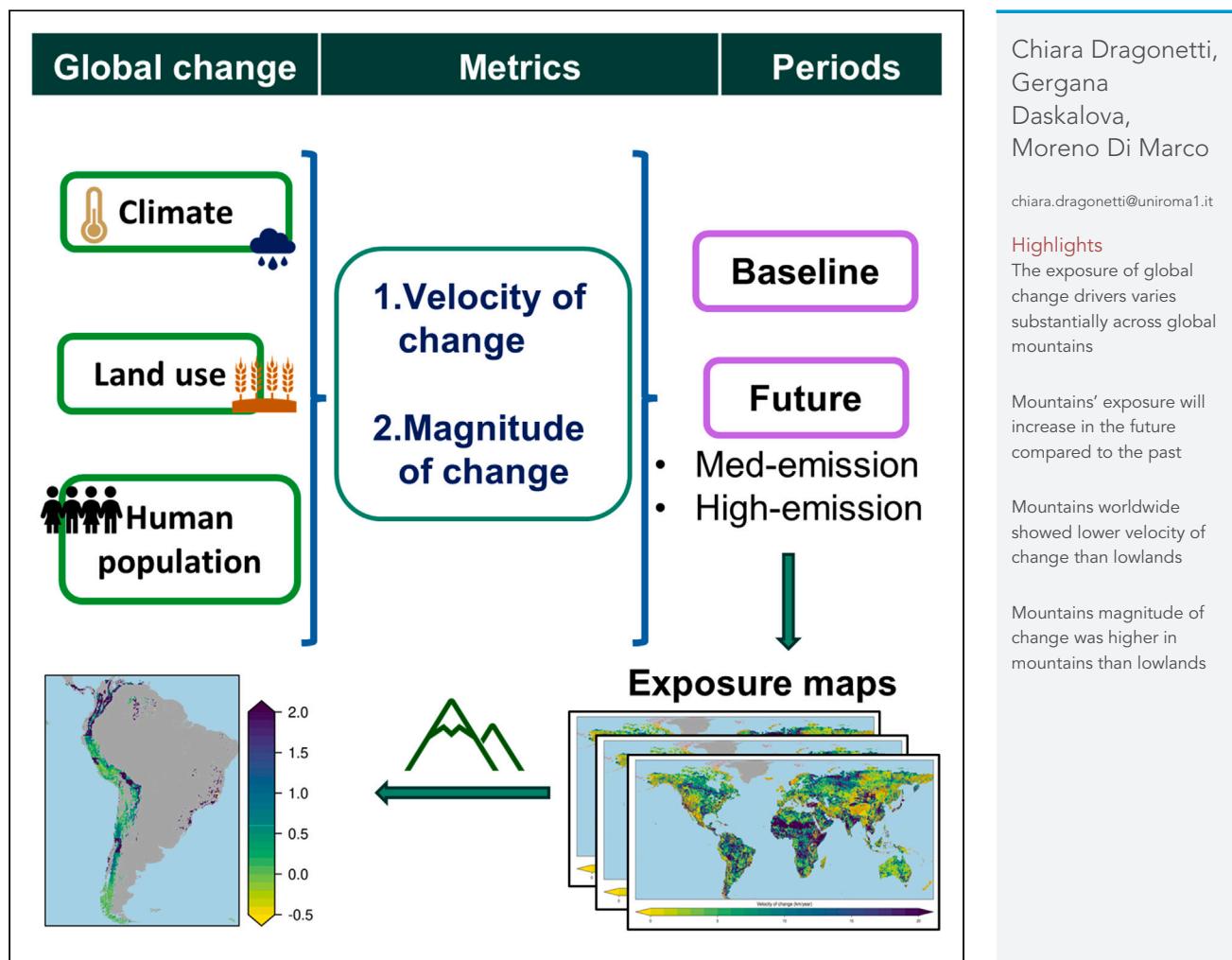


Article

The exposure of the world's mountains to global change drivers



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Chiara Dragonetti,^{1,3,*} Gergana Daskalova,² and Moreno Di Marco¹

SUMMARY

Global change affects mountain areas at different levels, with some mountains being more exposed to change in climate or environmental conditions and others acting as local refugia. We quantified the exposure of the world's mountains to three drivers of change, climate, land use, and human population density, using two spatial-temporal metrics (velocity and magnitude of change). We estimated the acceleration of change for these drivers by comparing past (1975–2005) vs. future (2020–2050) exposure, and we also compared exposure in lowlands vs. mountains. We found Africa's tropical mountains facing the highest future exposure to multiple drivers of change, thus requiring targeted adaptation and mitigation strategies to preserve biodiversity. European and North America's mountains, in contrast, experience more limited exposure to global change and could act as local refugia for biodiversity. This knowledge can be used to prioritize local-scale interventions and planning long-term monitoring to reduce the risks faced by mountain biodiversity.

INTRODUCTION

Human activities during the Anthropocene have caused direct and indirect impacts on biodiversity, by driving climate change, habitat degradation, and pollution.^{1–4} The rate of global warming over the 50 years interval 1959–2009 is almost twice as fast as the prior period⁵ and higher than any 50-year period in the past two millennia.⁶ In parallel, the frequency and intensity of heavy precipitation have increased since the 1950s over most global land areas.⁶ Future projections suggest that climate change will likely occur at an extraordinary rate for Earth's history,⁷ reaching a global warming of 2.1°C–3.5°C during 2081–2100 above pre-industrial temperatures, under a business-as-usual scenario.⁶ This accelerating speed can be disruptive for many global biological systems.⁸ If the rate of these global changes outpaces the capacity of species to adapt to new climates, many species will face a high risk of extinction.^{9–11}

Mountains worldwide face direct and indirect drivers of change, such as climate change, land-use change, and human population growth.^{12,13} Covering less than 20% of the earth's surface, mountains are extraordinarily important for both humans and biodiversity.¹⁴ From a human and demographic perspective, mountains host between 10% and 20% of world's population, depending on the mountain definition applied,^{14,15} and they provide both mountain and lowland communities with essential ecosystem services.^{16–18} From a biodiversity perspective, mountains sustain approximately one-third of the diversity of terrestrial species¹⁹ and are home to half of the 34 globally recognized biodiversity hotspots.²⁰ Mountain areas have served as refugia to different species during past climatic change events, and it is anticipated that they will act as refugia also under future climate change.^{21–23} The local topography creates in fact a diverse mosaic of microclimates, which allows species to relocate to suitable habitats within a short linear distance when climate change occurs.^{24,25} However, for the same reason of environmental heterogeneity, mountains host many ecosystems and species that are particularly sensitive to climate changes.^{26,27} Many mountain species are shifting their ranges to higher elevations or northern latitudes,²⁸ but species restricted to high elevations (i.e., mountain tops) frequently face a progressive reduction in their distribution and an increased probability of extinction.^{27,29–31} Moreover, species movement is limited by habitat availability and connectivity¹³; thus the effects of climate change on mountain biota are often exacerbated by other drivers, such as land-use and land-cover change.³²

