

1 **Montane species and communities track rising temperatures better in the tropics**

2

3 Benjamin G. Freeman^{1,2*}, Yiluan Song³, Kenneth J Feeley⁴, Kai Zhu³

4

5 ¹ Biodiversity Research Centre, University of British Columbia, Vancouver, BC, Canada

6 ² Department of Zoology, University of British Columbia, Vancouver, BC, Canada

7 ³ Department of Environmental Studies, University of California, Santa Cruz, CA USA

8 ⁴ Department of Biology, University of Miami, Coral Gables, FL 33156 USA

9

10

11 Abstract

12 Many species are responding to recent climate change by shifting their distributions
13 upslope to higher elevations, but the observed rates of shifts vary considerably among
14 studies. Here we test the hypothesis that latitudinal position in part explains this variation,
15 using two independent datasets—resurveys of species’ elevational ranges, and repeatedly
16 surveyed tree plots. We find that communities are shifting 18.6 m per decade upslope, but
17 these upslope shifts are slightly faster in the tropics (25.1 m per decade on average) than
18 the temperate zone (13.1 m per decade on average). Faster upslope shifts in the tropics
19 are surprising because rates of warming are faster in the temperate zone. Consequently,
20 tropical communities are tracking changing temperatures 2.5 times (resurvey dataset) and
21 10.0 times (tree plot dataset) more than their temperate counterparts. For the amount of
22 warming expected to lead to a 100 m upslope shift, tropical communities have shifted
23 upslope by an average of 81 m while temperate communities have shifted upslope by an
24 average of only 32 m. Similarly, for the amount of warming expected to lead to a 1 °C
25 increase in CTI, tropical tree plots have increased in CTI by an average of 0.44 °C while
26 temperate tree plots have increased by an average of only 0.044 °C. This latitudinal
27 gradient in responsiveness to recent warming suggests tropical montane biotas are
28 disproportionately sensitive to ongoing global warming.

29 Introduction

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

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

51 2019). It is unknown, however, whether these scattered reports are general across taxa
52 and continents.

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

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

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

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

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

101

102 Materials and methods

103

104 Resurvey data

105 Our aim was to compile a comprehensive list of studies that have measured recent range
106 shifts for species in mountainous regions in response to recent warming (within the past ~
107 100 years). First, we conducted a Web of Science search on 11 July 2019 with the
108 keywords “climate change” OR “global warming” AND “range shift” AND “mountain”
109 OR “elevation” OR “altitude*”. This search returned 1827 hits. We retained studies that
110 met the following three criteria: (1) they measured recent range shifts at species’ lower
111 elevation limits, mean (or optimum) elevations, or upper elevational limits; (2) range
112 shifts were reported for all species or the entire community, not just species with
113 significant range shifts; and (3) range shifts were measured over a time period of ≥ 10
114 years. Second, we located additional studies that met these three criteria by examining
115 recent papers synthesizing the range shift literature (Chen et al., 2011; Freeman, Lee-
116 Yaw, Sunday, & Hargreaves, 2018; Lenoir & Svenning, 2015; Rumpf, Hülber,
117 Zimmermann, & Dullinger, 2019; Wiens, 2016). There were three cases for which
118 multiple publications reported elevational range shifts for the same community using the

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

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

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

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

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

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

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

171

172 Forest Inventory Data

173 We compiled our forest inventory plot dataset using Forest Inventory and Analysis (FIA)
174 plots from the United States and previously published inventory plot data from Central
175 and South America (Feeley *et al.* 2013; Fadrique *et al.* 2018). We filtered for FIA plots
176 that were fully forested and have not received observable treatment, including cutting,
177 site preparation, artificial regeneration, natural regeneration, and other silvicultural
178 treatment (Smith 2002). We also filtered for FIA plots that have not experienced
179 disturbances in at least five years. Because we were interested in changes in just
180 mountain forests, we selected FIA plots that fell within mountainous areas using the
181 global mountains raster map derived from the 250 m global Hammond landforms product
182 (Karagulle *et al.* 2017). We included only FIA plots that had been surveyed at least twice.
183 We collected the species identity of all individual adult trees (diameter at breast height >
184 12.7 cm, or 5 inches) for each survey of each FIA plot. We then calculated the
185 community temperature index (CTI) of the plot as the average of optimal temperature of
186 each species weighted by basal area, following the method of Fadrique *et al.* (Fadrique *et*

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

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

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

211 For each plot, we calculated the rate of temperature change as the linear trend of
212 mean annual temperature over time, using monthly mean temperature estimates from
213 1980 to 2013 from the CHELSA time-series dataset (Karger & Zimmermann 2019). As
214 with the resurvey data, we calculated the thermal tracking score for each plot as the ratio
215 of observed changes (rate of change in thermophilization rate) and expected changes (rate
216 of change of mean annual temperature).

