated the significance of regression coefficients for fixed effects using the conditional standard error of regression coefficients.

Results

Resurvey dataset

Resurvey data show that tropical montane taxa are tracking temperature increases "better" (i.e., have higher temperature tracking scores) than are temperate montane species (Fig. 2a-2d, Fig. S3). Tropical communities had temperature tracking scores 2.5 times greater than temperate communities (Fig. 2a, Table S2; temperature tracking scores for tropical and temperate communities = 0.81 ± 0.16 vs. 0.32 ± 0.077, $p = 0.0058$; estimates ± standard errors from mixed-effects models), and tropical species had temperature tracking scores 2.2 times greater than temperate species (Fig, 2c, Table S3; temperature tracking scores for tropical and temperate species = 0.86 ± 0.18 vs. 0.40 ± 0.085, $p = 0.018$).

Results were similar when we modeled temperature tracking from resurvey data as a continuous function of position along the latitudinal gradient. Temperature tracking scores decreased by an average of 0.15 ± 0.050 and 0.12 ± 0.054 per 10° increase in latitude for communities and species, respectively (Figs. 2b and 2d, Tables S4 and S5). For resurvey data, estimates from linear mixed models are that communities at the equator have a tracking score of 0.97 ± 0.21 but 0.32 ± 0.077 at 45° latitude (averaged over levels of fixed effects; the equivalent values for the species-level model are 0.94 ± 0.23 and 0.39 ± 0.88). Hence, tropical communities and species are closely tracking temperature changes while temperate zone communities and species are not, though the explanatory power of community models was much greater (marginal R^2 values from linear mixed-effects models = 0.10 and 0.0091 respectively).

Methodological covariates included in models had minimal explanatory power, with the exception that temperature tracking scores tended to be larger at species' upper elevational limits compared to at their lower elevational limits or mean elevations (Tables S2-S5). Results for communities all held when considering only communities with 10 or more species (Fig. S4, Tables S6 and S7), indicating that the results are not driven by the inclusion of depauperate communities. In addition, all results held when subsetting the resurvey dataset to only studies of birds (Fig. S5, Tables S8-S11).

Last, absolute responses to recent climate change tended to be greater in the tropics, though this difference was not statistically significant (Tables S12-S15). On average tropical communities have shifted upslope 25.1 meters per decade while temperate communities have shifted upslope 13.1 meters per decade ($p = 0.093$); the equivalent estimates for the species-level analysis are 20.8 meters per decade (tropics) and 13.7 meters per decade (temperate; $p = 0.30$). Estimated rates of upslope shifts from models that did not include latitude were 18.6 meters per decade (communities) and 14.5 meters per decade (species-level).

Forest inventory dataset

Tropical montane trees are also tracking temperature increases better than temperate montane trees (Fig. 2e and 2f, Fig S6, Tables S16-S17). Tropical montane forest plots had higher temperature tracking scores (0.44 ± 0.11) than temperate montane forest plots (0.044 ± 0.044; $p = 0.00099$; Table S16). Latitude is a strong predictor in the linear mixed model: a 10° increase in latitude corresponds to a 0.13 ± 0.039 decrease in the temperature tracking score (Table S17). The model-based estimate is that tree plots have

a tracking score of 0.56 ± 0.0043 at the equator, but -0.038 ± 0.0043 at 45° latitude. Results were unchanged when using only species-level climatic optima data (Tables S18, S19).

The greater temperature tracking in tropical inventory plots was due to faster changes in CTI in the tropics, also known as the thermophilization rate. Tropical plots had thermophilization rates of 0.095 ± 0.020 °C per decade vs. 0.017 ± 0.012 °C per decade for temperate plots (Fig. S6). Thus, while the rate of warming was faster at high latitudes in our dataset-- 0.31 ± 0.0065 °C per decade for temperate plots vs. 0.22 ± 0.010 °C per decade for tropical plots (Fig. S6), there were still greater absolute responses to recent warming in the tropics.

Discussion

We found evidence that tropical montane species and communities are tracking recent temperature increases better than temperate montane species. Temperature tracking was greater in the tropics in each of three datasets: (1) community-level data from resurvey studies, (2) species-level data from resurvey studies, and (3) repeatedly-censused forest inventory tree plots. On average, tropical montane species track temperature increases, while temperate montane species do not. This tighter temperature tracking in the tropics means that absolute responses to recent warming are also greater in the tropics, despite faster rates of warming in the temperate zone.