Almost 60% of the world's mountains are under intense human pressure, resulting in overexploitation of natural resources and land-use change toward infrastructural development, pastureland, and cropland.¹³ The magnitude and the impact of human activities in mountains vary spatially across economic development levels and elevational gradients.³³ In many developing countries there is a significant increase in mountain land-use change associated with population growth.^{34–37} For instance, tropical mountains in Central America, East Africa, the Middle East, and parts of South-East Asia have recently experienced population growth which is often linked to an increased urbanization.¹⁵ From a human perspective, many mountain populations are already modifying the extent and intensity of their land-use activities to cope with climate change,^{15,36,38–40} for instance, relocating their activities to higher elevations. This process can initiate a synergistic

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interplay with climate-induced alterations, leading to great consequences on biodiversity. In this sense, even if demography is considered an indirect pressure in mountain areas, it holds particular significance especially in regions such as the Himalaya and the East African Mountains,⁴¹ where population growth has been significant over the last three decades, leading to an unregulated urbanization and land-use change.^{38,42} On the other hand, mountain areas in developed countries, such as certain regions of the European Alps, have been experiencing an increasing human depopulation and land abandonment, often leading to the cessation of pastoralism and other traditional land-use practices.^{43,44}

Quantifying the exposure of mountain ecosystems to different anthropogenic pressures is crucial for gaining insights into the degree of transformation these ecosystems undergo and, consequently, the effects on the species living within them. By comparing the future level of exposure with the past one,⁴⁵ it is possible to anticipate the risks to which mountain biodiversity will be exposed in the future and plan long-term adaptive biodiversity monitoring as well as adaptive management and conservation.

Regions with a low projected exposure can potentially serve as local climatic refugia, i.e., areas that offer protection to species against long-term environmental variations, as described in previous research.^{46–48} In these areas species would only need to make short-range migrations to temporarily adapt to changing environmental conditions.⁴⁹ To effectively act as refugia, these regions need to be protected from anthropogenic pressures such as overexploitation, or unsustainable tourism.^{50,51} In contrast, regions which showed novel climate conditions (i.e., higher exposure) may experience a loss of biodiversity due to the extinction of species that are unable to keep pace with the new environmental conditions.^{22,52,53} These areas require conservation intervention to help species adaptation, such as the restoration of habitat conditions (including microhabitat) and environmental connectivity, which will in turn require long-term monitoring.⁵⁴

Here we assessed the past and future exposure of mountain areas to three global change drivers: climate change, land-use change, and human population density change.

Our objectives were to

- (1) determine whether mountain areas worldwide will experience increased exposure to environmental changes in the future compared to the past;
- (2) assess which global change factor will have a predominant influence in the different mountain areas;
- (3) identify mountain areas which will experience more stable conditions in the future (i.e., low exposure); and
- (4) assess whether mountain areas will be globally more or less exposed than lowlands.

We used two metrics of change to estimate the exposure, the velocity and the magnitude. The velocity of change is a common metric used to quantify the exposure of a system to climate change,^{52,55–58} representing the speed and the direction in which a given organism needs to move to maintain the same climatic conditions.⁷ This metric can also be used to assess the exposure of an area to other drivers of change, such as land-use change.^{59,60} The magnitude of change is used to measure how much the conditions of a location have changed (or will change) over time.^{50,52} As these metrics provide different and complementary information, it is essential to combine them to assess the exposure of an area.^{25,60}

RESULTS

We estimated the velocity of change and the magnitude of change of each driver under alternative future scenarios (time-slice 2020–2050) (Figure 1; Figures S1–S3), as well as for a reference baseline period (time-slice 1975–2005). We looked at two different Shared Socio-economic Pathways (SSP) coupled with two Representative Concentration Pathways (RCP). SSP-RCP 2–4.5 and SSP-RCP 5–8.5,⁶¹ respectively, depicting a business-as-usual socio-economic pathway (achieving a global warming of 2.1°C–3.5°C by 2100 above pre-industrial temperatures) and a high-emissions pathway (achieving a global warming of 3.3°C–5.7°C). We compared the velocity and magnitude of change of all drivers across 13 mountain areas, classified according to continents and latitude^{33,62} (Figure 2). We also compared the exposure to global change drivers of world's mountains with the one in the lowlands, in terms of both absolute exposure (e.g., velocity of change in the future) as well as relative exposure (e.g., future vs. past velocity or "acceleration"). We identified mountain areas that could act as potential future refugia from global change, and those which will be more exposed to a change for one or more drivers.

Global change within mountain areas

Mountains' velocity of change was projected to increase in the future compared to the past, with the highest climate velocity under high-emissions scenario (median velocity in mountains = 0.54 km/year, se = 0) and the highest land-use velocity under intermediate-emissions scenario (median velocity in mountains = 2.99 km/year, se = 0.014) (Table S1). In contrast, we found that human population density growth in mountain areas decelerates in the future (median velocity intermediate-emissions scenario = −0.05 km/year, se = 0; median velocity high-emissions scenario = −0.13 km/year, se = 0) compared to the past (median velocity = 0.54 km/year, se = 0.005).

The relative magnitude of climate change in mountain areas was higher in the baseline epoch (median = 2.24, se = 0) compared to the future intermediate-emissions scenario (median = 1.80, se = 0), but the highest value was under the high-emissions scenario (median = 3.55, se = 0) (Table S2). Land-use magnitude was much lower in the past (median = 0.55, se = 0.002) compared to the future (median intermediate-emissions scenario = 8.95, se = 0.018; median high-emissions scenario = 4.33, se = 0.026). The magnitude of change of human population also increased in both future scenarios in mountains (median intermediate-emissions scenario = 3.34, se = 0.001; median high-emissions scenario = 2.89, se = 0) compared to the past (median = 2.39, se = 0.171).