217 In order to focus on the response of organisms to the warming climate, we
218 selected plots with significant warming trends (plots with $p < 0.05$ in a regression of
219 mean temperature versus year). As FIA plots are generally smaller in size compared to
220 the plots in Central and South America (168 m² for FIA plots compared to 1-hectare for
221 most tropical plots), we aggregated FIA plots into 1 degree diameter hexagons that
222 contain approximately 30 plots each, averaging the thermophilization rate and
223 temperature tracking score weighted by total basal area. We removed hexagons with <5
224 plots from subsequent analysis. We examined the relationships between latitude and the
225 temperature tracking score by fitting linear mixed-effects models using the “nlme”
226 package in R (Pinheiro *et al.* 2017). We included both latitude (either the factor
227 “tropical/temperate”, or absolute latitude) and elevation as fixed effects. Due to the close
228 proximity of hexagons/plots and spatial dependence in the residuals of non-spatial linear
229 models, we modeled spatial random effects that follow Gaussian covariance functions,
230 and then evaluated the significance of regression coefficients for fixed effects using the
231 conditional standard error of regression coefficients.

232

233 Results

234 *Resurvey dataset*

235 Resurvey data show that tropical montane taxa are tracking temperature increases
236 “better” (i.e., have higher temperature tracking scores) than are temperate montane
237 species (Fig. 2a-2d, Fig. S3). Tropical communities had temperature tracking scores 2.5
238 times greater than temperate communities (Fig. 2a, Table S2; temperature tracking scores
239 for tropical and temperate communities = 0.81 ± 0.16 vs. 0.32 ± 0.077 , $p = 0.0058$;
240 estimates \pm standard errors from mixed-effects models), and tropical species had
241 temperature tracking scores 2.2 times greater than temperate species (Fig. 2c, Table S3;
242 temperature tracking scores for tropical and temperate species = 0.86 ± 0.18 vs. $0.40 \pm$
243 0.085 , $p = 0.018$).

244 Results were similar when we modeled temperature tracking from resurvey data
245 as a continuous function of position along the latitudinal gradient. Temperature tracking
246 scores decreased by an average of 0.15 ± 0.050 and 0.12 ± 0.054 per 10° increase in
247 latitude for communities and species, respectively (Figs. 2b and 2d, Tables S4 and S5).
248 For resurvey data, estimates from linear mixed models are that communities at the
249 equator have a tracking score of 0.97 ± 0.21 but 0.32 ± 0.077 at 45° latitude (averaged
250 over levels of fixed effects; the equivalent values for the species-level model are $0.94 \pm$
251 0.23 and 0.39 ± 0.88). Hence, tropical communities and species are closely tracking
252 temperature changes while temperate zone communities and species are not, though the
253 explanatory power of community models was much greater (marginal R^2 values from
254 linear mixed-effects models = 0.10 and 0.0091 respectively).

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

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

270

271 *Forest inventory dataset*

272 Tropical montane trees are also tracking temperature increases better than temperate
273 montane trees (Fig. 2e and 2f, Fig S6, Tables S16-S17). Tropical montane forest plots
274 had higher temperature tracking scores (0.44 ± 0.11) than temperate montane forest plots
275 (0.044 ± 0.044 ; $p = 0.00099$; Table S16). Latitude is a strong predictor in the linear mixed
276 model: a 10° increase in latitude corresponds to a 0.13 ± 0.039 decrease in the
277 temperature tracking score (Table S17). The model-based estimate is that tree plots have

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

281 The greater temperature tracking in tropical inventory plots was due to faster
282 changes in CTI in the tropics, also known as the thermophilization rate. Tropical plots
283 had thermophilization rates of 0.095 ± 0.020 °C per decade vs. 0.017 ± 0.012 °C per
284 decade for temperate plots (Fig. S6). Thus, while the rate of warming was faster at high
285 latitudes in our dataset-- 0.31 ± 0.0065 °C per decade for temperate plots vs. 0.22 ± 0.010
286 °C per decade for tropical plots (Fig. S6), there were still greater absolute responses to
287 recent warming in the tropics.

288

289 Discussion

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

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

301 6.1 m per decade reported nearly two decades ago (Parmesan & Yohe 2003). Hence, as
302 temperatures continue to warm and more resurvey datasets are published (e.g. 83
303 communities in the present study versus 30 in the Chen et al. 2011 study), estimated rates
304 of upslope shift continue to increase, counter to the more common pattern wherein effect
305 sizes tend to decline over time (Camerer *et al.* 2018). Further, we find evidence that rates
306 of upslope shift depend in part on latitude, with average upslope shifts for communities
307 of 25.1 m per decade in the tropics but only 13.1 m per decade in the temperate zone,
308 though this difference is marginally significant.

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

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

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

328 Latitude is a much better predictor of temperature tracking when considering
329 communities (a set of species aggregated together) than for individual species. Individual
330 species show a wide variation in their temperature tracking scores (Freeman et al., 2018;
331 Moritz et al., 2008; Rumpf et al., 2019). While latitude is a statistically significant
332 predictor of temperature tracking in the species-level model, its explanatory power is low.
333 Combined, these results imply that despite a clear latitudinal pattern of temperature
334 tracking for communities, we still have only a limited ability to predict changes in
335 individual species' elevational distributions associated with warming temperatures
336 (Angert *et al.* 2011). Range shifts at the species-level may be more predictable in the
337 marine realm, where most species appear to closely track temperature (Lenoir et al.,
338 2020; Pinsky, Eikeset, McCauley, Payne, & Sunday, 2019).