The overall rate of upslope shift for communities that we document of 18.6 m per decade is 67% higher than the average overall shift for communities of 11.1 m per decade reported nearly a decade ago (Chen et al., 2011), which was itself double the estimate of

6.1 m per decade reported nearly two decades ago (Parmesan & Yohe 2003). Hence, as temperatures continue to warm and more resurvey datasets are published (e.g. 83 communities in the present study versus 30 in the Chen et al. 2011 study), estimated rates of upslope shift continue to increase, counter to the more common pattern wherein effect sizes tend to decline over time (Camerer *et al.* 2018). Further, we find evidence that rates of upslope shift depend in part on latitude, with average upslope shifts for communities of 25.1 m per decade in the tropics but only 13.1 m per decade in the temperate zone, though this difference is marginally significant.

Our resurvey results appear to be robust to the heterogeneity present within our datasets. Despite nearly two decades of research documenting elevational range shifts associated with recent warming, the number of studies for most taxonomic groups remains low, particularly in the tropics (Feeley *et al.* 2017). Birds are the only taxonomic group with reasonable sampling across temperate and tropical zones, and we find strong temperature tracking in tropical—but not temperate—birds. This means that we have evidence for a latitudinal gradient in temperature tracking in both birds and trees (comparing tropical birds to temperate birds, and tropical trees to temperate trees), while data is lacking for other individual groups.

Resurvey and forest inventory plot datasets show marked latitudinal patterns in temperature tracking, but differences in temperature tracking scores across latitudes were higher for the resurvey dataset. This difference could reflect a biological difference in generation time between species included in the datasets. Trees have long generation times that lead to slow rates of community turnover and range shifts (Lenoir *et al.* 2008; Feeley *et al.* 2012). In comparison, the resurvey dataset consists primarily of taxa with

much shorter generation times such as birds, mammals, and herbaceous plants. An alternative explanation is that methodological differences between resurveys and forest tree inventory plots, both in data collection and analysis, explain why temperature tracking scores are higher in the resurvey dataset.

Latitude is a much better predictor of temperature tracking when considering communities (a set of species aggregated together) than for individual species. Individual species show a wide variation in their temperature tracking scores (Freeman et al., 2018; Moritz et al., 2008; Rumpf et al., 2019). While latitude is a statistically significant predictor of temperature tracking in the species-level model, its explanatory power is low. Combined, these results imply that despite a clear latitudinal pattern of temperature tracking for communities, we still have only a limited ability to predict changes in individual species' elevational distributions associated with warming temperatures (Angert *et al.* 2011). Range shifts at the species-level may be more predictable in the marine realm, where most species appear to closely track temperature (Lenoir et al., 2020; Pinsky, Eikeset, McCauley, Payne, & Sunday, 2019).

Multiple mechanisms may explain why tropical species are tracking temperature changes better than temperate species. The leading explanation is that tropical species are more physiologically sensitive to climate change than are temperate species. This explanation implies that the mean annual temperature is a more important driver of species' elevational distributions in the tropics than at higher latitudes. An additional possibility is that both tropical and temperate species are tracking recent warming, but that temperate species are using phenological shifts to do so (Socolar *et al.* 2017). Seasonal temperature fluctuations in the tropics are minimal, meaning that tropical

species are unlikely to be able to track climate via phenological shifts. In other words, temperate-zone species may track changing climate by shifting in time, while tropical species track changing climate by shifting in space. If so, we may expect a decoupling of biodiversity change and carbon dynamics in the temperate zone.

Several limitations of our study deserve explicit mention. First, we followed previous analyses in calculating temperature tracking scores based on mean annual temperature (Chen et al., 2011). Analyses that incorporate temperature variability (i.e., seasonality) and other climatic variables have also proven powerful (Crimmins *et al.* 2011; Tingley *et al.* 2012), but are inherently more difficult to implement and interpret. Second, our analyses do not take into account variation in microclimate, which may be a strong driver of range shifts or the lack thereof (Lembrechts *et al.* 2019; Zellweger *et al.* 2020). It is not clear how microclimate availability varies along a latitudinal gradient, but a greater availability of microclimates and climate refugia in the temperate zone than the tropics is an alternative explanation for our results. We were similarly unable to analyze climatic factors that occur at intermediate spatial scales along mountain slopes, such as cold-air pooling (Curtis *et al.* 2014). Third, future studies should address landscape-level changes due to habitat loss or other disturbances (Larsen 2012; Lenoir & Svenning 2015; Campos-Cerqueira *et al.* 2017; Guo *et al.* 2018). The resurveys and forest plots in our dataset took place in landscapes that have not undergone intensive deforestation or other land-use change. Given that highly modified landscapes predominate across most of the globe, further tests of the interactions between landscape change and climate change are needed. Fourth, the patterns we document are not without exceptions. For example, Puerto Rican frogs and birds are not closely tracking temperature despite their tropical

latitude (Campos-Cerqueira & Mitchell Aide 2017; Campos-Cerqueira *et al.* 2017), though this could potentially reflect increasing forest cover on this island (Battey *et al.* 2019). Conversely, some temperate zone communities are closely tracking recent warming (Kelly & Goulden 2008; Menéndez *et al.* 2014).

