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**Climate velocities and lagged species elevational shifts in mountain ranges**

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Abstract

Mountain ranges support concentrations of climate-endangered endemic species, and are potential refugia for species retreating from the lowlands under anthropogenic climate change. Predicting the outcome for biodiversity requires knowledge of whether species are shifting uphill at the same rate as temperature isotherms (i.e. whether they are successfully tracking the velocity of climatic changes). Here, we provide a global assessment of the velocity of climate change in mountain ranges: applying thermal dynamic theory, deriving moist adiabatic lapse rates (MALR) using local surface temperature and water vapor. MALR varied substantially around the world, from 3 to 9°C cooling per km elevation increase. Consider the rate of terrestrial surface warming from 1971 to 2015, 24 regions can be identified as exhibiting high velocities where the isotherms have shifted more than one standard deviation of the global mean value (> 8.45 m yr⁻¹). High velocities are typically found in relatively dry parts of the world, but also occur in wet regions with low lapse rates, such as in Northern Sumatra, Western Guiana Shield, Northern Andes, Costa Rica, Nepal, and Madagascar. Analysis of biodiversity data in relation to mountain-specific velocities revealed more cases of tracking between species and isotherms than previously suggested and more likely occurred at lower climate velocity. Nevertheless, upslope migrations of montane species have generally been lagging behind climate velocity. Such lags could continue to effect change even if the climate were to stabilize immediately. Reducing emissions would be expected to minimize lags, as well as slow the velocities of warming and required responses everywhere.
Main text

Mountainous regions represent 25% of the Earth’s land surface but harbor disproportionately rich biodiversity, due in part to their steep climatic gradients and complex topography\textsuperscript{3,4}. Thus, assessing the responses of montane biotas to anthropogenic climate change is particularly important for species conservation.

Uphill movements of species towards cooler climates have been widely observed around the globe\textsuperscript{2,5-9} yet whether species are keeping pace with shifting climates remains unclear. The sparsity of meteorological stations in many mountain ranges\textsuperscript{10}, combined with the climatic heterogeneity of complex topographies, make it difficult to determine the ‘expected’ responses of species if they were track climatic changes precisely. The simplest approach, which we adopt here, is to quantify the magnitude of climate isotherm shifts (i.e. the velocity of climate change) in each mountain range, and then estimate differences between observed range changes and isotherm shifts\textsuperscript{1,9,11-15}. We find that uphill movements are generally lagging behind climates and species have no opportunity to track climate effectively unless the velocity is low.

The velocity of thermal isotherm shifts (in km of elevation yr\textsuperscript{−1}) can be derived by dividing the temperature lapse rate (temperature decrease while ascending altitude, in °C km\textsuperscript{−1}) by the surface temperature change (in °C yr\textsuperscript{−1}). However, lapse rates (i.e. 5.5°C km\textsuperscript{−1} in the tropics or 6.5°C km\textsuperscript{−1} elsewhere) that are widely-applied have been inferred from limited ground observations\textsuperscript{2,8}. Actual thermal lapse rates can vary substantially in different regions and this has not been explicitly considered in ecological research. Temperature lapse rate is the decrease of temperature with increasing altitude. The pressure of the air decreases when a parcel of air molecules rises and expands with negligible heat transfer conduction and radiation from outside, which costs internal energy, cooling the parcel. The consequent rate of cooling is referred as adiabatic lapse rate (“adiabatic” meaning that no external source of energy
was involved, and the value often used is 9.8°C km$^{-1}$. However, if the air condenses moisture as it cools, it gains some heat of condensation, which slows the rate of cooling. Thus, realized or “moist adiabatic” lapse rates (MALR) are often lower (e.g. 6.5°C km$^{-1}$) than the adiabatic lapse rate. As a consequence, temperature lapse rates are determined by water vapor changes and latent heat release, which are linked to surface temperature, elevation and moisture content in the region of interest$^{16}$.

Importantly, the limited data available indicates that temperature lapse rates differ between regions and seasons$^{16,17}$. For example, lapse rates range from 4.1°C km$^{-1}$ to 6.8°C km$^{-1}$ for different times and seasons along the slopes of the central Himalayas$^{18}$. In the Washington Cascades mountains in North America, the values of lapse rates vary from 2.5 km$^{-1}$ to 7.5°C km$^{-1}$ in late summer and spring$^{19}$.

Nonetheless, the mechanisms underlying temperature lapse rate are well established in thermodynamic theory, with MALR being a function of local temperature and vapor pressure$^{20}$. Here, we use this knowledge to assess the velocity of mountain climate changes on a global scale, and then evaluate whether species are keeping pace with shifting isotherms. Mountain areas were represented by grids with 0.5° resolution of mean elevation above 1,000 m$^{21}$ (Figs. 1,2). The velocity is represented by the vertical isotherm shifts (i.e. how far an isothermal line rises from the surface), calculated by dividing the rate of warming in each mountain grid by its MALR, derived from terrain-surface conditions. We estimate MALR (usually noted as $\Gamma_w$) as:

$$\Gamma_w = g \frac{1 + \frac{H_v \gamma}{R_{sd} T}}{C_{pd} + \frac{H_v^2 \gamma \varepsilon}{R_{sd} T^2}}$$

where $\gamma$ is the mixing ratio of the mass of water vapor per unit mass of dry air, which is also influenced by air pressure; $T$ represents the air temperature (other parameters are constants; see Methods). We use mean annual temperature and water vapor
pressure at terrain surface from 2011 to 2015 from CRU TS 3.24 to calculate MALR and consider the rate of warming from 1971 to 2015 for each mountain grid. The MALR formula predicts that higher surface temperature or water vapor leads to curvilinear decreases in MALR (Fig. 1a). Given the widely varied temperature and water vapor differences between mountain grids (Fig. 1 b,c), our estimates show that temperature lapse rates of global mountains vary from 3 to 9°C km$^{-1}$ (Fig 1d).