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

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

351 Several limitations of our study deserve explicit mention. First, we followed
352 previous analyses in calculating temperature tracking scores based on mean annual
353 temperature (Chen *et al.*, 2011). Analyses that incorporate temperature variability (i.e.,
354 seasonality) and other climatic variables have also proven powerful (Crimmins *et al.*
355 2011; Tingley *et al.* 2012), but are inherently more difficult to implement and interpret.
356 Second, our analyses do not take into account variation in microclimate, which may be a
357 strong driver of range shifts or the lack thereof (Lembrechts *et al.* 2019; Zellweger *et al.*
358 2020). It is not clear how microclimate availability varies along a latitudinal gradient, but
359 a greater availability of microclimates and climate refugia in the temperate zone than the
360 tropics is an alternative explanation for our results. We were similarly unable to analyze
361 climatic factors that occur at intermediate spatial scales along mountain slopes, such as
362 cold-air pooling (Curtis *et al.* 2014). Third, future studies should address landscape-level
363 changes due to habitat loss or other disturbances (Larsen 2012; Lenoir & Svenning 2015;
364 Campos-Cerqueira *et al.* 2017; Guo *et al.* 2018). The resurveys and forest plots in our
365 dataset took place in landscapes that have not undergone intensive deforestation or other
366 land-use change. Given that highly modified landscapes predominate across most of the
367 globe, further tests of the interactions between landscape change and climate change are
368 needed. Fourth, the patterns we document are not without exceptions. For example,
369 Puerto Rican frogs and birds are not closely tracking temperature despite their tropical

370 latitude (Campos-Cerqueira & Mitchell Aide 2017; Campos-Cerqueira *et al.* 2017),
371 though this could potentially reflect increasing forest cover on this island (Battey *et al.*
372 2019). Conversely, some temperate zone communities are closely tracking recent
373 warming (Kelly & Goulden 2008; Menéndez *et al.* 2014).

374

375 *Conclusions*

376 The latitudinal gradient in temperature tracking we document has multiple implications
377 for the conservation of montane floras and faunas. The weak temperature tracking of
378 temperate montane species and communities indicates that acclimation and adaptation,
379 rather than elevational shifts, will likely be key processes in determining if temperate
380 montane species can persist in the face of continued warming. It is an open question
381 whether adaptation and acclimation will be able to keep pace with rates of warming that
382 are unprecedented in recent evolutionary time (Visser 2008; Feeley *et al.* 2012). In
383 contrast, the strong temperature tracking of tropical montane species indicates that they
384 may be able to persist despite warming temperatures by shifting their distributions
385 upslope, at least when protected elevational corridors provide suitable habitats at higher
386 elevations. On the other hand, this implies that the “escalator to extinction”—wherein
387 montane species respond to warming temperatures by shifting upslope until they run out
388 of available habitat on mountaintops (Freeman, Scholer, Ruiz-Gutierrez, & Fitzpatrick,
389 2018)—runs faster in the tropics. Notably, such mountaintop extinctions may occur well
390 below the actual mountaintop, as pervasive anthropogenic modifications of high-
391 elevation tropical systems effectively limit the ability of the tree line to shift upslope
392 (Rehm & Feeley 2015). Indeed, local extinctions and range contractions associated with

393 recent warming appear to be most common in tropical montane species (Freeman et al.,
394 2018; Wiens, 2016).

395 The sixth mass extinction in Earth's history is now underway (Ceballos *et al.*
396 2017). The tropics have the highest species diversity of any biome, and tropical
397 mountains have the highest diversity of all (Rahbek *et al.* 2019). The relatively small
398 temperature changes in the tropics should minimize the impact of climate change, but the
399 disproportionately sensitive responses of tropical montane species have instead placed
400 this whole biota on an escalator to extinction. The degree to which predictions of
401 widespread species extinctions in tropical mountains (Sekercioglu *et al.* 2008) come true
402 will depend on our ability to protect elevational corridors that enable species to persist
403 while shifting upslope (Feeley & Rehm 2012), and, ultimately, on whether humanity is
404 able to slow global warming.

405

406 Acknowledgements

407 We thank the many scientists who have published resurvey data and measured forest
408 inventory plots. The Feeley lab, Schluter lab, R. Yorque, J. Lembrechts and two
409 anonymous reviewers provided useful comments that improved this manuscript. BGF
410 was supported from postdoctoral fellowships from Banting Canada (379958), and the
411 Biodiversity Research Centre, and YS was supported by a Regents' fellowship from the
412 University of California, Santa Cruz. KZ and KJF are supported by the US National
413 Science Foundation (NSF grants DEB 1926438 to KZ and DEB-1350125 to KJF).

