Montane species and communities track recent warming more closely in the tropics

Running head: temperature tracking across latitudes

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Abstract

Tropical species have been hypothesized to be particularly sensitive to temperature increases because of their physiological specialization to stable climates. Here we use two independent datasets to test whether tropical montane species are tracking recent warming via upslope range shifts better than temperate montane species. First, we compiled published data documenting recent elevational shifts of plants and animals. For this resurvey data, we analyzed temperature tracking for both entire communities (N = 83) and for individual species (N = 2871). Second, we calculated temperature tracking of tree community structure using data from repeatedly surveyed forest inventory plots from mountainous regions of the Americas (N = 300). We defined temperature tracking scores as the ratio of observed changes vs. expected changes based on estimates of local warming. Both datasets show that tropical montane taxa are tracking changing temperatures significantly better than their temperate counterparts. On average, tropical communities are tracking temperature 2.6 times more than temperate communities (0.84 ± 0.15 vs. 0.32 ± 0.074), tropical species are tracking temperature 2.3 times more than temperate species (0.91 ± 0.18 vs. 0.40 ± 0.083), and tropical tree plots are tracking temperature 4.4 times more than temperate tree plots (0.44 ± 0.11 vs. 0.099 ± 0.042). This latitudinal gradient in temperature tracking is consistent with accumulating evidence that tropical montane biotas are disproportionately sensitive to ongoing global warming.

Keywords: global warming, latitudinal gradient, mountaintop extinction, range shift, upslope shift

Introduction

One consequence of global warming is the upslope shift, or "migration", of many montane species' ranges to higher, cooler elevations (I.-C. 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 approximate that of concurrent warming (I. C. 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 concurrent warming (Rumpf et al., 2018), and some birds in northeastern North America are shifting their ranges *downslope* despite recent warming (DeLuca & King, 2017; Zuckerberg, Woods, & Porter, 2009).

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 low in the tropics compared to 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; Perez, Stroud, & Feeley, 2016; Sunday, Bates, & Dulvy, 2012). Several studies have reported that tropical montane species are moving rapidly upslope associated with recent warming (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 may 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. Note that not all studies that reported range shifts for communities also reported range shifts for the individual species that comprised the community. 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 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 (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, lower temperature tracking scores 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 256 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). 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.

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. 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 (I.-C. 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 (Kusrini et al., 2017; Moret, Aráuz, Gobbi, & Barragán, 2016). For these studies, we estimated local temperature changes using data from high-resolution gridded data provided by the Climatic Research Unit (Harris, Jones, Osborn, & Lister, 2013). When studies did not report local adiabatic lapse rates, we assumed a lapse rate of 0.55°C / 100 m elevation, which was the mean lapse rate from the 14 studies that reported locally measured lapse rates. 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. To do so, we fit linear mixed-effects models using the "lme4" package (Bates, Maechler, Bolker, & Walker, 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. These models were the same as those described above, but with the absolute value of latitude as a fixed effect. 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). We did not include taxa as a predictor variable in the community or species-level models because latitudinal sampling was poor for most taxonomic groups.

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 (Fadrique et al., 2018; Feeley, Hurtado, Saatchi, Silman, & Clark, 2013). Because we were interested in changes in mountains, we selected FIA plots (Smith, 2002) 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