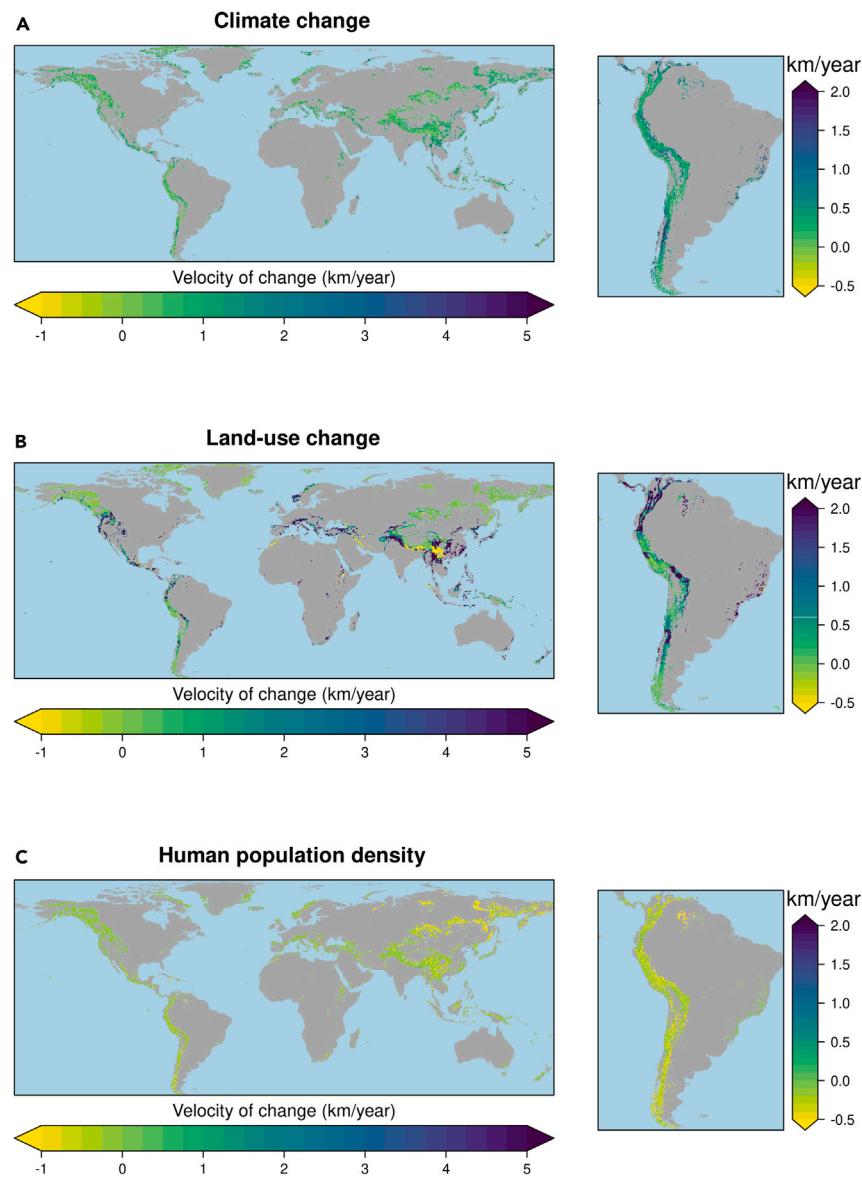


Figure 1. The velocity of change of the three global change drivers

Panel of maps showing the velocity of change (km/year) in mountain areas under the high-emissions scenario, for the three different drivers: (A) climate change, B) land-use change, C) human population density.

Comparison of the drivers across mountain areas

We compared the velocity and magnitude of change of all drivers of change across 13 mountain areas, classified according to continents and latitude³³ (Figure 2). We also reported the specific results for 289 main mountain ranges according to Global Mountain Biodiversity Assessment (GMBA)⁶² (Tables S9–S14).

High-emissions scenario

Under high-emissions scenario two mountain areas showed overall higher exposure than the others for the all drivers of change (in terms of magnitude and velocity of change): Low Africa and Middle South Africa (Figure 3; Tables S3–S8; Figures S8 and S9). Within these areas, mountain ranges such as those in the Cameroon Island Chain showed a higher exposure for both land-use change (median velocity = 7.81 km/year, median magnitude = 338.36) and climate change (median velocity = 0.26 km/year, median magnitude = 4.48), and a high magnitude of change for human population density (3.83) (Tables S9–S14). Conversely, mountain areas with an overall lower exposure to climate and land-use change are found in Middle South America and High North America (i.e., magnitude of climate change

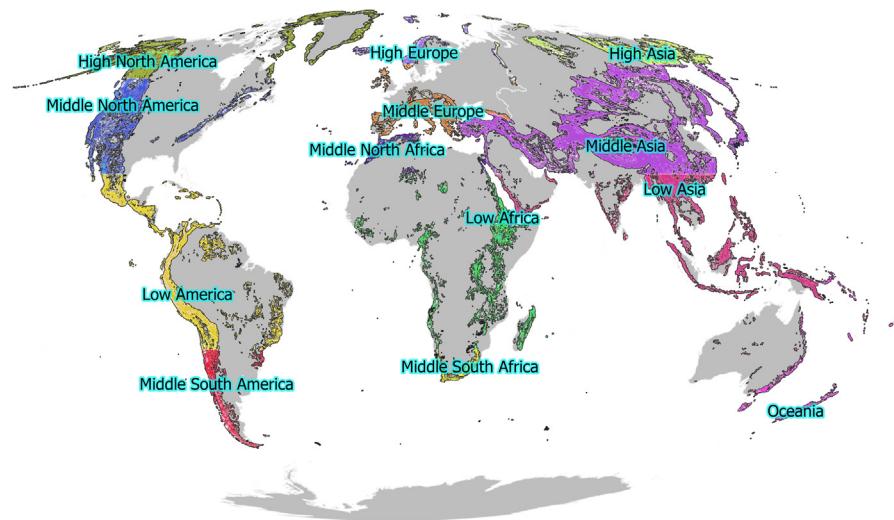


Figure 2. The mountain areas of the world

The mountain areas classified according to latitude and continents, following Nogués-Bravo et al. 2007.

of South Atlantic Islands = 1.77, velocity of land-use change in Mackenzie mountains in High North America = 0) ([Tables S12](#) and [S10](#)). Human population velocity of change showed negative values in all mountain areas, with few exceptions very close to 0 ([Table S5](#)). The magnitude of population density change is similar for all mountain areas (~3), except for Oceania, High Asia, and High North America ([Table S8](#)).

Intermediate-emissions scenario

Under the intermediate-emissions scenario, mountains in the Low Africa, Middle North Africa, and Low Asia areas were the ones most exposed to global changes, both in terms of velocity and magnitude ([Figures S4, S6, and S7](#)). Central Highlands in India for instance showed high velocities for both climate and land-use (medians respectively of 1.51 km/year and 14.5 km/year) ([Tables S9](#) and [S10](#)). Areas with an overall low exposure to climate and land-use change under intermediate-emissions scenario were High Europe and High North America (e.g., Iceland showed low values of climate change velocity and magnitude, respectively 0.34 km/year and 1.16) ([Tables S9](#) and [S12](#)). Under this future scenario the velocity of change of human population density is close to 0 in all mountain areas.