414

415

416 References

- 417 Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J. & Chunco, A.J.
418 (2011). Do species' traits predict recent shifts at expanding range edges? *Ecol. Lett.*,
419 14, 677–689.
- 420 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). lme4: Linear mixed-effects
421 models using Eigen and S4.
- 422 Battey, C.J., Otero, L.M., Gorman, G.C., Hertz, P.E., Lister, B.C., García, A., *et al.*
423 (2019). Why Montane Anolis Lizards are Moving Downhill While Puerto Rico
424 Warms. *bioRxiv*, 751941.
- 425 Camerer, C.F., Dreber, A., Holzmeister, F., Ho, T.H., Huber, J., Johannesson, M., *et al.*
426 (2018). Evaluating the replicability of social science experiments in Nature and
427 Science between 2010 and 2015. *Nat. Hum. Behav.*, 2, 637–644.
- 428 Campos-Cerqueira, M., Arendt, W.J., Wunderle, J.M. & Aide, T.M. (2017). Have bird
429 distributions shifted along an elevational gradient on a tropical mountain? *Ecol.*
430 *Evol.*, 7, 9914–9924.
- 431 Campos-Cerqueira, M. & Mitchell Aide, T. (2017). Lowland extirpation of anuran
432 populations on a tropical mountain. *PeerJ*, 2017.
- 433 Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017). Biological annihilation via the ongoing
434 sixth mass extinction signaled by vertebrate population losses and declines. *Proc.*
435 *Natl. Acad. Sci. U. S. A.*, 114, E6089–E6096.
- 436 Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011). Rapid range
437 shifts of species associated with high levels of climate warming. *Science*, 333,
438 1024–1026.

- 439 Chen, I.C., Shiu, H.J., Benedick, S., Holloway, J.D., Chey, V.K., Barlow, H.S., *et al.*
440 (2009). Elevation increases in moth assemblages over 42 years on a tropical
441 mountain. *Proc. Natl. Acad. Sci.*, 106, 1479–1483.
- 442 Crimmins, S., Dobrowski, S., Greenberg, J., Abatzoglou, J. & Mynsberge, A. (2011).
443 Changes in climatic water balance drive downhill shifts in plant species' optimum
444 elevations. *Science*, 331, 324–327.
- 445 Curtis, J.A., Flint, L.E., Flint, A.L., Lundquist, J.D., Hudgens, B., Boydston, E.E., *et al.*
446 (2014). Incorporating cold-air pooling into downscaled climate models increases
447 potential refugia for snow-dependent species within the Sierra Nevada Ecoregion,
448 CA. *PLoS One*, 9.
- 449 DeLuca, W. V. & King, D.I. (2017). Montane birds shift downslope despite recent
450 warming in the northern Appalachian Mountains. *J. Ornithol.*, 158, 493–505.
- 451 Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak,
452 D.C., *et al.* (2008). Impacts of climate warming on terrestrial ectotherms across
453 latitude. *Proc. Natl. Acad. Sci.*, 105, 6668–6672.
- 454 Fadrique, B., Báez, S., Duque, Á., Malizia, A., Blundo, C., Carilla, J., *et al.* (2018).
455 Widespread but heterogeneous responses of Andean forests to climate change.
456 *Nature*, 564, 207–212.
- 457 Feeley, K.J., Hurtado, J., Saatchi, S., Silman, M.R. & Clark, D.B. (2013). Compositional
458 shifts in Costa Rican forests due to climate-driven species migrations. *Glob. Chang.*
459 *Biol.*, 19, 3472–3480.
- 460 Feeley, K.J. & Rehm, E.M. (2012). Amazon's vulnerability to climate change heightened
461 by deforestation and man-made dispersal barriers. *Glob. Chang. Biol.*, 18, 3606–