185 included only FIA plots that had been surveyed at least twice. We collected the species
186 identity of all individual adult trees (diameter at breast height > 12.7 cm) for each survey
187 of each FIA plot. We then calculated the community temperature index (CTI) of the plot
188 as the weighted average of optimal temperature of each species, following the method of
189 Fadrique et al. (Fadrique et al., 2018). Specifically, we downloaded all georeferenced
190 plant location records available through the BIEN database (version 4.1.1 accessed in
191 November 2018 via BIEN package in R) for the New World (North America, Central
192 America, and South America, but excluding the Caribbean islands). The BIEN database
193 provides collated observation and collection data from multiple sources and provides a
194 base level of data filtering and standardization. We used BIEN's default download
195 preferences to exclude records of known introduced species and cultivated individuals.
196 We further filtered the records to include only those that were georeferenced and that list
197 the year of collection/observation as being between 1970 and 1980 (we restricted records
198 to just this 10-year window to minimize errors due to species migrating through time).
199 For each species, we then extracted the estimated mean annual temperature (BIOCLIM1)
200 at all retained collection coordinates from the CHELSA v1.2 raster of "current" (i.e.,
201 mean of 1979-2012) climate at 30 arc-second resolution and estimated the thermal optima
202 (MAT_{opt}) of each species as the mean MAT of all collections. If species had fewer than
203 10 records, we estimated MAT_{opt} at the genus-level using combined records of all
204 congeners. Genera with <10 records were excluded from subsequent analyses. We next
205 used the collection records to calculate the community temperature index (CTI) of each
206 plot in each census as the mean MAT_{opt} for species in the plot weighted by their relative
207 basal area.

We then calculated the thermophilization rate of each FIA plot as the linear trend of CTI over time, and obtained previously published thermophilization rates for 10 sites in Costa Rica and 63 sites in the tropical Andes (Fadrique et al., 2018; Feeley et al., 2013). Using these data, we calculated the rate of temperature change for all sites using monthly mean temperature estimates from 1980 to 2013 from the CHELSA time-series dataset (Karger & Zimmermann, 2019). Specifically, we calculated the rate of temperature change at each site as the linear trend of mean annual temperature over time. 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. We removed hexagons with <5 plots from subsequent analysis. 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 a significant warming trend ($p < 0.05$) and examined the relationships between absolute latitude and the temperature tracking score by fitting linear mixed-effects models using the "spaMM" package in R (Rousset, 2017). We included both absolute latitude and elevation as fixed effects. Due to the close proximity of 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 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). We first 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. Tropical communities had temperature tracking scores 2.6 times greater than temperate communities (Fig. 2a, Table S2; temperature tracking scores for tropical and temperate communities = 0.84 ± 0.15 vs. 0.32 ± 0.074, p = 0.0021; estimates ± standard errors from mixed-effects models), and tropical species had temperature tracking scores 2.3 times than temperate species (Fig, 2c, Table S3; temperature tracking scores for tropical and temperate species = 0.91 ± 0.18 vs. 0.40 ± 0.083, p = 0.0082).

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 0.16 ± 0.049 and 0.13 ± 0.053 per 10 degrees latitude for communities and species, respectively (Figs. 2b and 2d, Tables S4 and S5). 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 = 0.12 and 0.010 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.

Forest inventory data also show that tropical montane taxa are tracking temperature increases better than temperate montane species (Fig. 2e and 2f, Fig S5, Tables S8-S9). Tropical montane forest plots had higher temperature tracking scores (0.44 ± 0.11) than temperate montane forest plots (0.099 ± 0.042; $p = 0.0038$; Table S8). Latitude is a strong predictor in the linear mixed model: a 10-degree increase in latitude corresponds to a 0.14 ± 0.039 decrease in the temperature tracking score (Table S9). 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. 0.033 ± 0.011 °C per decade for temperate plots (Fig. S6). In contrast, the rate of warming was faster at high latitudes in our dataset: 0.31 ± 0.0061 °C per decade for temperate plots vs. 0.22 ± 0.010 °C per decade for tropical plots (Fig. S6).

Discussion

We found strong evidence that tropical montane species 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. Moreover, the effect of latitude is large, with tropical montane species tightly tracking temperature increases (temperature tracking scores ~ 1, which indicates perfect

temperature tracking) and temperate montane species tracking temperature increases only weakly (temperature tracking scores closer to 0; 0 would indicate a complete lack of temperature tracking. Specifically, for resurvey data, estimates from linear mixed models are that communities have a tracking score of 1.02 ± 0.20 at the equator, but 0.32 ± 0.074 at 45° latitude (averaged over levels of fixed effects; the equivalent values for the species-level model are 0.99 ± 0.22 and 0.39 ± 0.86). For forest tree plot data, the model-based estimate is that tree plots have a tracking score of 0.63 ± 0.0069 at the equator, but -0.00080 ± 0.0068 at 45° latitude.