Given these MALR estimates and the rates of surface temperature change (Fig. 2 a,b), the climate velocities in global mountains vary considerably from -16.67 m yr$^{-1}$ (Saltillo, Mexico) to +16.80 m yr$^{-1}$ (Mashhad, Iran), with global average elevational isotherm increases of +5.42 ± 0.03 m yr$^{-1}$ in mountain ranges (Fig. 2c; Extended Data Fig. 1). We identify high climate-velocity mountains where the isotherms have shifted more than one standard deviation of the global mean value (higher than 8.45 m yr$^{-1}$) (Fig. 2d). Defined in this way, about 16% of mountainous areas are exposed to high climate velocity and many are well-recognized biodiversity hotspots, such as Northern Sumatra, Hengduan, Nepal, Southern Ghats, Madagascar, Mediterranean basin, Northern Sahara, Brazilian Highlands, Northern Andes, Costa Rica, and Western America and Mexico (Supplementary Table 1). Other high velocity mountains may also be of concern, including most of the Middle East mountains (which includes endemics) and central Asia, Siberia, and the Alaska-Yukon region (Supplementary Table 1). The approach delineates that high climate velocity can be due to high rates of temperature warming or to low lapse rates. It is intuitive that higher warming rate results in high climate velocity (Extended Data Fig. 2a) and this is often observed in drier regions with low mean annual precipitation (MAP), possibly due to the limited heat capacity of arid regions$^{22-24}$ (Supplementary Table 1). Yet, high climate velocities are also observed in mountain ranges that have relatively modest levels of warming but low lapse rates, which can occur at areas with high water
vapour pressure and/or high surface temperatures (Extended Data Fig. 2b, and Supplementary Table 1). Many of these areas coincide with wet climates (high MAP), such as in Northern Sumatra, Western Guiana Shield, Northern Andes Mts, Costa Rica, and Nepal (Extended Data Fig. 2b, and Supplementary Table 1). Mountain climate velocities emerge from the interactions of lapse rates and water vapor pressure, interacting with mountain topographies and levels of regional warming.

We also applied our framework to mountains on islands that harbor a high proportion of endemic species and provide refuges for shifting species otherwise constrained by the ocean\textsuperscript{25,26}. We define islands as landmasses that are smaller than Australia and surrounded by water\textsuperscript{21}. We examined the velocity of climate change in island mountains globally (only 14 islands have mountain grid cells higher than 1,000 m, based on our dataset) and found a mean shift of 3.35 m yr\textsuperscript{-1}, which was lower than the global average (5.42 m yr\textsuperscript{-1}). Two island regions—Madagascar and Japan—were found to have high climate velocity (>8.45 m yr\textsuperscript{-1}) (Fig. 3a-c). In Japan, high climate velocity is mainly caused by the surface temperature warming (Fig. 2b, Supplementary Table 1) but, interestingly, Madagascar is not adjacent to ocean with particularly high levels sea surface warming\textsuperscript{27} (Fig. 2b, Supplementary Table 1); for Madagascar, high water vapour levels generate a low lapse rate, and hence the high climate velocity (Supplementary Table 1). High climate velocity in these islands may lead to considerable biodiversity loss, which illustrates the importance of developing climate adaptation strategies\textsuperscript{28}.

Growing evidence shows that the rate of warming varies with elevation\textsuperscript{10}. The sparse long-term meteorological stations in mountain areas have hampered a global test of elevation dependent warming\textsuperscript{29}. Our study reveals a complex pattern of elevation-dependent climate velocity (Fig. 3d-f and Extended Data Fig. 3).
Accelerated climate velocity with elevation can be observed in the low latitudes (ca. 10°N/S) but high velocity occurs mostly at low elevation near the equator and at 30-40°N, 60-70°N and 20-30°S, in line with the projections of the IPCC Fifth Assessment Report. These complex patterns support the call for greater understanding of the patterns and causes of elevation-dependent warming.

Since factors such as whether the slopes face the sun may have a major impact on the mountain climate, we further explored how the topography of the mountains, including the aspect and orientation of the mountains, affects climate velocity. We investigate how mountain climate velocities differ among different aspects and orientations. Apart from commonly known North-South and East-West orientations, we further defined two categories: mountains facing east and equator are called East-Equator mountains; facing west and equator, West-Equator mountains (Extended Data Fig. 4a). We found that climate velocities are higher in East-facing and West-facing slopes than other slopes ($\chi^2 = 11.06$, $p = 0.011$, d.f. = 3) (Extended Data Fig. 4b), which are associated with the higher water vapor in these aspects of slopes than the others ($\chi^2 = 687.76$, $p<0.001$, d.f. = 3) (Extended Data Fig. 4c) even though the warming rates were lower than the other slopes ($\chi^2 = 267.62$, $p<0.001$, d.f. = 3) (Extended Data Fig. 4d). Regarding the orientation, climate velocities are significantly higher in East-Equator (orientations illustrated in Extended Data Fig. 4) and North-South mountains than mountain ranges of other orientations ($\chi^2 = 765.72$, $p<0.001$, d.f. = 3) (Extended Data Fig. 4e). Water vapor values are significantly higher in East-Equator mountains ($\chi^2 = 521.72$, $p<0.001$, d.f. = 3, Extended Data Fig. 4f) but surface temperature changes are significantly higher in North-South mountains, compared to East-West and West-Equator mountains (E-W: $z = -9.05$, $p<0.001$; W-Equator: $z = -7.98$, $p<0.001$) (Extended Data Fig. 4g). This observation is generally
consistent in mountain orientations of different aspects (Extended Data Fig. 5).