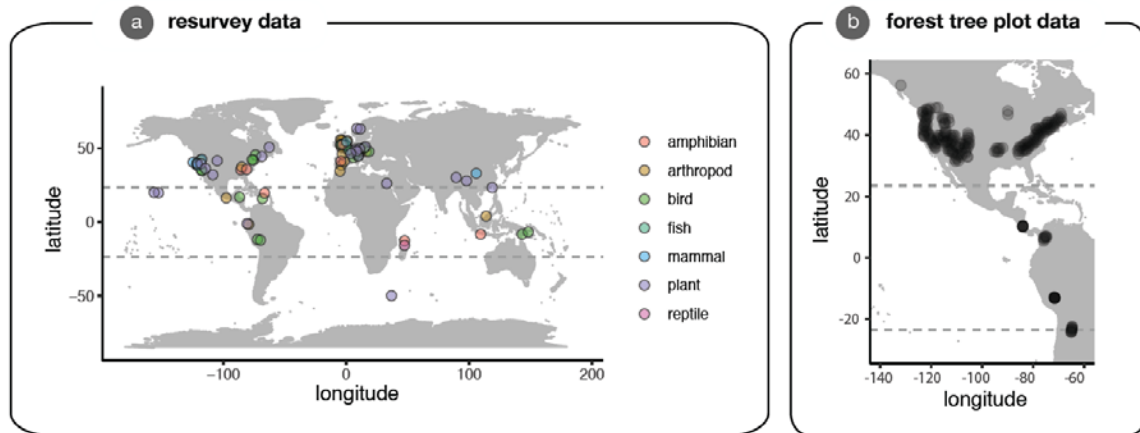
- 462 3614.
- 463 Feeley, K.J., Rehm, E.M. & Machovina, B. (2012). The responses of tropical forest
464 species to global climate change: acclimate, adapt, migrate, or go extinct? *Front.*
465 *Biogeogr.*, 4, 69–84.
- 466 Feeley, K.J., Stroud, J.T. & Perez, T.M. (2017). Most ‘global’ reviews of species’
467 responses to climate change are not truly global. *Divers. Distrib.*, 23, 231–234.
- 468 Freeman, B.G. & Class Freeman, A.M. (2014). Rapid upslope shifts in New Guinean
469 birds illustrate strong distributional responses of tropical montane species to global
470 warming. *Proc. Natl. Acad. Sci.*, 111, 4490–4494.
- 471 Freeman, B.G., Lee-Yaw, J.A., Sunday, J.M. & Hargreaves, A.L. (2018a). Expanding,
472 shifting and shrinking: The impact of global warming on species’ elevational
473 distributions. *Glob. Ecol. Biogeogr.*, 27, 1268–1276.
- 474 Freeman, B.G., Scholer, M.N., Ruiz-Gutierrez, V. & Fitzpatrick, J.W. (2018b). Climate
475 change causes upslope shifts and mountaintop extirpations in a tropical bird
476 community. *Proc. Natl. Acad. Sci. U. S. A.*, 115, 11982–11987.
- 477 Guo, F., Lenoir, J. & Bonebrake, T.C. (2018). Land-use change interacts with climate to
478 determine elevational species redistribution. *Nat. Commun.*, 9, 1-7.
- 479 Harris, I., Jones, P.D., Osborn, T.J. & Lister, D.H. (2013). Updated high-resolution grids
480 of monthly climatic observations—the CRU TS3. 10 Dataset. *Int. J. Climatol.*, 34,
481 623-642.
- 482 Karagulle, D., Frye, C., Sayre, R., Breyer, S., Aniello, P., Vaughan, R., *et al.* (2017).
483 Modeling global Hammond landform regions from 250-m elevation data. *Trans.*
484 *GIS*, 21, 1040–1060.

- 485 Karger, D.N. & Zimmermann, N.E. (2019). Climatologies at High resolution for the
486 Earth Land Surface Areas CHELSA V1 . 2: Technical specification. *Sci. Data*, 4,
487 170122.
- 488 Kelly, A.E. & Goulden, M.L. (2008). Rapid shifts in plant distribution with recent
489 climate change. *Proc. Natl. Acad. Sci.*, 105, 11823–11826.
- 490 Kusrini, M.D., Lubis, M.I., Endarwin, W., Yazid, M., Darmawan, B., Ul-Hasanah, A.U.,
491 *et al.* (2017). Elevation range shift after 40 years: The amphibians of Mount Gede
492 Pangrango National Park revisited. *Biol. Conserv.*, 206, 75–84.
- 493 Larsen, T.H. (2012). Upslope range shifts of Andean dung beetles in response to
494 deforestation: compounding and confounding effects of microclimatic change.
495 *Biotropica*, 44, 82–89.
- 496 Laurance, W.F., Carolina Useche, D., Shoo, L.P., Herzog, S.K., Kessler, M., Escobar, F.,
497 *et al.* (2011). Global warming, elevational ranges and the vulnerability of tropical
498 biota. *Biol. Conserv.*, 144, 548–557.
- 499 Lembrechts, J.J., Nijs, I. & Lenoir, J. (2019). Incorporating microclimate into species
500 distribution models. *Ecography*, 42, 1267–1279.
- 501 Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., *et al.* (2020).
502 Species better track climate warming in the oceans than on land. *Nature Ecol. &*
503 *Evol.*, 1-16.
- 504 Lenoir, J., Gegout, J.C., Marquet, P.A., De Ruffray, P. & Brisse, H. (2008). A significant
505 upward shift in plant species optimum elevation during the 20th century. *Science*,
506 320, 1768–1771.
- 507 Lenoir, J. & Svenning, J.C. (2015). Climate-related range shifts - a global