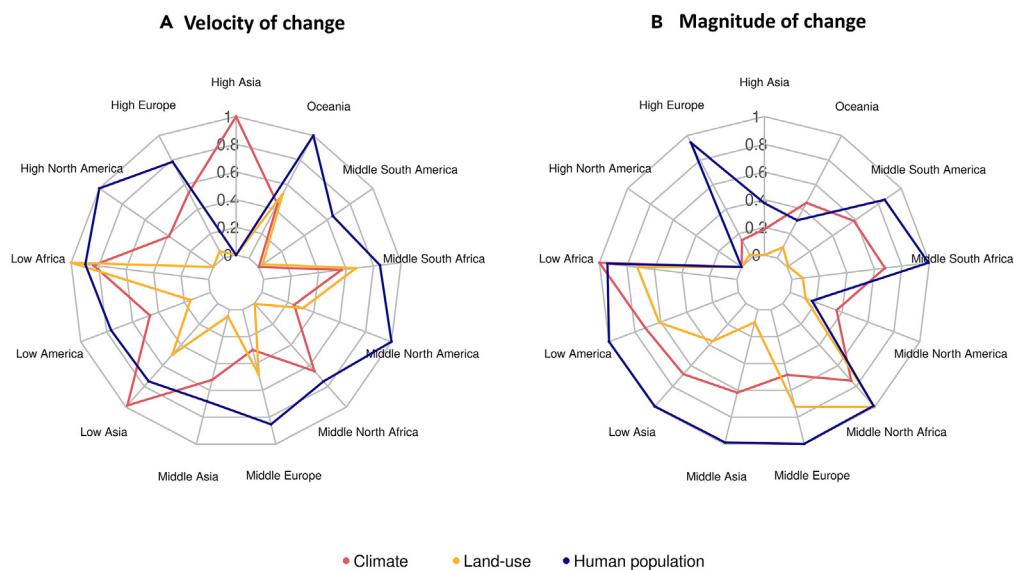
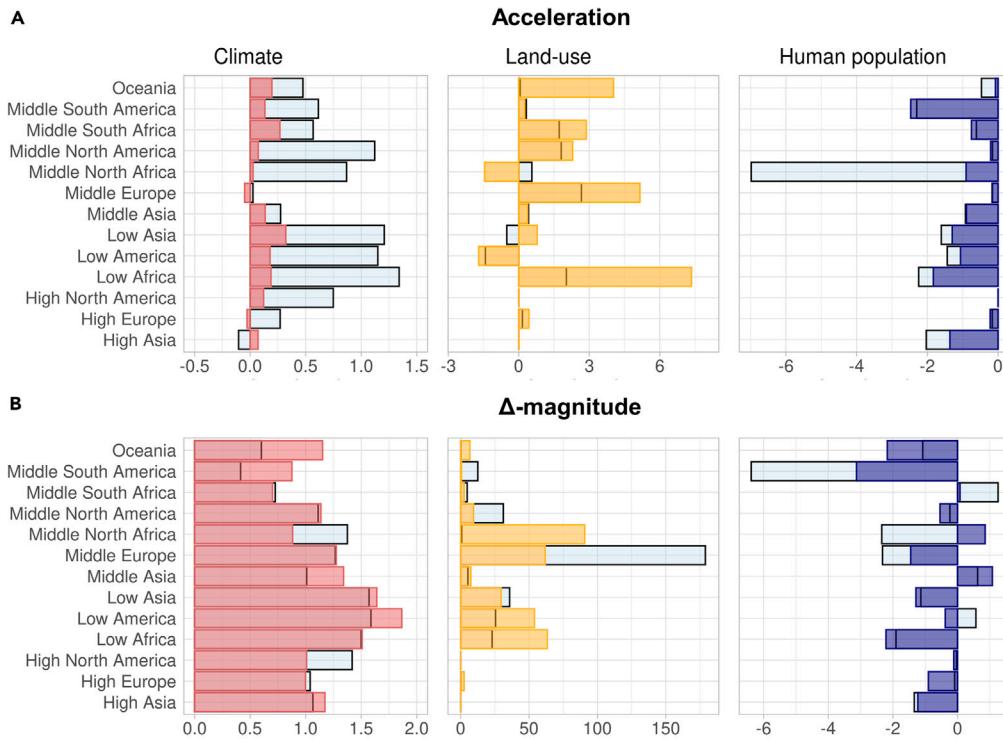


Figure 3. The exposure to global change drivers across mountains

Radial plots showing the values scaled independently for each variable (0–1) of the future velocity (A) and magnitude (B) of three global change drivers in different mountain areas, under future high-emissions scenario (period 2020–2050).

**Figure 4. The acceleration of the exposure to global change drivers across mountains**

Future acceleration, i.e., the difference in velocity of change between the future and the baseline epoch (A), and future Δ -magnitude of change, i.e., the difference in magnitude of change between the future and the baseline epoch (B) in the different mountain areas of the world, under high-emissions scenario. Colored bars represent the values of the acceleration for each mountain area, while empty bars represent the values of the acceleration for the reference lowland regions.

Baseline epoch

In the baseline epoch, High North America and High Europe were the areas with the lowest overall exposure, considering both the two metrics and the three drivers of change together (Figure S5). Considering climate change, Middle North Africa showed high values of both velocity and magnitude of change (median velocity = 0.56 km/year; median magnitude = 3.48) (Tables S3 and S6). Land-use change was instead particularly high in Middle South Africa (median velocity = 2.31 km/year; median magnitude = 4.94) (Tables S4 and S7). Human population density has been a relevant driver of past change for many mountain areas, in terms of both velocity and magnitude. Middle South America, for instance, showed the highest values in terms of both velocity and magnitude of human population change (median velocity = 2.22 km/year; median magnitude = 5.93), followed by Low Africa (median velocity = 1.76 km/year; median magnitude = 5.30) (Tables S5 and S8).

We also looked at the influence of topographic features and medium elevation on global change exposure (Figures S10 and S11). We found mountains of lower overall elevation and topographic complexity have the highest climate change velocity, in all scenarios. The magnitude of change did not substantially differ based on elevation, with the exception of land use, which showed the highest magnitude in low-elevation mountains, in all scenarios.

The acceleration of the exposure across mountain areas

High-emissions scenario

The acceleration, i.e., the difference in velocity of change between the future (high-emissions scenario) and the baseline epoch, was positive for climate change and land-use change across most mountainous areas. Conversely, acceleration of human population was negative (Figure 4A). Mountains of Low Asia and Middle South Africa areas showed the highest climatic acceleration (respectively +0.32 km/year and +0.27 km/year) (Table S3), while Low Africa and Middle Europe mountains showed the highest acceleration for land-use change (respectively +7.35 km/year and +5.15 km/year) (Table S4). Specifically, mountain ranges of Central Africa such as the Cameroon Island Chain showed the highest land-use acceleration (median = 24.78 km/year) (Table S10). The acceleration of the human population was instead negative in all mountain areas and their reference lowlands areas, meaning a decrease in the velocity of change from the baseline epoch to the future (Table S5).