Our study provides estimates of the rates of elevational shifts required by species and whether they tracked (kept pace with) temperature changes precisely or lagged behind. We compared these rate estimates with observed elevational shifts in montane species, taken from peer-reviewed articles reporting multi-species elevational redistributions (Supplementary Table 2). The global variation in predicted elevation shifts in different mountain ranges shows that rates of expected species uplifts are much lower (e.g. in Italy and France) than predicted in the original paper using widely applied empirical values (range from 5.5°C km\(^{-1}\) to 6.5°C km\(^{-1}\)) or a globally-averaged lapse rate of 5.5°C km\(^{-1}\) (Extended Data Fig. 6), and this may partially explain previous findings that mountain species appeared to be generally lagging behind climate changes\(^2\). To assess the probability of species tracking climate velocity, considering each taxon at each region as one data-point, we conducted bootstrapping to control the sample size effect and compare the probability of tracking in relation to climate velocity (Fig. 4a). Each dataset was subsampled and the mean shift was compared with its corresponding climate velocity, using Wilcoxon signed-rank test at significance level of 0.05. If the shifts of species are not significantly different from the climate velocity, we consider the species successfully track the climate velocity. We repeated the procedure for 1000 times (\(i = 1000\)) and used the percentage of numbers that are not significantly different from the climate velocity as the probability of tracking successfully (Fig. 4b-c; significant levels at \(p = 0.01\) and 0.001 were shown in Fig.4d & 4e). The probability of species tracking thus represents the variation within each data point and provided better assessment than comparing only the mean values of shifts, i.e. data points that are closer to the 1:1 diagnose line are not necessarily tracking better. Plotting the probability of species tracking demonstrated that mountain species are generally lagging behind the climate
velocities with exceptions more likely occurring at lower velocities (Fig. 4b, Extended Data Fig. 7).

By applying the well-established thermodynamic theory of MALR, we provide a global assessment of climate velocity in mountain ranges and identify 24 major regions with high climate velocities. In addition to dry regions with increasing surface temperatures, we identify mountains where high water vapor causes high climate velocity. Based on the newly calculated climate velocity, we also evaluate the probability of species tracking climate velocity in global mountains. Many ecological studies rely on average lapse rates collected by the sounding balloon method, tying a thermometer on a balloon in order to collect the temperature profile vertically, to estimate isothermal line shifts in mountain regions. The more accurate estimations of climate velocity provide potential explanations for the largely lagged upslope migrations previously documented in many species. Nevertheless, the biological impacts of climate change have largely been studied in North America and Europe, where the velocities of mountain climate change are relatively slower than most other parts of the world. We still have a limited understanding of whether species generally move uphill more slowly than the shift of isothermal lines and, if they do move more slowly, what the ecological impacts of climate change are for these lagging species.

Our estimation of global temperature lapse rates, based on the MALR formula considering the latent heat release and water vapor changes, provides a heuristic understanding of climate velocity in global mountains. However, many other mechanisms, such snow albedo, radiative flux changes, surface heat loss and aerosols, also influence the energy balance regimes, making a direct estimate of climate conditions and climate change in extremely difficult in mountain regions. Nevertheless, since mountains may effectively provide shelters for many rare and
endangered species, our study helps identify vulnerable regions with high climate velocity, which we suggest are priority regions for conservation. Given this vulnerability, extensive monitoring networks for both mountain climate and biological impacts are urgently needed.
Methods

The climatic data sources and the calculation of MALR

The climatic data, including mean annual temperature and water vapor pressure, and the corresponding global digital elevation model were derived from the gridded CRU TS3.24 database (0.5° resolution), which we averaged over every 5 years. Both mean annual temperature and water vapor pressure were derived from local weather stations and subsequently averaged across coarse spatial extent to obtain the final values.

MALR at each grid was generated by the MALR formula:

\[ \Gamma_w = g \frac{1 + \frac{H_v \gamma}{R_{sd} T}}{C_{pd} + \frac{H_v \gamma}{R_{sd} T^2}} \]

where \( \Gamma_w \) is the moist adiabatic lapse rate (K/m), \( g \) denotes the Earth's gravitational acceleration (9.8076 m/s\(^2\)), \( H_v \) denotes the heat of water vaporization (2,501,000 J/kg), \( R_{sd} \) denotes the specific gas constant of dry air (287 J kg\(^{-1}\) K\(^{-1}\)), \( \epsilon \) denotes the dimensionless ratio of the specific gas constant of dry air to the specific gas constant for water vapor (0.622), \( C_{pd} \) denotes the specific heat of dry air at constant pressure (1,005 J kg\(^{-1}\) K\(^{-1}\)), and \( T \) denotes the air temperature (K). \( \gamma \) is the mixing ratio of the mass of water vapor to the mass of dry air:

\[ \gamma = \frac{e}{p - e} \]

where \( e \) represents the water vapor pressure of the air and \( p \) represents the pressure of the air. Here, \( p \) was derived from the Barometric formula:

\[ p = p_b \times \exp \left[ -g \times M \times h \right] \frac{1}{R \times T} \]

where \( p_b \) denotes the static pressure (101,325.00 pascals), \( M \) denotes the molar mass of Earth's air (0.0289644 kg/mol), \( R \) denotes the universal gas constant for air (8.31432 N m mol\(^{-1}\) K\(^{-1}\)), \( h \) denotes the height above sea level (meters), and \( T \) denotes the standard temperature (K).
The preprocessing of climatic variables (from monthly data to annual data) and the calculation of basic climate velocity and climate velocity was computed by pySpark. Islands are defined as landmasses that are smaller than Australia and surrounded by water\textsuperscript{21}. Here, the input dataset is not the digital elevation model (DEM) from CRU but from SRTM, which is more conservative on defining terrestrial area (smaller terrestrial regions), so it is better for island detection (the islands near shores are not connected to continents). Greenland is not included as it is not surrounded by the ocean in the dataset. These analyses were run in Wolfram Mathematica 9. Though we only present the results when the anthropogenic warming accelerated (Extended Data Fig. 8) in our main text, the results from 1901 to 2015 can be found in Supplementary Fig. 1 & 2.