- 508 multidimensional synthesis and new research directions. *Ecography*, 38, 15–28.
- 509 Menéndez, R., González-Megías, A., Jay-Robert, P. & Marquéz-Ferrando, R. (2014).
- 510 Climate change and elevational range shifts: evidence from dung beetles in two
- 511 European mountain ranges. *Glob. Ecol. Biogeogr.*, 23, 646–657.
- 512 Moret, P., Aráuz, M. de los Á., Gobbi, M. & Barragán, Á. (2016). Climate warming
- 513 effects in the tropical Andes: first evidence for upslope shifts of Carabidae
- 514 (Coleoptera) in Ecuador. *Insect Conserv. Divers.*, 9, 342–350.
- 515 Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C. & Beissinger, S.R. (2008).
- 516 Impact of a century of climate change on small-mammal communities in Yosemite
- 517 National Park, USA. *Science*, 322, 261–264.
- 518 Moskwik, M. (2014). Recent elevational range expansions in plethodontid salamanders
- 519 (Amphibia: Plethodontidae) in the southern appalachian mountains. *J. Biogeogr.*, 41,
- 520 1957–1966.
- 521 Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change
- 522 impacts across natural systems. *Nature*, 421, 37–42.
- 523 Perez, T.M., Stroud, J.T. & Feeley, K.J. (2016). Thermal trouble in the tropics. *Science*,
- 524 351, 1392–1393.
- 525 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., *et al.*
- 526 (2017). *Nlme: Linear and Nonlinear Mixed Effects Models*, version 3(1).
- 527 Pinsky, M.L., Eikeset, A.M., McCauley, D.J., Payne, J.L. & Sunday, J.M. (2019). Greater
- 528 vulnerability to warming of marine versus terrestrial ectotherms. *Nature*, 569, 108–
- 529 111.
- 530 R Development Core Team. (2020). *R: A language and environment for statistical*

- 531 computing.
- 532 Rahbek, C., Borregaard, M.K., Antonelli, A., Colwell, R.K., Holt, B.G., Nogues-Bravo,
533 D., *et al.* (2019). Building mountain biodiversity: Geological and evolutionary
534 processes. *Science*, 365, 1114–1119.
- 535 Rehm, E.M. & Feeley, K.J. (2015). The inability of tropical cloud forest species to invade
536 grasslands above treeline during climate change: Potential explanations and
537 consequences. *Ecography*, 38, 1167–1175.
- 538 Rohatgi, A. (2017). WebPlotDigitizer 3.11.
- 539 Rumpf, S.B., Hülber, K., Klöner, G., Moser, D., Schütz, M., Wessely, J., *et al.* (2018).
540 Range dynamics of mountain plants decrease with elevation. *Proc. Natl. Acad. Sci.*,
541 201713936.
- 542 Rumpf, S.B., Hülber, K., Zimmermann, N.E. & Dullinger, S. (2019). Elevational rear
543 edges shifted at least as much as leading edges over the last century. *Glob. Ecol.*
544 *Biogeogr.*, 28, 533–543.
- 545 Sekercioglu, C.H., Schneider, S.H., Fay, J.P. & Loarie, S.R. (2008). Climate change,
546 elevational range shifts, and bird extinctions. *Conserv. Biol.*, 22, 140–150.
- 547 Sheldon, K.S. (2019). Climate Change in the Tropics: Ecological and Evolutionary
548 Responses at Low Latitudes. *Annu. Rev. Ecol. Evol. Syst.*, 50, 303–333.
- 549 Smith, W.B. (2002). Forest inventory and analysis: A national inventory and monitoring
550 program. *Environ. Pollut.*, 116, 233–242.
- 551 Socolar, J.B., Epanchin, P.N., Beissinger, S.R. & Tingley, M.W. (2017). Phenological
552 shifts conserve thermal niches in North American birds and reshape expectations for
553 climate-driven range shifts. *Proc. Natl. Acad. Sci.*, 201705897.

- 554 Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2012). Thermal tolerance and the global
555 redistribution of animals. *Nat. Clim. Chang.*, 2, 686–690.
- 556 Tingley, M.W., Koo, M.S., Moritz, C., Rush, A.C. & Beissinger, S.R. (2012). The push
557 and pull of climate change causes heterogeneous shifts in avian elevational ranges.
558 *Glob. Chang. Biol.*, 18, 3279–3290.
- 559 Visser, M.E. (2008). Keeping up with a warming world; assessing the rate of adaptation
560 to climate change. *Proc. R. Soc. B Biol. Sci.*, 275, 649.
- 561 Wiens, J.J. (2016). Climate-Related Local Extinctions Are Already Widespread among
562 Plant and Animal Species. *PLoS Biol.*, 14, 1–18.
- 563 Wu, C., Holloway, J.D., Hill, J.K., Ho, C., Thomas, C.D. & Chen, I. (2019). Reduced
564 body sizes in climate-impacted Borneo moth assemblages are primarily explained by
565 range shifts. *Nat. Commun.*, 1–7.
- 566 Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-
567 römermann, M., *et al.* (2020). Forest microclimate dynamics drive plant responses to
568 warming. *Science*, 368, 772–775.
- 569 Zuckerberg, B., Woods, A.M. & Porter, W.F. (2009). Poleward shifts in breeding bird
570 distributions in New York State. *Glob. Chang. Biol.*, 15, 1866–1883.
- 571
- 572