Conclusions

The latitudinal gradient in temperature tracking we document has multiple implications for the conservation of montane floras and faunas. The weak temperature tracking of temperate montane species and communities indicates that acclimation and adaptation, rather than elevational shifts, will likely be key processes in determining if temperate montane species can persist in the face of continued warming. It is an open question whether adaptation and acclimation will be able to keep pace with rates of warming that are unprecedented in recent evolutionary time (Visser 2008; Feeley *et al.* 2012). In contrast, the strong temperature tracking of tropical montane species indicates that they may be able to persist despite warming temperatures by shifting their distributions upslope, at least when protected elevational corridors provide suitable habitats at higher elevations. On the other hand, this implies that the "escalator to extinction"—wherein montane species respond to warming temperatures by shifting upslope until they run out of available habitat on mountaintops (Freeman, Scholer, Ruiz-Gutierrez, & Fitzpatrick, 2018)—runs faster in the tropics. Notably, such mountaintop extinctions may occur well below the actual mountaintop, as pervasive anthropogenic modifications of high-elevation tropical systems effectively limit the ability of the tree line to shift upslope (Rehm & Feeley 2015). Indeed, local extinctions and range contractions associated with

recent warming appear to be most common in tropical montane species (Freeman et al., 2018; Wiens, 2016).

The sixth mass extinction in Earth's history is now underway (Ceballos *et al.* 2017). The tropics have the highest species diversity of any biome, and tropical mountains have the highest diversity of all (Rahbek *et al.* 2019). The relatively small temperature changes in the tropics should minimize the impact of climate change, but the disproportionately sensitive responses of tropical montane species have instead placed this whole biota on an escalator to extinction. The degree to which predictions of widespread species extinctions in tropical mountains (Sekercioglu *et al.* 2008) come true will depend on our ability to protect elevational corridors that enable species to persist while shifting upslope (Feeley & Rehm 2012), and, ultimately, on whether humanity is able to slow global warming.

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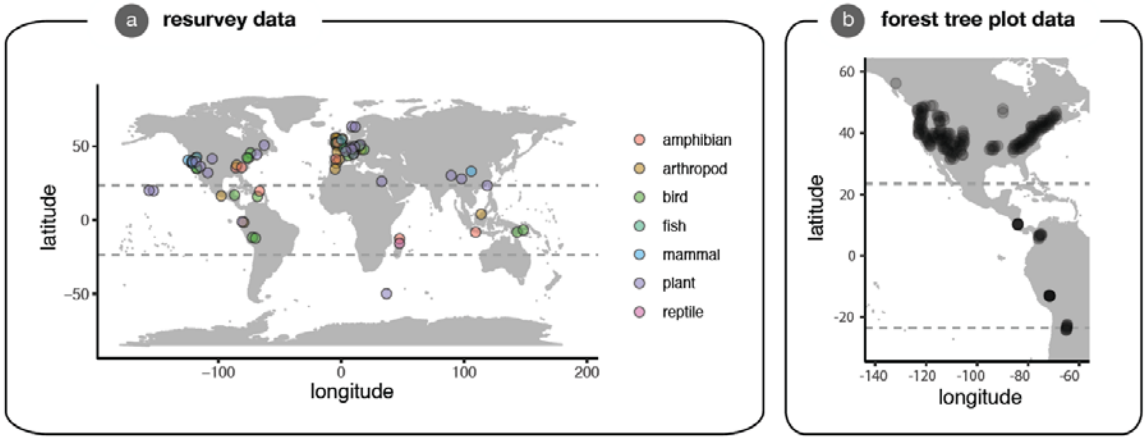

Figure 1. Maps of resurvey studies that measured elevational shifts associated with recent warming (a) and of forest inventory tree plots that have been repeatedly censused (b). Locations of resurvey studies are jittered slightly to improve clarity. The Tropics of Cancer and Capricorn (at 23.4° N and S, respectively) delimit the tropics, and are illustrated with dashed lines.