**Topographical analysis and corresponding data sources**

The surface aspect of each pixel was calculated by using the Surface Aspect Tool in ArcGIS Pro (the license of 3D analyst is required), and the input digital elevation model (DEM) is from CRU in order to match the climatic data. Two characters (elongation and orientation) were calculated for each mountain ranges previously defined in the literature\textsuperscript{36} in Wolfram Mathematica 9. Elongation is defined as \(1 - (\text{smallest axis of the best-fit ellipse} / \text{largest axis of the best-fit ellipse})\), and orientation is computed as the angle between the largest axis and the horizontal axis. The orientation of only those mountains having elongation value greater than 0.5 were further analyzed. To provide a better alignment with the definition of global mountains described in the main text, we then analyzed climatic data from elevations higher than 1,000 m (a.s.l.) within these ‘expert-identified’ mountains. For the clarity, we summarized the results based on categories of surface aspects and orientations of mountains (Extended Data Fig. 4a). Kruskal–Wallis test (non-parametric) was applied
to statistically quantify the differences across different aspects and orientations of
mountains. A Wilcoxon signed-rank test was then applied in paired-dataset
comparisons as a post Hoc analysis.

**Biological datasets**

We adapted published studies providing range- or boundary-shift information based
on an exhaustive literature review (Supplementary Table 2). Generally, literature was
collected based on Chen et al. 2011 and updated to 2017. Investigations of different
taxa within the same region were considered as different records (e.g., 37). Certain
records collected during this process were subsequently discarded from the dataset
when either: (1) the values returned two different studies in the same region were
evermore different, specifically exceeding a ratio of 5 (e.g., in Spain [Sierra
Nevada]38, the number of samples in two investigating periods were 1,168 V.S.
29,174); (2) the information provided in a large-scale (exceed 5 x 5 degree on the
map) research was insufficient, so we could not divide the records into geographical
regions (e.g., 39). Along with the raw datasets we used in our analysis, statistically
summarized information for all literature is also provided. The standard error was not
provided for studies with (1) only one record in a region or (2) insufficient
information from the original paper.

**Corresponding climate velocity to the biological data**

To pair biological records with the climate velocity derived from MALR, climate
velocities were assigned or statistically summarized based on the following criteria:
(1) if the spatial scale of a research was less than 1 x 1 degree (i.e. distributed within a
grid), the climate velocity at the same corresponding grid was used (eg. 40); (2) if the
scale of a study exceeded 1 x 1 degree (i.e., distributed on multiple grids), the regional
climate velocity was statistically calculated (provided as mean, variance, and sample size; e.g. \(^41\)); (3) if the study region exceeds 5 x 5 degrees, the biological records were grouped into different regions (e.g. \(^8\)), and the climate velocity of each region was derived based on criteria 1 and 2; (4) for studies encompassing multiple regions and periods, the corresponding spatiotemporal information was used in order to derive the most accurate climate velocity (eg., \(^42\)); (5) if a study investigated the same region multiple times in different temporal periods, the same geographical information was used (e.g. \(^43\)).

The probability of species tracking climate velocity—comparing biological data and climate velocity

In order to statistically compare the biological data with corresponding climate velocity, we calculated the probability of species tracking climate velocity after bootstrapping the data to meet a relatively constant sample size across regions and taxa. Some studies did provide detailed raw data (Supplementary Table 2), but for those only reporting statistical results—such as mean and variance/standard deviation/error (Extended Data Fig. 9)—we applied different probability distribution functions, normal distribution as well as non-normal distributions (log-normal and Student-t distribution), in our statistical analysis according to the statistical characteristics (mean and standard deviation/error) provided in the original reports. The nature of non-normally-distributed frequency in our dataset (Supplementary Fig. 3) was taken cared here, and the final probability reported was averaged from all three approaches with different probabilities.

The probability of species tracking climate velocity was then calculated as follows: First of all, we used the bootstrap technique to subsample the dataset to control the inconsistencies induced by having different sample sizes across studies. For each
taxon in each region, we set the sample size to $n$ and drew $n$ records ($n$ in Fig. 4a). If the total number of records for that taxon in that region is smaller than $n$, all records were used. For those only reporting statistical results (21 out of 47), we applied different probability functions to generate the drawn value as described in the previous paragraph. The drawn biological data were then compared to the corresponding climatic velocity using the non-parametric method—Wilcoxon signed-rank test—because many datasets did not satisfy the normal distributed assumption (Supplementary Fig. 3). This procedure (draw and comparison) was then iterated 1,000 times ($i$ in Fig. 4a), and we calculated the number of iterations at which the biological data showed no significant difference to the corresponding climate velocity (i.e., did not meet the significant level, 0.05; $p$ in Fig. 4 which implies the ability of tracking climate change; the lower $p$, the higher ability) and divided it by the total number of iterations (1,000; $i$ in Fig. 4a); the result was the probability of species tracking climate velocity. A logistic-type (probit) function was then applied to estimate the probability curve. We also ran a sensitivity analysis by setting different values for $n$ (30, 40, 50, 60, 70, 80, 90, and 100), and the results indicated that $n$ does not influence the probability of species tracking climate velocity (Supplementary Table 3), so we decided to set $n = 30$ to fairly address the small-sample-size research.

The data processing and statistical analysis in this section were done in R.

**Probability of species tracking using different lapse rate calculations**

The straightforward thought to test how better climate velocity derived from MALR (with the consideration of water vapor) is tracked by species should be: applying regression for water vapor and the residual that derived from the regression of biological records and local constant lapse rate (which does not consider water vapor).