573

574

Figure 1. Maps of resurvey studies that measured elevational shifts associated with

575

recent warming (a) and of forest inventory tree plots that have been repeatedly censused

576

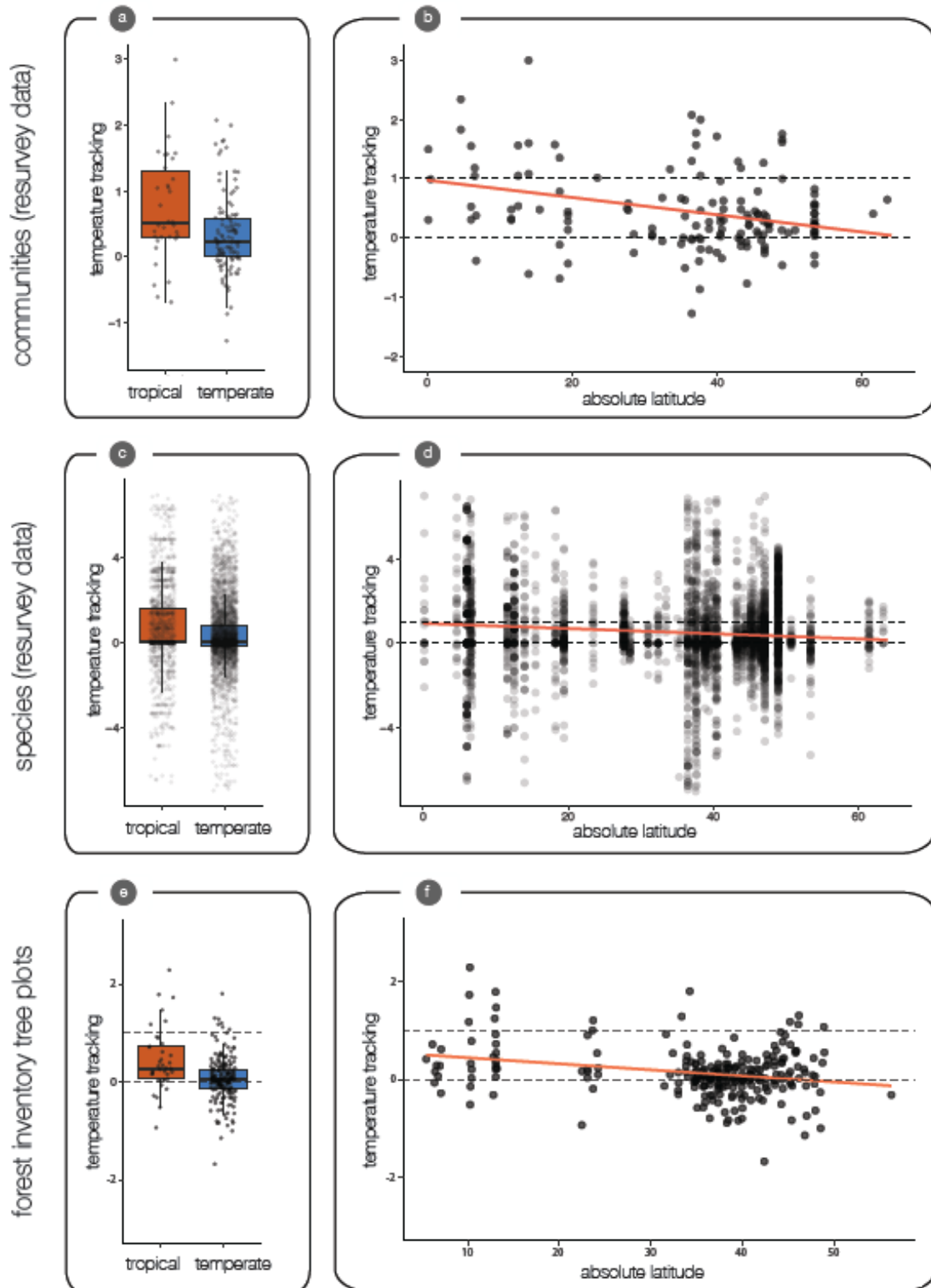
(b). Locations of resurvey studies are jittered slightly to improve clarity. The Tropics of

577

Cancer and Capricorn (at 23.4° N and S, respectively) delimit the tropics, and are

578

illustrated with dashed lines.