While both resurvey and forest inventory plot datasets show marked latitudinal patterns in temperature tracking, 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 (Feeley, Rehm, & Machovina, 2012; Lenoir, Gegout, Marquet, De Ruffray, & Brisse, 2008). In comparison, the resurvey dataset consists primarily of taxa with much shorter generation times such as birds, mammals, and herbaceous plants. An alternative explanation that requires testing is that methodological differences between resurveys and forest tree inventory plots, both in data collection and analysis, may explain why temperature tracking scores differ between these datasets.

Our model explains the observed variation in temperature tracking at the level of communities much better than for individual species. Individual species show a wide variation in their temperature tracking scores (Freeman, Lee-Yaw, et al., 2018; Moritz et al., 2008; Rumpf et al., 2019). Latitude is a significant predictor of temperature tracking

300 in the species-level model, but its explanatory power is low. Combined, these results
301 imply that despite a clear latitudinal pattern of temperature tracking for communities, we
302 still have only a limited ability to predict changes in individual species' elevational
303 distributions associated with warming temperatures (Angert et al., 2011). Range shifts at
304 the species-level may be more predictable in the marine realm, where most species
305 appear to closely track temperature (Lenoir et al., 2019; Pinsky, Eikeset, McCauley,
306 Payne, & Sunday, 2019).

307 Multiple mechanisms may explain why tropical species are tracking temperature
308 better than temperate species. The leading explanation is that tropical species are more
309 physiologically sensitive to climate change than are temperate species. This explanation
310 implies that the mean annual temperature is a more important driver of species'
311 elevational distributions in the tropics than at higher latitudes. An additional possibility is
312 that both tropical and temperate species are tracking recent warming, but that temperate
313 species are using phenological shifts to do so (Socolar, Epanchin, Beissinger, & Tingley,
314 2017). Seasonal temperature fluctuations in the tropics are minimal, meaning that tropical
315 species are unlikely to be able to track climate via phenological shifts. In other words,
316 temperate-zone species may track changing climate by shifting in time, while tropical
317 species track changing climate by shifting in space. If so, we may expect a decoupling of
318 biodiversity change and carbon dynamics in the temperate zone.

319 Several limitations of our study deserve explicit mention. First, we followed
320 previous analyses in calculating temperature tracking scores based on mean annual
321 temperature (I.-C. Chen et al., 2011). Analyses that incorporate temperature variability
322 (i.e., seasonality) and other climatic variables have also proven powerful (Crimmins,

Dobrowski, Greenberg, Abatzoglou, & Mynsberge, 2011; Tingley, Koo, Moritz, Rush, & Beissinger, 2012), but are inherently more difficult to implement and interpret. Second, future studies should address land use drivers of recent distribution changes in conjunction with climate drivers (Guo, Lenoir, & Bonebrake, 2018; Larsen, 2012; Lenoir & Svenning, 2015). Third, there remains a strong temperate zone bias in data on elevational range shifts associated with recent climate change (Feeley, Stroud, & Perez, 2017). Tropical studies are indeed underrepresented in our datasets, but the general trends we document are robust to the unbalanced samples. Fourth, the patterns we document are strong but not without exceptions. For example, Puerto Rican frogs and birds are not closely tracking temperature despite their tropical latitude (Campos-Cerqueira, Arendt, Wunderle, & Aide, 2017; Campos-Cerqueira & Mitchell Aide, 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, González-Megías, Jay-Robert, & Marquéz-Ferrando, 2014).

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 helping temperate montane species 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. 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, Lee-Yaw, et al., 2018; Wiens, 2016).