However, given that the relation between water vapor and lapse rate is non-linear
(MALR formula and Fig. 1a), the analysis based on the concept of regression should not work. In order to bridge the method, which is more familiar to readers, to our formal analysis (which is going to be described later), we firstly provide a set of intuitive but potentially biased histograms to show the different explanation powers among different lapse rate calculations (Extended Data Fig. 10a). The residual between mean observed shifting rate and the mean climate velocity derived from different lapse rate calculations for a taxon are shown. We can still find that the residual histogram of MALR is more normally distributed than that of others (i.e. it explains biological dataset better than others), yet please note that this method neglects the variance of different records of a taxon. Consequently, in order to formally compare different lapse rate calculations, the method with probability scope and subsampling is applied. Based on the results generated from the previous section, we further calculated the averaged probability of species tracking climate velocity (the concept behind this analysis is quite similar to the survival analysis). We sorted the data by ascending climate velocities and then calculated the cumulated probability for each record before dividing it by the cumulated number of records. For example, there are four records (format: probability of species tracking climate velocity, climate velocity): (0.98, 0.2), (0.90, 0.4), (0.75, 0.6), (0.6, 0.7). The averaged probability under a certain climate velocity would then be: (0.98, 0.2), (0.94, 0.4), (0.88, 0.6), (0.81, 0.7). 0.94 is from (0.98+0.90)/2; 0.88 is from (0.98+0.90+0.75)/3; 0.81 is from (0.98+0.90+0.75+0.60)/4. This result can be directly compared to the ultimate impacts of lapse rates derived from different methods (local constant lapse rate, constant lapse rate, and MALR) on the probability of species tracking climate velocity (Extended Data Fig. 10b). The analysis was done in R.
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**Data availability**
Source datasets are provided at
https://datadryad.org/stash/share/cvQWOmBfKEki5GoHVkl-7yeGvAwkoEQquwEO13wB4

**Code availability**
The code used for analysis can be found at
https://datadryad.org/stash/share/cvQWOmBfKEki5GoHVkl-7yeGvAwkoEQquwEO13wB4
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Author Contributions

S.-F.S. conceived the idea. S.-F. S., I.-C. C., and W.-P. C. designed the methodology. W.-P. C. performed the formal analysis. S.-F. S., I.-C. C., and W.-P. C. wrote the paper. All authors discussed results and provided input and edits on the manuscript.

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Competing interests

The authors declare no competing interests.
Figure 1 | The foundation of moist adiabatic lapse rate for assessing climate velocity in global mountains. (a) The nonlinear effect of surface temperature and water vapor on lapse rate. The mean surface temperature (b) and water vapor (c) and derived mean moist adiabatic lapse rates (2011-2015) in global mountains (d).
Figure 2 | The velocity of climate change in global mountains from 1971 to 2015.

Terrestrial (a) and sea (b) surface temperature change (1971-1975 V.S. 2011-2015) and derived elevational climate velocities in mountains (c). (d) The high climate-velocity mountains are defined as where the isotherms have shifted more than one standard deviation of the global mean value (higher than 8.45 m yr⁻¹).
Figure 3| The velocity of climate change (1971-2015) in mountain islands (a, b, c) and along latitude-elevation gradients (d, e, f). Please see the Supplementary Method and Extended Data Fig. 3 for how to project a latitude-longitude map on a latitude-elevation map. Mountain summits are labeled for reference. Results that include the full 20th century (1901-2015) can be found in Supplementary Fig. 1 & 2.
Figure 4 | The probability of tracking climate velocities for mountain species. (a) The diagram summarizing how the probability of tracking climate velocities was calculated (i.e., 1000) (b) The diagonal diagram for observed range shifts for mountain species and corresponding climate velocities. Blue labels represent cases that species track climate successfully (color-coded under $p = 0.05$ threshold). (c-e) The different probabilities of species tracking climate velocity under different $p$ thresholds. Only mean values are shown here. Panel c-e share the same color legend with panel b. For raw data points, please see Extended Data Fig. 9 for details.
Extended Data Figure 1 | Climate change velocity (1971-2015) derived from the MALR formula (a) and average lapse rates (b-c). (a) The histogram of MALR. b-c, Histograms derived from constant lapse rates 6°C km$^{-1}$ (b) and 5.5°C km$^{-1}$ (c). The dashed and solid lines represent the zero velocity and the mean velocity, respectively. The red regions indicate the seriously warming regions (exceeding 1 standard deviation). The values labeled above the solid lines and red regions are the mean velocity and the minimum velocity of the seriously warming regions. The result of 20th century (1901-2015) can be found in Supplementary Fig. 2.