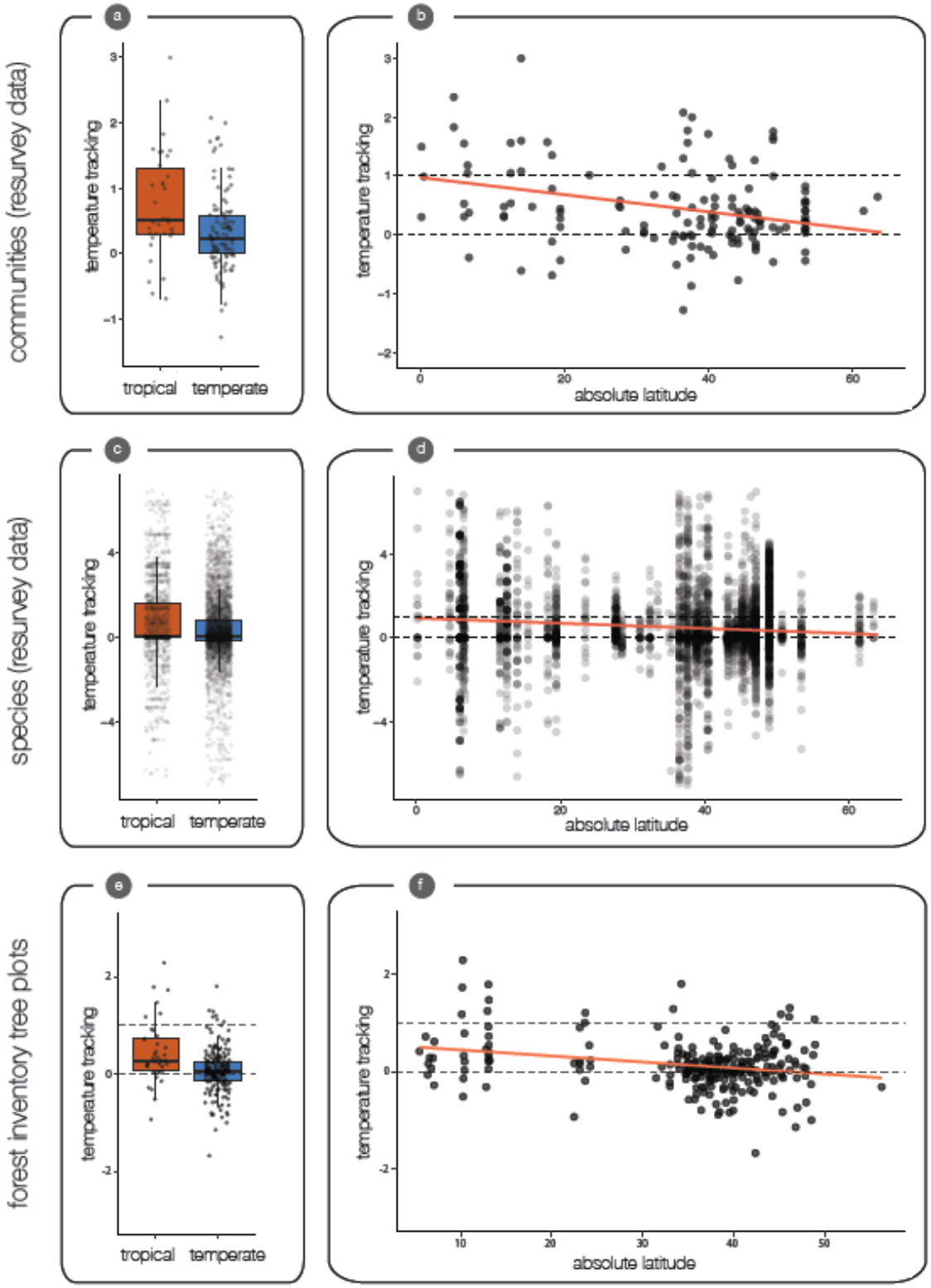

Figure 2. Tropical communities, species, and forest inventory tree plots have higher temperature tracking scores than their temperate zone counterparts. Raw data are shown

as points. Dashed lines illustrate both perfect temperature tracking (temperature tracking = 1) and zero temperature tracking despite warming temperatures (temperature tracking = 0). Trendlines illustrate predictions from mixed models. (a) temperature tracking for communities in tropical and temperate zones; (b) relationship between temperature tracking and absolute latitude (°) for communities; (c) temperature tracking for species in tropical and temperate zones (~ 0.5% of data has been removed for visualization); (d) relationship between temperature tracking and absolute latitude (°) for species; (e) temperature tracking for forest inventory tree plots in tropical and temperate zones; (f) relationship between temperature tracking and absolute latitude (°) for forest inventory tree plots.