Similar to the acceleration of velocity, the Δ -magnitude of climate change was positive under this future scenario in all mountain areas (Figure 4B; Table S6). This was also the case for land-use change (Table S7). Mountain areas with the highest Δ -magnitude of climate change were Low America (+1.86), Low Asia (median = +1.64), and Low Africa (+1.51). Middle North Africa and Low Africa showed the highest Δ -magnitudes for land-use change (respectively +90.70 and +63.34). Human population showed instead negative Δ -magnitude values except for

Middle Asia, Middle North Africa, and Middle South Africa ([Table S8](#)). Within those exceptions, the Himalaya for instance is one of the mountain ranges with the highest Δ-magnitude for this driver (+4.12) ([Table S14](#)).

Intermediate-emissions scenario

Under the intermediate-emissions scenario, climate showed an overall lower acceleration across mountains compared to the other scenario, while land-use generally showed a greater acceleration ([Figure S12A](#); [Tables S3](#) and [S4](#)). Climate change acceleration was even negative for mountains in Middle Europe, High Europe, and High Asia. The acceleration of land-use change was always positive instead, with the highest values for Middle South America (+7.21 km/year) and Low Africa (+7.10).

The Δ-magnitude of climate change showed negative values, except for mountains of High North America and High Asia, showing values very close to 0 ([Table S6](#)). Conversely, Δ-magnitudes of land-use change was high in all mountain areas, with the highest values in Middle North Africa and Middle South Africa mountains (respectively +80.19 and +36.66) ([Figure S12B](#); [Table S7](#)). Under this scenario human population driver of change showed very similar trends to high-emissions scenario, in terms of both velocity and magnitude ([Tables S5](#) and [S8](#)).

The exposure of mountains vs. lowlands

Mountains worldwide showed a lower velocity of land-use change and especially climate change compared to lowlands, both in the past and under future scenarios ([Table S1](#)). Conversely, the magnitude of change of all drivers was higher in mountains than lowlands, both in the past and under future scenarios ([Table S2](#)).

We compared the acceleration and the Δ-magnitude (i.e., the difference between future and past magnitude) of each mountain area with their lowland counterparts (i.e., the portion of the globe divided according to continent and latitude which contains that mountain area, excluding the mountain area itself) ([Figure 4](#); [Figure S12](#)).

High-emissions scenario

Under high-emissions scenario, all mountain areas showed the same positive or negative trends of their reference lowland regions in terms of climate acceleration, except for Middle North Africa and Low Asia mountains. Land-use acceleration was particularly higher in the mountains of Low Africa compared to the respective lowland area (respectively 7.34 km/year vs. 2.02 km/year). Δ-magnitude was generally higher in mountain areas than in the reference lowlands areas for both climate and land use, with a few exceptions (i.e., Middle North Africa and high North America for climate change and Middle Europe for land-use change). Human population showed globally a deceleration, with very similar values between mountains and reference lowlands areas. Middle North Africa was an exception, as the acceleration was much lower in lowlands than mountains (−6.98 km/year vs. −0.90 km/year).

Intermediate-emissions scenario

The intermediate-emissions scenario showed notable differences in climatic acceleration between mountain areas and lowlands, with the mountains generally showing lower accelerations. Δ-magnitude of climate change was more similar under this scenario between mountains and reference lowlands than the high-emissions scenario. Land-use change instead showed substantial differences in Middle South Africa and Middle North Africa, where mountains showed a much higher Δ-magnitude compared to the lowlands (respectively 36.66 vs. 18.33 and 80.19 vs. 4.10). The population under this scenario showed notable differences in the case of Middle South America, Middle South Africa, and Middle North Africa.

DISCUSSION

The exposure to global change drivers varies considerably across the world's mountains, but we observed some common trends. Human population density showed overall positive change in the past (both velocity and magnitude) but negative change in the future, thus being a more significant driver of change in the baseline epoch compared to the future one. Both the acceleration and the Δ-magnitude of climate and land use are positive in most mountain areas, resulting in an increasing future exposure of world's mountains to these two drivers. Specifically, mountains showed the highest climate change velocity under the high-emissions scenario (due to a significant increase of the temperature^{6,61}), but the highest anthropogenic land-use change velocity under the intermediate-emissions scenario, due to an increase in human land-use activities.² Notably the magnitude of climate change under the intermediate-emissions scenario is lower than that in the past. This is explained by a level of emissions quite stable by 2050 under this scenario, with a consequent low global warming and a substantial increase in temperature only after 2050.⁶¹

Mountain areas with a higher velocity and a higher magnitude of both climate change and land-use change will be especially at risk in the future (e.g., mountains of sub-Saharan Africa). In these areas, the significant impact of climate change will be exacerbated by the synergistic action of anthropogenic land-use change.⁶³ Areas with both low velocities and low magnitudes of climate change are instead areas that will likely retain more stable climates and could potentially act as local climate refugia^{46,47} (e.g., North Europe's or North America's mountains).

In our study, mountains showed lower velocities of climate and anthropogenic land-use change compared to the lowlands, in line with previous literature.^{7,9,22,55,56} However, we also found that the magnitude of change was higher in mountains than the lowlands, both in the past and under future emissions scenarios.^{24,50}

The relevance of considering different metrics and different drivers

The discrepancy in our findings between the velocity and the magnitude of change, with the former being higher in the lowlands and the latter being higher in the mountains, underlines the importance of considering the two metrics together to assess the whole exposure of mountain areas to global change drivers. The overall low velocities of change seen in our results highlight that mountain areas could act potentially as future climatic refugia, as they already did during past climatic shifts.^{21–23,64} The capacity of complex topography to provide a spatial buffer for climate change has been recognized qualitatively and assessed at different scales.^{7,22,56} However, when the magnitude of change exceeds the extent of the local spatial gradient, organisms might have to cross unsuitable conditions to reach a future environmental equivalent.²⁴

The velocity of change of a given variable is also intrinsically strongly related to the spatial gradient of that variable.²⁵ Thus, in general, mountains showed lower velocities of change than the lowlands, and mountains with higher spatial gradients (i.e., topographic complexity) showed lower velocities of change than plateaus or highlands⁵² as is the case for Low America and Middle South America (e.g., the Cordillera Occidental and Central in the Northern Andes). However, topographic complexity can hinder organisms' dispersal, posing risk to species with more limited movement ability.^{13,24} Furthermore, a species may find suitable climatic conditions nearby, but unsuitable habitat conditions due, for instance, to a change in land use or a higher level of fragmentation.^{13,27,59} Interestingly, our results showed a magnitude of future anthropogenic land-use change much greater than the past one, and in general much higher than the magnitude of the other drivers. Land use already plays a crucial role as a driver of change in mountain areas, especially in ecosystems at and below the treeline⁴¹ and is expected to do the same in the future according to our results. Anthropogenic land-use change might occur in areas previously not affected by this phenomenon. This means that even a low percentage increase in anthropogenic land use might result in a high magnitude of change, if anthropogenic land use was minimal or null during the first period. For instance, the Pyrenees showed a median land-use magnitude of change of 107 under the high-emissions scenario, but a null increase in cropland and pastureland and an increase of urbanization of just 1%. However, our metrics computed for the driver of anthropogenic land-use change offer less informative insights compared to others when making a general assessment of the exposure experienced by organisms. This is due to the large spatial scale (~25 km) associated with this specific driver.