The sixth mass extinction in Earth's history is now underway(Ceballos, Ehrlich, & Dirzo, 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, Schneider, Fay, & Loarie, 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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Author contributions

BGF compiled resurvey dataset; YS, KZ and KJF compiled forest inventory tree plot dataset; BGF, YS and KZ conducted analyses; BGF led the writing process with extensive input from KJF, YS and KZ.

Author contributions

The authors declare no competing interests.

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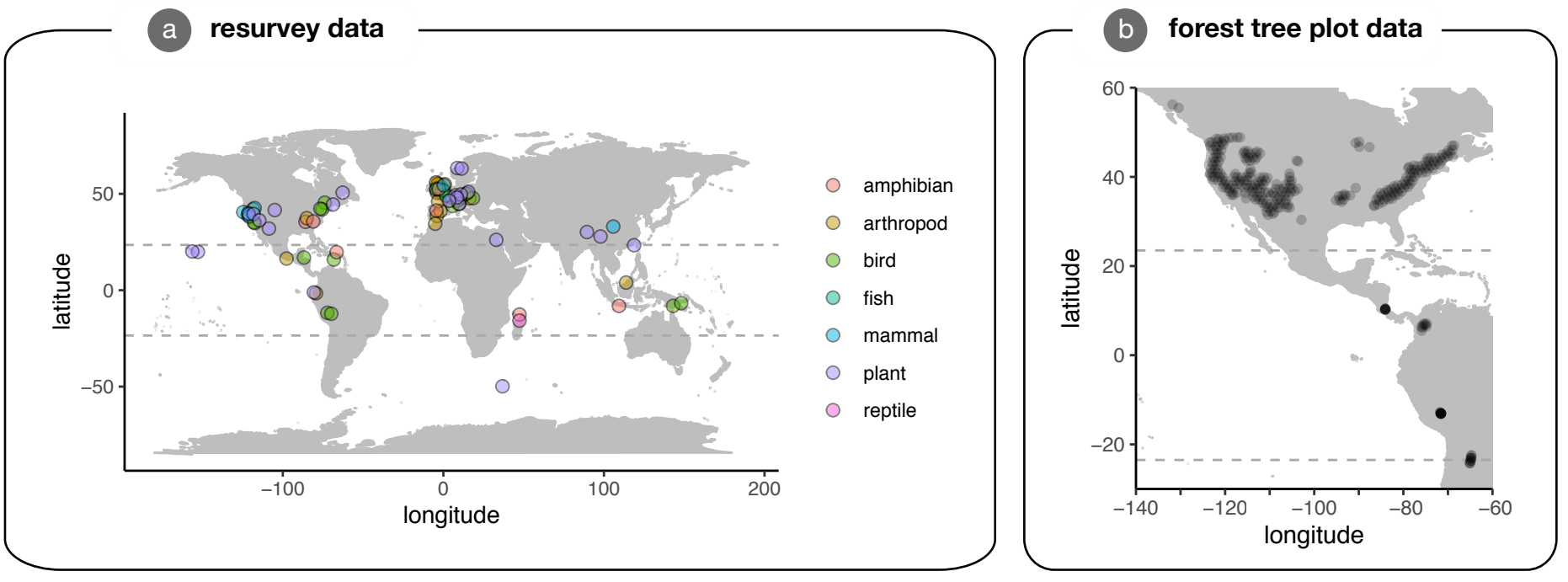
Fig 1. Maps of resurvey studies that measured elevational shifts associated with recent warming (a) and of forest inventory tree plots that have been repeatedly censused (b). Locations of resurvey studies are jittered slightly to improve clarity. The Tropics of Cancer and Capricorn (at 23.4° N and S,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

