The ranges of plants and animals are moving in response to recent changes in climate. As temperatures rise, ecosystems with ‘nowhere to go’, such as mountains, are considered more threatened. However, species survival may depend as much on keeping pace with moving climates as the climate’s ultimate persistence. Here, we present a new index of the velocity of temperature change (km yr⁻¹), derived from spatial gradients (C km⁻¹) and multimodel ensemble forecasts of rates of temperature increase (C yr⁻¹) in the 21st century. This index represents the instantaneous local velocity along Earth’s surface needed to maintain constant temperatures, and has a global mean of 0.42 km yr⁻¹ (A1B emission scenario). Due to topographic effects, the velocity of temperature change is lowest in mountainous biomes such as tropical and subtropical coniferous forests (0.08 km yr⁻¹), temperate coniferous forest, and montane grasslands. Velocities are highest in flooded grasslands (1.26 km yr⁻¹), mangroves, and deserts. High velocities suggest that the climates of only 8% of global protected areas have residence times exceeding 100 years. Small protected areas exacerbate the problem in mediterranean-type and temperate coniferous forest biomes. Large protected areas may mitigate the problem in desert biomes. These results suggest management strategies for minimizing biodiversity loss from climate change. Montane landscapes may effectively shelter many species into the next century. Elsewhere, reduced emissions, a much expanded network of protected areas, or efforts to increase species movement may be necessary. As climate changes in this century, the current distribution of climatic conditions will be rearranged on the globe; some climates will disappear entirely, and novel (no-analog) climates are expected in wide regions. For species to survive, the persistence of suitable climates is not sufficient. Species must also keep pace with climates as they move. To summarize the speed at which climate is changing, we compute the instantaneous horizontal velocity of temperature change (Fig. 1e) derived from the ratio of temporal (Fig. 1d) and spatial (Fig. 1c) gradients of mean annual near-surface temperature (Fig. 1b) (C yr⁻¹ ÷ C km⁻¹ = km yr⁻¹). As exemplified by California, the spatial gradient of temperature change is greatest on mountain slopes (Fig. 1c): modest displacements in space, moving up or down-slope, result in a large change in temperature. As a result, relatively small velocities (Fig. 1e) are required to keep pace with the rate of temperature change (assuming that the climate persists and does not disappear). In contrast, high velocities are required in flatter areas such as California’s Central Valley where large geographic displacements are required to change temperature appreciably. The magnitude of these results depends on the emissions scenario (Fig. 2a) and also the period of time over which the temporal gradient is calculated (Fig. 2b). However, velocity patterns of global temperature change are similar across scenarios, with the highest velocities in flat landscapes at higher latitudes (Fig. 2c). Using temperature change calculated from 2000-2099 under the intermediate A1B emissions scenario, the geometric mean velocity was 0.42 (0.11-1.46) km yr⁻¹. (Throughout we summarize uncertainty in the mean by listing upper and lower, ±1 s.d., estimates in parenthesis). (See Supplementary Fig. S17 for other emissions scenarios.)
Land-cover change results in formidable barriers to species movement. Thus, keeping pace with climate change is more feasible within protected areas where landscapes may be less fragmented. The sizes of protected areas vary greatly across biomes (see Supplementary Fig. S20). To explore the interaction between protected area sizes and velocities required to keep pace with climate change, we calculated residence times, defined as the diameter of each protected area divided by velocity (km yr⁻¹). Assuming protected areas are circular and disconnected, this index can be interpreted as the time for current climate to cross a protected area. Such residence times exceed 100 years for only 8.02% (2.67 - 16.49%) of protected areas. Fig. 4 summarizes these data by biome, ordered by decreasing residence time. The order of residence times is generally the inverse of velocities, across biomes. For example, the three biomes with the slowest velocities have among the four longest residence times. There are also notable differences. For example, the limited size of protected areas in mediterranean-type, temperate broadleaf and coniferous forest biomes decreases the residence time in these biomes despite relatively low velocities.

To guide interpretation of these results, we make three clarifications. First, climate change involves complex interactions among temperature, precipitation, and seasonal and historic variability. We focus on mean annual temperature for several reasons. Mean annual temperature is a useful summary of both historic and projected climate change. The direction and magnitude of temperature change is much less uncertain than precipitation change. Growing numbers of examples document the latitudes and elevations of species distributions responding as expected to changing temperatures. We repeated all analyses with precipitation (see Supplementary Fig. S19). Interestingly, precipitation spatial gradients are also greatest in mountainous areas due to the influence of rain shadows and orographic effects. As a result the mean velocity, 0.22 (0.08-1.90) km yr⁻¹, and overall patterns are similar to those derived by temperature.