Trends of the exposure in anthropogenic land-use change are frequently correlated with the ones of human population density. For instance, in Europe, a low velocity of land-use change is associated with a low velocity of human population change, indicating a correlation between land abandonment and population decline, especially in Mediterranean mountains.⁶⁵ In contrast, mountain ranges of Central Africa (Low Africa) exhibit a strong increase in exposure to both land use and population.

Our results showed that human population density, being an indirect driver of change, was the less relevant driver, showing negative velocities in the future and negative acceleration and Δ-magnitudes. Human population velocity of change can also assume negative values in our analysis, indicating a decrease in human population density over time. From our results this is a trend that emerges especially in some areas characterized by what is often defined as the "rural exodus,"^{41,65} which characterizes many areas of Europe. Analyzing the individual mountain ranges, however, a substantial increase in the population is observed in some areas, such as Central Africa or the Himalaya.⁴¹

Mountain areas at risk

We identified mountains with a high velocity and a high magnitude of both climate and anthropogenic land-use change (e.g., African mountains). These areas also showed a higher relative exposure (i.e., higher acceleration and high delta magnitude), meaning that in the future they will be more exposed to global changes than they were in the past. Here, we might assist to an overall decline in biodiversity, due to the extinction of specialized species that cannot adapt to the new environmental conditions and will likely suffer competition from rapidly expanding generalist species that exploit the new conditions.^{22,31,52,53}

We found that high exposure characterizes mountain areas in very different geographical contexts, but tropical mountains and specifically African mountains will be especially at risk. Tropical mountain ranges might experience strong human population growth and land-use intensification in the future, which may have negative consequences for biodiversity.^{19,66–68} Our results showed how all the mountains of sub-Saharan Africa will be particularly affected by the synergistic action of the three drivers of change. Climate change has been particularly relevant in the African continent over the last century^{69,70} and is now interacting with habitat destruction, land-use change, and fragmentation with negative effects on biodiversity and human communities.^{71–73} Specifically in East Africa we found numerous mountain ranges with a high exposure. Here, climate change is acting in synergy with land-use change to alter species distributions^{74,75} and their migratory patterns (e.g., for large herbivores), increasing conflicts with humans and leading to species decline.⁷⁶ In Ethiopian and Kenyan mountain areas, projections of climate change by the mid-21st century are characterized by an increase of temperature, increased frequency of extreme events, and alteration of precipitation patterns, with wetter rainy seasons in Kenya and prolonged aridity in Ethiopian highlands.⁷⁷ In these areas, population growth will also play a key role, showing the highest magnitude values in our analyses.⁷⁸ Even under an intermediate-emissions scenario, by 2050 in those areas human population and activities will be concentrated at high elevations, triggering cascade effects on remaining forest cover, biodiversity, and ecosystem services.³⁸

Mountain areas as climate refugia

We found mountains of Europe and North America (High Europe and Middle North America) having both low velocity and low magnitude of climate change. These regions may serve as local climatic refugia, protecting species from exposure to current climate shifts.^{46,48,79,80} Three main dimensions must be considered in identifying species' refugia: space, time, and species ecology. Our metrics of exposure encompasses both spatial and temporal aspects.⁸¹ In this sense, regions with low projected exposure may potentially act as local climatic refugia, as species

residing there would only need to make short-distance movements to adapt to climate changes.⁴⁹ As we did not consider the third dimension (i.e., species ecology), we cannot define specific refugia for each taxon, as not all species face the same level of risk from high exposure.⁸² When species-specific ecological data are considered together with biophysical and sociopolitical factors, our metrics can be integrated into a multifaceted prioritization process to identify potential macro- and microrefugia.^{28,79,81,83} Additionally, we did not account for microclimatic conditions in our analysis. These conditions define the niche of each species and may remain stable even in highly exposed regions, defining microrefugia that we cannot identify.⁸⁴

To effectively act as local refugia, these regions require proactive conservation, e.g., protection from pressures such as overexploitation or unsustainable tourism.^{59,85} Moreover, integrating the potential refugia identification with the measurements of functional connectivity would also be necessary to increase the ecological meaning of velocity-based climate exposure.^{81,86} In this sense, our study is useful as a starting point to identify areas able to connect current and future climate analogues along paths that minimize exposure to different climates.^{24,51,87}

Mapping different metrics of climate and land-use change enables identifying areas where species may undergo rapid shifts in their optimal climatic conditions while simultaneously having their potential movement constrained by land-use change. Global climate mitigation is paramount to reduce the risk of high magnitude and velocity of change in mountains, but this needs to be coupled with sustainable land-use policy that together prevent local degradation of important areas for biodiversity.⁸⁸

By considering both magnitude and velocity together, we identified regions facing higher exposure to global change drivers and regions expected to act as refugia. Coarse filter metrics such as those we estimated in this study could be complemented with fine-filter (species-specific) metrics where that information is available, to identify potential macro- and microrefugia that in combination maximize both transient and long-term resilience to climate change.⁸¹ In this sense, our results can serve as a starting point for guiding long-term monitoring projects and prioritizing areas for conservation efforts. Starting or maintaining monitoring programs in areas projected to experience rapid environmental change is essential to provide a deeper comprehension of how biodiversity reacts to unprecedented levels of environmental change as well as the true potential for adaptation.⁸⁹ Untangling the interacting effects of global change drivers and identifying macro-scale trends contribute to laying the groundwork for the establishment of global programs focused on preserving natural resources in mountainous areas,⁴¹ including those historically instituted by the Convention on Biological Diversity (CBD; <https://www.cbd.int>).

Limitations of the study

In our analysis, we assessed the exposure that global mountain areas face concerning different global change drivers, including climate, land use, and human population, through the estimation of both the velocity and magnitude of change. A limitation of our study pertains to the spatial resolution of our analysis. The spatial resolution of the original data used for calculating the metrics restricts our ability to capture the intricate climatic and environmental variations that occur over short distances in mountain regions, especially regarding land use (~ 25 km). Nevertheless, we were constrained by the availability of the datasets, which were the only ones meeting the criteria required for our analyses, including global coverage and annual temporal resolution for both historical and future data. Another limitation was our inability to account for the change in the intensity of land use. Those changes, particularly in agricultural or pastoral areas, can have a substantial impact on biodiversity, but quantifying it is challenging due to the lack of global-scale datasets with a resolution of ≤ 25 km that represent this specific variable. We also recognized that based on the chosen dataset the mountain population size can vary a lot,^{15,90} but since our aim is to carry out comparisons (between eras and between mountain areas), we believe that the bias does not significantly affect our results.