Fig. 2. Tropical communities, species, and forest inventory tree plots have higher temperature tracking scores than their temperate zone counterparts. (a, c, e) Temperature tracking scores in tropical and temperate zones; (b, d, f) relationship between temperature tracking and absolute latitude. 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.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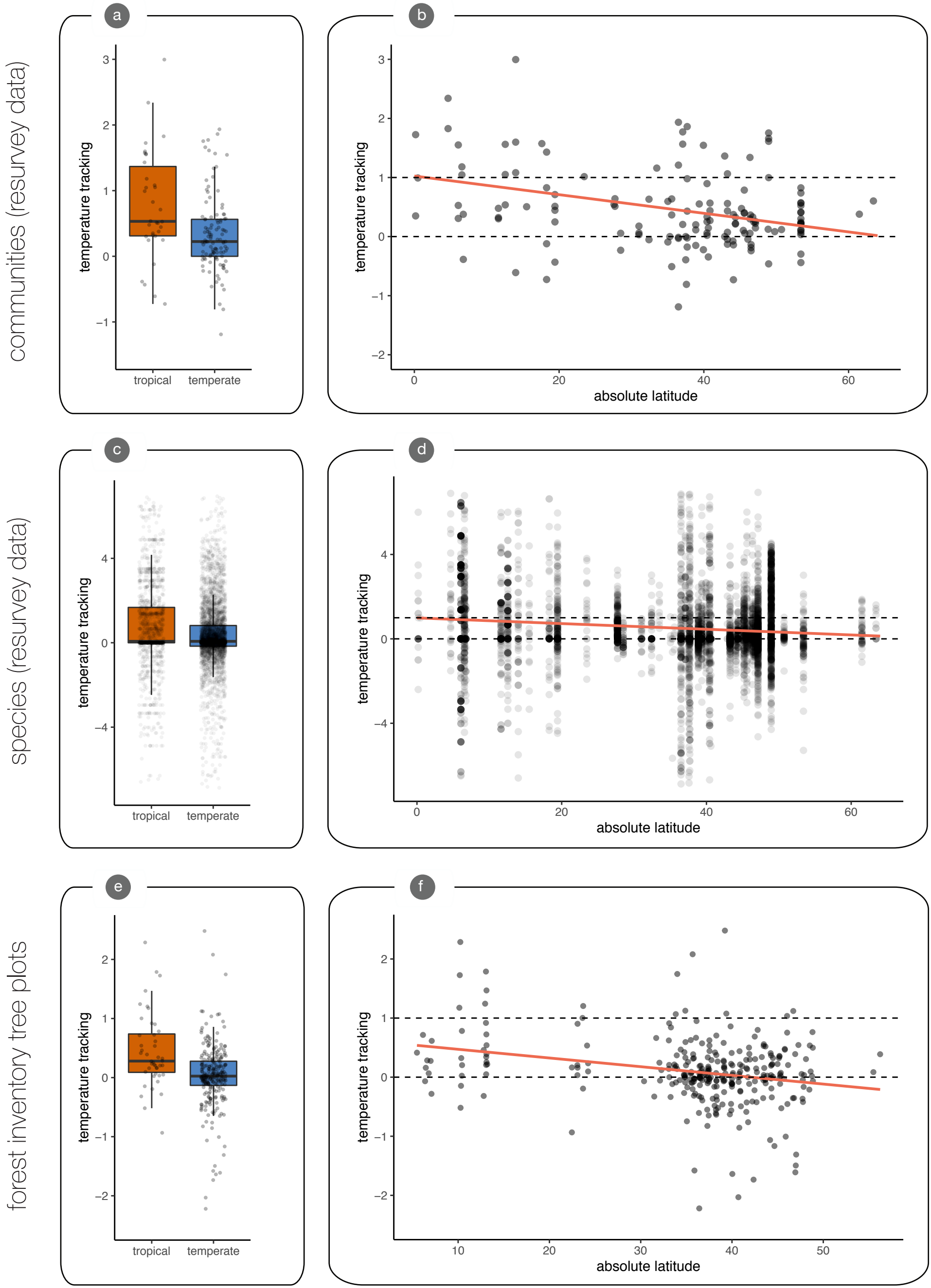
communities (resurvey data)
species (resurvey data)
forest inventory tree plots
a
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temperature tracking
tropical
temperate
absolute latitude