Second, there is uncertainty in both the spatial and temporal gradients of climate change. We estimated uncertainty in both of these contributing factors and propagated them through to lower and upper estimates of velocity and residence time (see Supplementary Material). Additionally, we note the instantaneous velocity is sensitive to the grain of the analysis and the size of the kernels used to compute spatial and temporal gradients. Throughout this study, we use a ~1 km spatial grain size, the finest available for global mean annual temperature, and a 9 grid cell spatial kernel, standard for creating gridded slopes from digital elevation models. We chose the fine spatial grain because both yearly dispersal capabilities for many species and large temperature changes often occur on the order of a few kilometres. In some cases, even finer resolution responses on the scale of meters may be sufficient to offset climate change as populations move from south to north facing slopes within a habitat.

Third, our index estimates the velocities and residence times of climates, not species. We make no assumptions about the tolerances of individual species. Implications for individual species depend on the breadth of tolerance, and our velocities apply to range edges, ecotones, and other features that reflect climate isolines. For species with small tolerances, the velocity estimates closely approximate migration speeds required to potentially avoid extinction. For species with large tolerances, the residence times are underestimates. We also note that species do not move at constant rates and, in some instances, the velocity of movements downhill may differ from those uphill; similarly leading edge expansion and trailing edge contraction will be different, reflecting the contrasting mechanisms. As a result of these caveats, we interpret these velocities as a relative...
It is, however, interesting to compare the magnitude and spatial patterns of the velocities with migration rate studies. Malcolm et al.\textsuperscript{17} calculated the minimum distances between modelled current and future biomes from two Global Vegetation Models (GVM) and interpreted them as necessary speeds for species migration. The study used similar emissions and temporal scales, a much coarser spatial grain (0.5-degrees), and projections from an older generation of global climate models than those explored here. Accounting for uncertainty, the probability density function of our velocities are the same as those found by Malcolm et al.\textsuperscript{17}. For example, we calculated 28.8 (0.3-66.9) % of the globe had migration rates greater than 1 km yr\textsuperscript{-1} compared with 17.4% and 21.1% from the two GVM’s used by Malcolm et al.\textsuperscript{17}. These similarities are interesting given the many differences in the approaches used to explore migration rates. (See supplementary material for further comparisons.)

We project that large areas of the globe (28.8\%) will require velocities faster than the more optimistic plant migration estimates from a landscape before anthropogenic fragmentation. Velocities on montane landscapes, in contrast, may fall within historic rates. The ability of complex topography to provide a spatial buffer for climate change has been recognized qualitatively\textsuperscript{21} and evaluated over small geographic areas\textsuperscript{22}, but was muted in previous, coarser scale global analyses\textsuperscript{17}. Considering these factors adds an important dimension to management strategies for addressing climate change, highlighting the greater vulnerability of large, extensive areas such as the lowland tropics and desert regions. In landscapes where small velocities are required, moderate sized protected areas may be able to contain moving climates and ecosystems. Elsewhere, additional steps must be taken. These include slowing

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the temporal gradient of climate change through reduced emissions, increasing the ability of plants and animals to disperse through managed relocation\(^1\), or increasing the size of protected areas through habitat corridors and new reserves\(^4\).

**Methods Summary**

Detailed methods are in the supplemental materials. In brief, for current climate, we used the 30-arcsec WorldClim Version 1.4 Annual Mean Temperature and Total Annual Precipitation bioclimatic variable\(^2\). Spatial gradients were calculated from a 3-by-3 grid cell neighbourhood using the average maximum technique\(^3\) modified to accommodate different cell-widths at different latitudes. Future temperature projections for each emissions scenario were averages of 16 global climate models statistically downscaled to 0.5-degrees\(^4\). We computed temporal gradients as the slope of a linear model fit through each year of the time period of interest. Velocity is the ratio of the temporal gradient to the spatial gradient, and log transformed for visualization due to a highly skewed distribution. We report geometric means of the velocity to accommodate this skew. We compiled biomes from the World Wildlife Fund Terrestrial Ecoregions\(^6\) and protected areas from the World Database on Protected Areas (WDPA) Annual Release 2009 (web download version), February 2009. For each protected area centroid we sampled the velocity and biome to compare with estimates of reserve diameter. We discuss precipitation and uncertainty propagation in the supplementary material.

**References**

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Author Contribution Statement