Extended Data Figure 2 | The rising temperature and mean water vapor of the 17 high climate velocity regions in global mountains. For each region, orange dots denote the climate velocity (1971-2015), green bar represent surface temperature change (1971-1975 V.S. 2011-2015) (a); blue bars represent mean water vapor pressure (2011-2015) (b). Biodiversity hotspot regions are labeled in red. Detailed information on each region can be found in Supplementary Table 1 & Data availability section.
Extended Data Figure 3 | Illustrations explaining how to project latitude-longitude maps onto latitude-elevation maps. (a) a gray-scale latitude-elevation map as Fig. 3b; the red box is shown in b. (c) a latitude-elevation map; the red box is shown in d. (d) The green pixels represent the latitudinal band of 40° and the altitudinal band of 2,000-2,200 m; yellow pixels represent the latitudinal band of 31° and the altitudinal band of 1,400-1,600 m. The green and yellow pixels in d are averaged to the green and yellow pixels in b.
Extended Data Figure 4| The definition mountain aspects and orientations (a) and associated mean climate velocity (b,e), mean water vapor (c,f), temperature change (d,g). Median and its 95% confidence interval is shown at the center of each box.
Extended Data Figure 5| Combined effect of mountain orientation and aspect on mean climate velocity, mean water vapor, and temperature change. Median and its 95% confidence interval is shown at the center of each box.
Extended Data Figure 6 | Comparison among elevational climate velocity derived from MALR, a globally averaged lapse rate of 5.5 °C / km (yellow) and empirical lapse rates in the original paper (red). The regions of outliers are labelled.
Extended Data Figure 7 | The maximum trackable climate velocity based on (a, b) constant lapse rate (5.5 °C / km) and (c, d) empirical lapse rates in the original paper. The relationships between observed shifting rate and elevational climate velocity are shown in a and c. Only mean values are shown here. The probabilities that species may track climate velocity are shown in b and d.
Extended Data Figure 8 | The temporal extents we used in this study and an example explaining how we derived climate velocity through a period of time. The temperature trend from 1900 to 2015, and the target periods discussed in our main text and supplementary materials are labeled as orange and blue bars, respectively.
Extended Data Figure 9 Raw biological data points used in our analyses. All data points from papers that provided raw data are shown (in green). Otherwise, mean and standard deviation (reported in the original paper) are shown (in blue). Since a proportion of original reports providing only mean and variance from a location, the number of data points are highly overlapped. See Supplementary Table S2 for the corresponding information and Data availability section for the dataset.
Extended Data Figure 10 | Residual frequency distribution and the probability of climate tracking and climate velocity under different lapse rate calculations. (a) The residual frequency distribution simply derived from the difference between mean of observed range shift velocity and predicted climate velocity. This result shows clearly how better the climate velocity calculated by MALR, but it contains bias because it compares only the mean value of observed records (ignoring the variance of observed records). (b) an advanced analysis showing how climate velocity be tracked under different lapse rate. Please see Supplementary Methods for details.
Supplementary Figure 1 | Projections of the climate velocity (1901-2015) in global mountain regions of (a, b, c) islands and (c, d, e) continents. Please see the Supplementary Method and Extended Data Fig. 3 for how to project a latitude-longitude map on a latitude-elevation map. Some mountains are labeled as triangles. The sample size (b, e) and standard error (c, f) are shown.
Supplementary Figure 2|Climate change velocity (1901-2015) derived from the MALR formula (a) and average lapse rates (b - c). (a) The histogram of MALR. b-c, Histograms derived from constant lapse rates 6°C km⁻¹ (b) and 5.5°C km⁻¹ (c). The dashed and solid lines represent the zero velocity and the mean velocity, respectively. The red regions indicate the seriously warming regions (exceeding 1 standard deviation). The values labeled above the solid lines and red regions are the mean velocity and the minimum velocity of the seriously warming regions.
Supplementary Figure 3 | Normality tests and qq plots for all biological raw datasets. Those datasets only reporting statistical summaries are not included. The p-values of Shapiro-Wilk normality tests for each dataset are shown in the lower-right corner of each panel.
Supplementary Figure 3| (Continued) the normality tests and qq plots for all biological raw datasets.
### Supplementary Table 1: Statistical information on major regions of high-velocity regions