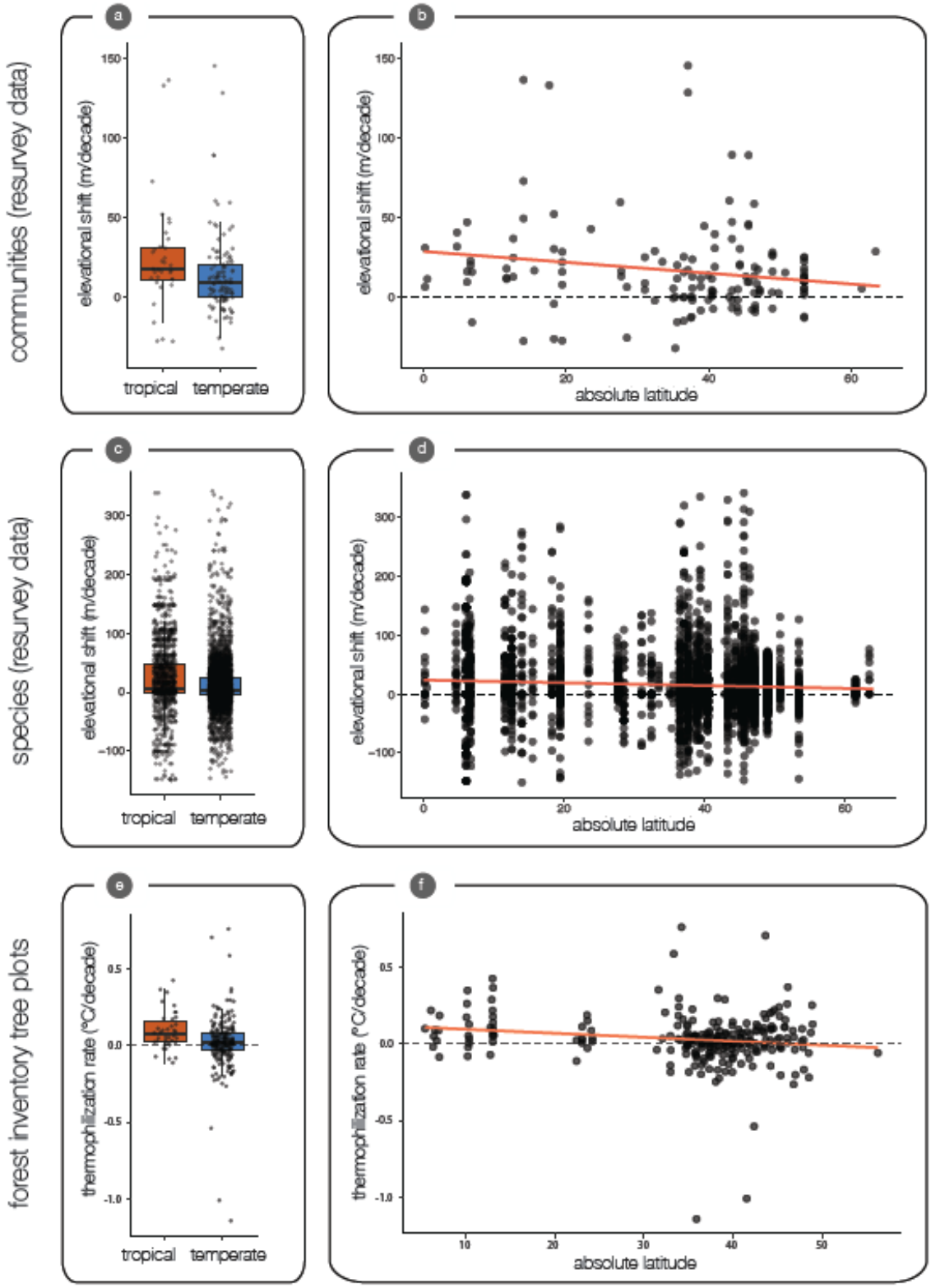

Figure 3. Tropical communities and species have undertaken larger upslope shifts, and forest inventory tree plots greater thermophilization, than their temperate zone

counterparts. Raw data are shown as points. Trendlines illustrate predictions from mixed models. (a) elevational shifts for communities in tropical and temperate zones; (b) relationship between elevational shifts and absolute latitude (°) for communities; (c) elevational shifts for species in tropical and temperate zones (~ 0.5% of data has been removed for visualization); (d) relationship between elevational shifts and absolute latitude (°) for species; (e) thermophilization rate for forest inventory tree plots in tropical and temperate zones; (f) relationship between thermophilization rate and absolute latitude (°) for forest inventory tree plots.