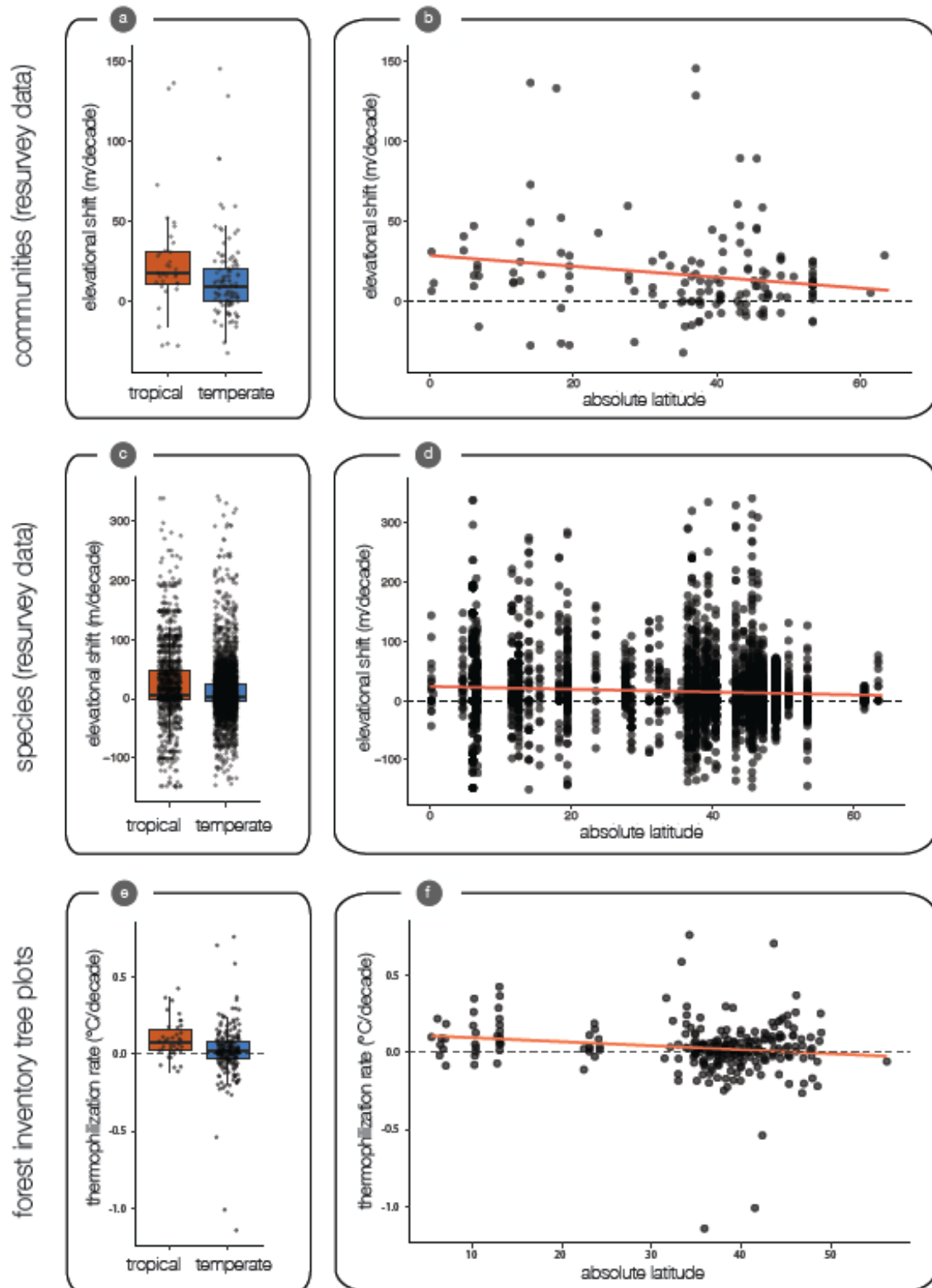


579

580 **Figure 2.** Tropical communities, species, and forest inventory tree plots have higher

581 temperature tracking scores than their temperate zone counterparts. Raw data are shown

582 as points. Dashed lines illustrate both perfect temperature tracking (temperature tracking
583 = 1) and zero temperature tracking despite warming temperatures (temperature tracking =
584 0). Trendlines illustrate predictions from mixed models. (a) temperature tracking for
585 communities in tropical and temperate zones; (b) relationship between temperature
586 tracking and absolute latitude ($^{\circ}$) for communities; (c) temperature tracking for species in
587 tropical and temperate zones (~ 0.5% of data has been removed for visualization); (d)
588 relationship between temperature tracking and absolute latitude ($^{\circ}$) for species; (e)
589 temperature tracking for forest inventory tree plots in tropical and temperate zones; (f)
590 relationship between temperature tracking and absolute latitude ($^{\circ}$) for forest inventory
591 tree plots.



592

593 **Figure 3.** Tropical communities and species have undertaken larger upslope shifts, and

594 forest inventory tree plots greater thermophilization, than their temperate zone

595 counterparts. Raw data are shown as points. Trendlines illustrate predictions from mixed
596 models. (a) elevational shifts for communities in tropical and temperate zones; (b)
597 relationship between elevational shifts and absolute latitude ($^{\circ}$) for communities; (c)
598 elevational shifts for species in tropical and temperate zones (~ 0.5% of data has been
599 removed for visualization); (d) relationship between elevational shifts and absolute
600 latitude ($^{\circ}$) for species; (e) thermophilization rate for forest inventory tree plots in tropical
601 and temperate zones; (f) relationship between thermophilization rate and absolute latitude
602 ($^{\circ}$) for forest inventory tree plots.