| ID | Region                          | Area ² | MALR † (2011-2015) | MAP ‡ (1971-2015) | Water vapor § (2011-2015) | Surface temp. change || Elevation || BD.# hotspot |
|----|---------------------------------|--------|--------------------|-------------------|---------------------------|------------------------|--------------|-------------|--------------|
| A  | Alaska-Yukon region             | 26.28  | 5.47 (0.02)        | 366.72 (8.71)     | 46.12 (0.38)              | 5.69 (0.04)             | 1299.29     | (10.84)     | N            |
| B  | West America and Mexico         | 14.84  | 4.46 (0.02)        | 349.98 (10.06)    | 86.86 (1.27)              | 4.63 (0.05)             | 1498.11     | (19.44)     | Y            |
| C  | Costa Rica                      | 0.05   | 3.05 (NA)          | 3769.9 (NA)       | 183.27 (NA)               | 2.69 (NA)               | 1741 (NA)   | Y           |
| D  | Northern Andes Mts              | 1.73   | 3.02 (0.03)        | 1718.4 (109.76)   | 195.09 (4.92)             | 3.26 (0.09)             | 1612.94     | (63.36)     | Y            |
| E  | Western Guiana Shield           | 0.15   | 2.93 (0.07)        | 2519.71 (387.52)  | 224.72 (10.19)            | 2.55 (0.07)             | 1125 (73.38) | N           |
| F  | Brazilian Highlands             | 0.54   | 3.24 (0.02)        | 1441.88 (24.15)   | 176.3 (2.78)              | 3.2 (0.07)              | 1108.55     | (20.34)     | Y            |
| G  | Mediterranean basin             | 3.75   | 4.46 (0.02)        | 770.9 (39.87)     | 82.56 (0.96)              | 4.32 (0.05)             | 1243.74     | (29.71)     | Y            |
| H  | Northern Sahara                 | 3.16   | 4.38 (0.03)        | 295.7 (9.43)      | 90.47 (1.81)              | 4.47 (0.07)             | 1352.42     | (40.95)     | Y            |
| I  | Sudan                           | 0.99   | 4.46 (0.05)        | 263.3 (28.35)     | 95.84 (2.63)              | 4.53 (0.07)             | 1104.4      | (25.32)     | N            |
| J  | Great Rift Valley              | 15.48  | 3.21 (0.01)        | 868.95 (16.03)    | 179.74 (1.75)             | 3.19 (0.02)             | 1451.66     | (22.08)     | N            |
|   | Area            | Longitude | Latitude  | Unique ID | Longitude Error | Latitude Error | Mean Ht in m | Longitude Error | Latitude Error | Mean Ht in m | Longitude Error | Latitude Error | Mean Ht in m | Longitude Error | Latitude Error | Mean Ht in m | Longitude Error | Latitude Error | Mean Ht in m | Longitude Error | Latitude Error | Mean Ht in m |
|---|-----------------|-----------|-----------|-----------|-----------------|----------------|--------------|----------------|----------------|--------------|----------------|----------------|--------------|----------------|----------------|--------------|----------------|----------------|--------------|----------------|----------------|--------------|
| K | Southern Africa | 7.25      | 3.74      | 0.03      | 308.57          | 12.9           | 135.96       | 2.33           | 0.03           | 1180.22      | 13.73          | 1231.71       | 40.52         | Y             | 1549.16       | 21.03         | N             | 1538.5        | 51.97         | Y             | 1540.16       | 21.03         | N             |
| L | Turkey          | 0.3       | 4.5       | 0.05      | 364             | 13.17          | 79           | 3.26           | 0.06           | 1445         | 119.39         | 1231.71       | 40.52         | Y             | 1549.16       | 21.03         | N             | 1538.5        | 51.97         | Y             | 1540.16       | 21.03         | N             |
| M | Hejaz Mts       | 2.86      | 3.82      | 0.06      | 121.76          | 5.58           | 132.63       | 4.04           | 0.06           | 1259.76      | 32.08          | 1231.71       | 40.52         | Y             | 1549.16       | 21.03         | N             | 1538.5        | 51.97         | Y             | 1540.16       | 21.03         | N             |
| N | Madagascar      | 0.69      | 3.16      | 0.01      | 1423.1          | 73.13          | 183.09       | 2.74           | 0.01           | 1231.71      | 40.52          | 1231.71       | 40.52         | Y             | 1549.16       | 21.03         | N             | 1538.5        | 51.97         | Y             | 1540.16       | 21.03         | N             |
| O | Iran-Pakistan region | 17.11 | 4.66 | 0.03 | 221.42 | 6.45 | 78.46 | 1.17 | 4.85 | 1549.16 | 21.03 | 1549.16 | 21.03 | N |
| P | Nepal           | 0.05      | 3.23      | NA        | 1616.12         | NA             | 168.53       | NA             | 2.96           | 1467         | NA             | Y             | 1549.16       | 21.03         | N             | 1538.5        | 51.97         | Y             | 1540.16       | 21.03         | N             |
| Q | Southern Ghats Mts | 0.1 | 2.92 | NA | 1054.4 | NA | 223.46 | NA | 2.75 | 1199 | NA | Y |
| R | Central Siberia | 0.79      | 6.82      | 0.03      | 373.95          | 5.87           | 22.51        | 0.4            | 6.58           | 1092         | 19.15          | N             | 1549.16       | 21.03         | N             | 1538.5        | 51.97         | Y             | 1540.16       | 21.03         | N             |
| S | Northwestern Mongolia | 0.79 | 5.24 | 0.02 | 360.49 | 24.49 | 51.71 | 0.81 | 4.65 | 1233.13 | 40.5 | N |
| T | Central-northern China | 0.2 | 4.99 | 0.07 | 163.82 | 7.25 | 63.58 | 2.71 | 4.36 | 1309.75 | 83.26 | N |
| U | Tarim Basin region | 0.39 | 4.78 | 0.05 | 64.66 | 6.79 | 72.78 | 1.69 | 4.18 | 1263.5 | 19.17 | N |
| V | Hengduan Mts     | 2.27      | 3.4       | 0.03      | 1001.3          | 19.89          | 154.06       | 4.25           | 3.27           | 1538.5       | 51.97          | Y             | 1549.16       | 21.03         | N             | 1538.5        | 51.97         | Y             | 1540.16       | 21.03         | N             |
| W | Northern Sumatra | 0.25      | 2.82      | 0.02      | 2375.73         | 239.68         | 244.57       | 3.34           | 3.28           | 1122         | 26.14          | Y             | 1549.16       | 21.03         | N             | 1538.5        | 51.97         | Y             | 1540.16       | 21.03         | N             |
| X | Japan           | 0.1       | 4.17      | NA        | 1310.04         | NA             | 95.09        | NA             | 3.56           | 1109.5       | NA             | N             | 1549.16       | 21.03         | N             | 1538.5        | 51.97         | Y             | 1540.16       | 21.03         | N             |
Percentage of each region divided by the total area of high-velocity regions in global mountains. (Unit: %)