We identified regions with lower overall exposure, which could potentially serve as refugia for species. However, it is important to note that the concept of climate velocity, and exposure in general, lacks key biological details, such as species-specific dispersal capacity, landscape permeability, habitat suitability, and inter-species interactions.⁵² Our models did not incorporate species-specific information, including sensitivity, life history, natural dispersal capabilities, and phenotypic plasticity, which are pivotal for species to adapt to new climate conditions.^{54,91} Additionally, it is crucial to recognize that not all species face the same level of risk from high exposure.⁸² This absence of biological data leads to climate velocities being somewhat general metrics. Enhancing the concept with a more realistic biological perspective could significantly bolster its utility in conservation efforts.

Furthermore, in our work, we have focused only on some of the key drivers of change, even if there are other drivers which could be important in specific contexts such as unsustainable tourism.⁸⁵ Likewise our global-scale assessment of human pressure did not consider other climatic variables which might be locally important, especially for some species, such as microclimatic conditions,^{52,92} solar radiation, wind direction, and substrate.^{93–96}

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2024.109734>.

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Conceptualization, C.D. and M.D.M.; methodology, C.D., M.D.M., and G.D.; writing – original draft, C.D.; writing – review and editing, C.D., M.D.M., and G.D.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Global mountain inventory v2	Global Mountain Biodiversity Assessment (GMBA) (Snethlage et al. ⁶²)	https://www.earthenv.org/mountains
Climate data	CHELSA V1.2 (Karger et al. ⁹⁷)	https://envicloud.wsl.ch/#/?prefix=chelsa%2Fchelsa_V1
Land-use data	Land-use Harmonization (Hurtt et al. ⁹⁸)	https://luh.umd.edu/data.shtml
Human population density data for future	High-resolution global population projections dataset developed with CMIP6 RCP and SSP scenarios for year 2010–2100 (Olén & Lehsten ⁹⁹)	https://dataguru.lu.se/app#worldpop
Human population density for the baseline epoch	Global Population Count Grid Time Series Estimates. NASA Socioeconomic Data and Applications Center (SEDAC)- Gao et al. ¹⁰⁰	https://sedac.ciesin.columbia.edu/data/set/popdynamics-global-pop-count-time-series-estimates/data-download
Velocity of change and magnitude of change final rasters	This paper	https://doi.org/10.5281/zenodo.10521813
Software and algorithms		
RStudio (version 4.2.2)	RStudio Team	http://www.rstudio.com/
Geographic Resources Analysis Support System (GRASS) Software (version 7.8.6)	Open Source Geospatial Foundation.	https://grass.osgeo.org
gVoCC package	Garcia Molinos et al. ¹⁰¹	https://rdrr.io/github/JorGarMol/VoCC/

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Chiara Dragonetti (chiara.dragonetti@uniroma1.it).

Materials availability

This study did not generate new unique materials.

Data and code availability

Data

This paper analyzes existing, publicly available data. Data sources are listed in Zenodo, in the README.txt file
<https://doi.org/10.5281/zenodo.10521813>.

Code

Original codes and final rasters are reported in Zenodo <https://doi.org/10.5281/zenodo.10521813>.

Additional information requests

Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

METHODS DETAILS

Delineation of mountain areas

We used the standard version of the mountain inventory v2 dataset produced by the Global Mountain Biodiversity Assessment (GMBA) to identify mountainous areas worldwide.⁶² This inventory of the world's mountain is generated after a manual digitalization of the range's general shape and after a definition of the mountain terrain based on ruggedness, defined as highest minus lowest elevation in meter within eight circular neighborhood analysis windows (NAWs) of different sizes (from 1 pixel (~250 m) to 20 (~5 km) around each point, combined with empirically derived thresholds for each NAW. This dataset also contains a selection of 289 polygons representing the main mountain ranges of the globe, the results of which we have reported specifically ([Tables S9–S14](#)). We also reported the exposure of the 289 mountain ranges in

relation to topography and medium elevation. The latter was calculated in a new analysis based on the DEM (digital elevation model) at a resolution of 1 km (Figures S10 and S11). We then grouped mountain ranges into different areas, following Nogués-Bravo et al., 2007,³³ which grouped the World Mountain Map¹⁰² by continents and latitude using the Holdridge classification.¹⁰³ Thus, 13 different mountain areas were considered: (1) America high-latitude mountains at northern hemisphere (High North America); (2) America mid-latitude mountains at northern hemisphere (Middle North America); (3) America low-latitude mountains (Low America); (4) America mid-latitude mountains at southern hemisphere (Middle South America); (5) Europe high-latitude mountains (High Europe); (6) Europe mid-latitude mountains (Middle Europe); (7) Africa mid-latitude mountains at northern hemisphere (Middle North Africa); (8) Africa low-latitude mountains (Low Africa); (9) Africa mid-latitude mountains at southern hemisphere (Middle South Africa); (10) Asia high latitude mountains (High Asia); (11) Asia mid-latitude mountains (Middle Asia); (12) Asia low-latitude mountains (Low Asia); (13) Australia and New Zealand (Oceania) (Figure 2). We then associated each mountain area with a reference area, i.e., the area outside mountains in each continent and latitudinal band considered.

Drivers of global change

We quantified the exposure of the world's mountain areas to three major global change drivers: climate change, land-use change, and human population density. We focused on two different climatic variables: yearly mean temperature (C°) and yearly mean precipitation amount (g/m3), extracted from CHELSA V1.2 database.⁹⁷ Temperature is the standard variable used in calculating the velocity of climate change^{7,59,60} and we decided to also consider precipitation, often included in climate-velocity analyses, as it regulates the distribution and productivity of plant communities.^{52,59} We averaged monthly minimum and maximum temperature data extracted from CHELSA V1.2 database across each year, obtaining a raster with the mean temperature estimated for each pixel, for each year, worldwide. Similarly, we obtained the yearly mean precipitation by averaging the mean monthly precipitation across each year.

We extracted yearly land use data from the Land-Use Harmonization (LUH2) dataset.⁹⁸ We decided to focus on anthropic land-use categories which are considered to have overall negative impacts on biodiversity¹⁰⁴: cropland, pastureland, and urban.