† Moist adiabatic lapse rate derived from mean temperature and mean water vapor. (Unit: °C / km; format: mean [S.E.])

‡ Mean annual precipitation. (Unit: mm / yr; format: mean [S.E.])

§ Mean water vapor pressure; used as the parameter to derive MALR (2011-2015) in order to calculate climate velocity. (Unit: Pa; format: mean [S.E.])

|| Temperature velocity. (1971-1975 V.S. 2011-2015; Unit: 0.01°C /yr; format: mean [S.E.])

¶ Averaged elevation. (Unit: meter; format: mean [S.E.])

# Biodiversity hotspot. This cell is filled by “Y” for any regions with biodiversity hotspots (45).
Supplementary Table 2 | Biological datasets.

| Pub_ID | Location                  | 1st yr of 1st investigation | 2nd yr of 1st investigation | 1st yr of 2nd investigation | 2nd yr of 2nd investigation | Taxon       | Reference |
|--------|---------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-------------|-----------|
| 1      | Switzerland               | 1880                        | 1920                        | 1980                        | 2005                        | Plants      | 46        |
| 2      | Malaysia (Mt. Kinabalu)   | 1965                        | 1965                        | 2007                        | 2007                        | Insects     | 2         |
| 3      | Spain (Sierra de Guadarrama) | 1967                     | 1973                        | 2004                        | 2004                        | Insects     | 47        |
| 4      | Madagascar (Tsaratanana Massif) | 1993                    | 1993                        | 2003                        | 2003                        | Herptiles   | 48        |
| 5      | France (Giffre valley)    | 1978                        | 1980                        | 2001                        | 2002                        | Aves        | 49        |
| 6      | France (Mont Ventoux alt.) | 1973                        | 1974                        | 2000                        | 2001                        | Aves        | 49        |
| 7      | Italy (Alta Valsessera)   | 1992                        | 1994                        | 2003                        | 2005                        | Aves        | 50        |
| 8      | USA (New York State)      | 1980                        | 1985                        | 2000                        | 2005                        | Aves        | 51        |
| 9      | USA (Yosemite Nationa Park) | 1914                       | 1920                        | 2003                        | 2006                        | Mammals     | 52        |
| 10     | Italy (Rhaetian Alps)     | 1954                        | 1958                        | 2003                        | 2005                        | Plants      | 53        |
| 11     | USA (Mt. Santa Rosa, CA)  | 1977                        | 1977                        | 2006                        | 2007                        | Plants      | 54        |
| 12     | West Europe (SW France)   | 1905                        | 1985                        | 1986                        | 2005                        | Plants      | 55        |
|   | Country/Region          | Start Year | End Year | Start Year | End Year | Taxon Type | Code |
|---|-------------------------|------------|----------|------------|----------|------------|------|
| 13 | Switzerland (12 Mts in Grisons) | 1893 | 1893 | 2004 | 2004 | Plants | 41 |
| 14 | Marion Island (sub-Antarctic) | 1965 | 1966 | 2005 | 2007 | Plants | 56 |
| 15 | Czech Republic | 1951 | 1980 | 1995 | 2001 | Insects | 57 |
| 16* | UK (Great Britain) | 1970 | 1982 | 2004 | 2005 | Insects | 58 |
| 17* | UK (Great Britain) | 1970 | 1982 | 1995 | 1999 | Insects | 37 |
| 18* | UK (Great Britain) | 1970 | 1980 | 1990 | 2000 | Insects | 37 |
| 19* | UK (Great Britain) | 1960 | 1970 | 1985 | 1995 | Insects | 37 |
| 20* | UK (Great Britain) | 1960 | 1970 | 1985 | 1995 | Insects | 37 |
| 21* | UK (Great Britain) | 1965 | 1975 | 1990 | 2000 | Insects | 37 |
| 22* | UK (Great Britain) | 1965 | 1975 | 1985 | 1995 | Arachnids | 37 |
| 23* | UK (Great Britain) | 1965 | 1975 | 1990 | 2000 | Insects | 37 |
| 24* | UK (Great Britain) | 1965 | 1975 | 1990 | 2000 | Insects | 37 |
| 25* | UK (Great Britain) | 1965 | 1975 | 1990 | 2000 | Millipedes | 37 |
| 26* | UK (Great Britain) | 1960 | 1970 | 1985 | 1995 | Insects | 37 |
| 27* | UK (Great Britain) | 1965 | 1975 | 1990 | 2000 | Arachnids | 37 |
| No. | Location               | Year1  | Year2  | Year3  | Year4  | Taxonomic Category | Code |
|-----|------------------------|--------|--------|--------|--------|--------------------|------|
| 28* | UK (Great Britain)     | 1960   | 1970   | 1985   | 1995   | Malacostraca       | 37   |
| 29* | UK (Great Britain)     | 1965   | 1975   | 1990   | 2000   | Fishes             | 37   |
| 30* | UK (Great Britain)     | 1968   | 1972   | 1988   | 1991   | Aves               | 37   |
| 31* | UK (Great Britain)     | 1960   | 1970   | 1985   | 1995   | Mammals            | 37   |
| 32* | UK (Great Britain)     | 1960   | 1970   | 1985   | 1995   | Herptiles          | 37   |
| 33  | Peru                   | 2003   | 2004   | 2007   | 2008   | Plants             | 59   |
| 34* | Peru                   | 1969   | 1969   | 2010   | 2010   | Aves               | 60   |
| 35  | Norway                 | 1922   | 1932   | 2008   | 2008   | Plants             | 61   |
| 36  | Taiwan                 | 1969   | 1969   | 2006   | 2006   | Plants             | 43   |
| 37  | USA (Lassen, CA)       | 1924   | 1928   | 2006   | 2007   | Aves               | 42   |
| 38  | USA (Yosemite, CA)     | 1915   | 1919   | 2003   | 2004   | Aves               | 42   |
| 39  | USA (Southern Sierra, CA) | 1911   | 1911   | 2008   | 2009   | Aves               | 42   |
| 40  | India                  | 1849   | 1850   | 2007   | 2010   | Plants             | 62   |
| 41  | USA                    | 1977   | 1981   | 2006   | 2011   | Aves               | 63   |
|   | Country                    | Year(s) | Species | Data Year(s) | Data Year(s) |
|---|---------------------------|---------|---------|--------------|--------------|
|42*| France (South-western Alps)| 1992-1993| 2007    |              | 2007         | Insects 38 |
|43*| Spain (Sierra Nevada)     | 1981-1982| 2006    |              | 2007         | Insects 38 |
|44 | New Guinean (Mt. Karimui) | 1955-1964| 2002    |              | 2011         | Aves 8    |
|45 | New Guinean (Karkar Island)| 1959-1968| 2002    |              | 2011         | Aves 8    |
|46 | USA (California)          | 1895-1970| 1971    |              | 2009         | Plants 64 |
|47*| Canada                    | 1970-1970| 2012    |              | 2012         | Plants 65 |

* Only mean and variance/standard deviation/error are available from the literature
The probability of tracking climate velocity based on Wilcoxon signed-rank test under different sample sizes (n).

| Pub_ID | n = 30 | n = 40 | n = 50 | n = 60 | n = 70 | n = 80 | n = 90 | n = 100 |
|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| 1      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 2      | 0      | 0      | 0.022  | 0.003  | 0      | 0      | 0      | 0      |
| 3      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 4      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 5      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 6      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 7      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 8      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 9      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 10     | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 11     | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 12     | 0.002  | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 13     | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 14     | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 15     | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 16     | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 17     | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 18     | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 19     | 0      | 0      | 0.2813 | 0.33   | 0      | 0      | 0      | 0      |
| 20     | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 21     | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 22     | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 23     | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 24     | 0.024  | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 25     | 0.0033 | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 26     | 0.0227 | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 27     | 0.1507 | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 28     | 0.2827 | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 29     | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 30     | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 31     | 0.4327 | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 32     | 0.0017 | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| 33     | 0.0287 | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