We extracted human population density data from the human population's count scenarios of the dataset of Olén & Lehsten, 2022,⁹⁹ at 5-year intervals. Since we did not have past human population data from Olén & Lehsten, we used a different dataset¹⁰⁰ to extrapolate them, after verifying the spatial correlation between the two data in the present (Pearson's coefficient = 0.80). We added a value of 1 to the raster layers of the human population count used for interpolation to avoid having NA or infinite values in the final raster.

Data had a native original resolution of 1 km for population data, 5 km for climate, and 25 km for land-use. We re-aggregated human population data at a resolution of 5 km to reduce the difference with land-use data, summing the number of individuals of the twenty-five adjacent pixels. We performed the analyses with the other datasets at their native resolution. We then ultimately downscaled the velocity and magnitude of change of land use at 5 km, to obtain a consistent resolution across the results.

Metrics of global change

Velocity of change

For each driver of global change, we estimated two different metrics, the velocity and the magnitude of change, globally. We estimated each metric for a time slice of 30 years, both in the past (1975–2005) and in the future (2020–2050), under two different emissions scenarios, the SSP-RCP 2–4.5 (i.e., intermediate-emissions) and the SSP-RCP 5–8.5 (i.e., high-emissions).⁶¹ According to the intermediate-emissions scenario, global warming is estimated to be between 2.1°C and 3.5°C in 2100, with development trends remaining mostly consistent with historical patterns.^{6,105} The high-emissions scenario projects the highest emissions, with global warming of 3.3°C–5.7°C by 2100^{6,106}.

We estimated the "acceleration" of each driver as the difference between the past and future velocity of change, and the Δ-magnitude as the difference between the past and future magnitude of change.

The velocity of change is a vector that describes the velocity and the direction that a point on a gridded map would need to move to maintain the same environmental conditions in a certain time frame.⁵² We measured the velocity of change following the gradient-based approach,⁷ and using the gVoCC package¹⁰¹ implemented in R (version 4.2.2¹⁰⁷). Here the velocity of change is defined as the ratio between a temporal trend (the rate of change of each variable through time, estimated as a regression slope) and the corresponding spatial gradient of that variable (i.e., vector sum of longitudinal and latitudinal pairwise differences at each focal cell using a 3 × 3-cell neighborhood):

$$\frac{\text{slope} \left(\frac{\text{unit}}{\text{year}} \right)}{\text{spatial gradient} \left(\frac{\text{unit}}{\text{km}} \right)} = \text{VoCC (km / year)} \quad (\text{Equation 1})$$

To estimate climate change velocity, we focused on mean temperature (C°) and precipitation amount (g/m3). We estimated the velocity of change separately for mean temperature and precipitation, and then we added the absolute values of the two climatic variables to consider the combined effect of climate change.⁵⁹ We decided to use the absolute values to account for the fact that both positive (e.g., increased temperature) and negative (e.g., decreased precipitation) velocities might be detrimental for biodiversity, and represent a change from the original climatic conditions.⁵²

We considered 4 Global Circulation Models (GCMs) for each future scenario, derived from the Coupled Model Intercomparison Project 5 (CMIP5): ACCESS 1–3, CESM1-BGC, CMCC-CM, MIROC 5. We obtained the climate velocity for each GCM under each emissions scenario,

and we averaged velocity estimates between GCMs for the same variable within each RCP scenario to produce an ensemble estimate. We also measured the uncertainty of the estimates by calculating the standard error across values.

We estimated the future velocity of change of land-use according to the same emissions scenarios considered for climate (intermediate-emissions and high-emissions). In this case, we calculated distinct land-use change velocities for each of the three classes considered (urban, cropland, pastureland). We then aggregated the real values of these velocities to avoid any duplication of change within a specified pixel. For instance, if there is a 3% loss in cropland (negative cropland velocity) that transforms into a 3% gain in urban area (positive urban velocity), the two velocities offset each other, resulting in a net detrimental velocity of 0.¹⁰⁸

A velocity of change of 0.99 km/year means that an organism would need to move at that speed to maintain the same degree of land use that is experiencing in the origin pixel.

We estimated the velocity of change of the human population density, extracting human population's count scenarios of Coupled Model Intercomparison Project 6 (CMIP6) from the dataset of Olén & Lehsten.⁹⁹ For this variable, we scaled all values in log10 to reduce the skewness of data. A velocity of change of the human population of 0.30 km/year, for example, means that a species must move at that speed to find the same levels of human density as currently experienced. Human population and land use velocity of change, unlike the velocities of climate change, can also assume negative values. In this case, a negative velocity means a decrease in human population density/detrimental land-use change over time, and a consequently lower pressure on the environment.

The choice to use two different CMIPs, respectively CMIP5 for climate and CMIP6 for population density, was forced by the need of data with the finest possible temporal resolution, to estimate the velocity of change. However, this has not affected our evaluation of multiple global change drivers, as we scaled the velocity and magnitude of each driver for our comparison.

To quantify the acceleration of global change across the world's mountains, we calculated the difference between the median of the future velocity of change and the median velocity of change of the baseline epoch. This allowed us to compare the velocity of change between the past and the future.

Magnitude of change

We estimated the magnitude of change for the same variables used to estimate velocity (i.e., climate, land use, human population density), for the baseline epoch (1975–2005) and future epoch (2020–2050). We estimated the magnitude of change as the standardized Euclidean distance of values between two-time steps, *sensu* Williams et al. 2007¹⁰⁹:

$$M = \sqrt{\sum \frac{(X^{t2} - X^{t1})^2}{sd^{t12}}} \quad (\text{Equation 2})$$

Where x_{t1} and x_{t2} represent values for the variable x at the beginning and at the end of the period considered (e.g., for the baseline epoch, $t1 = 1975$, $t2 = 2005$).

To estimate values of the climatic variables, we considered the average values of the 10 years before and the 10 years after the reference year. For instance, for the historical epoch we considered the average values from 1965 to 1985 to estimate 1975 ($t1$) and the average values from 1995 to 2005 to estimate 2005 ($t2$).

As we did for the velocity of change, we considered different Global Circulation Models under two emissions scenarios (i.e., intermediate-emissions and high-emissions), and then we averaged the magnitude estimates between GCMs within an RCP scenario to produce an ensemble estimate. We quantified the difference in magnitude of change across the world's mountains (Δ -magnitude), as the difference between the median future magnitude and the median magnitude in the baseline epoch. Such Δ -magnitude for climate is estimated as the sum of the absolute values of the differences estimated separately for temperature and precipitation.

Within the results, we reported the medians as a comparison value, both across mountains and between mountains and lowlands. We did not perform statistical tests to determine the significance of the differences observed between different epochs and regions, as in each comparison we considered the entire statistical population of values (i.e., every pixel). We represented the entire distribution of values for each region (mountain and lowland reference) and each epoch to allow for a full comparison (Figures S13–S18).