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# Accelerating global mountain forest loss threatens biodiversity hotspots

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## SUMMARY

The frontier of forest loss has encroached into mountains in some regions. However, the global distribution of forest loss in mountain areas, which are home to >85% of the world's birds, mammals, and amphibians, is uncertain. Here we combine multiple datasets, including global forest change and selected species distributions, to examine spatiotemporal patterns, drivers and impacts of mountain forest loss. We find 78.1 Mha of montane forest was lost during 2001–2018 and annual loss accelerated significantly, with recent losses being 2.7-fold greater than those at the beginning of the century. Key drivers of mountain forest loss include commercial forestry, agriculture, and wildfire. Areas with the greatest forest loss overlap with important tropical biodiversity hotspots. Our results indicate protected areas within mountain biodiversity hotspots experienced lower loss rates than their surroundings. Increasing the area of protection in mountains should be central to preserving montane forests and biodiversity in the future.

# INTRODUCTION

Mountains are vital to the world's terrestrial biodiversity as they provide habitat to more than 85% of the world's bird, mammal, and amphibian species[1]. Montane forests serve as important refuges for large numbers of rare and endangered species with small geographical distributions, making them represent regions of high conservation significance[2]. As many montane species have narrow ranges[3], even relatively small reductions in forest habitat may increase their risk of extinction. Unfortunately, forest loss and degradation pose significant threats to the persistence of forest dwelling species that rely on specific microenvironments worldwide[4]. In addition, climate change is forcing many montane species to move to higher elevations in search of suitable habitats[5,6], but their ability to do so is potentially limited by topographic constraints and the integrity of the habitat[7]. Understanding the dynamics of mountain forest loss worldwide is therefore crucial for predicting and mitigating the potential impacts on sensitive forest species[8].

Mountain forest loss was historically limited in many areas as high elevations and steep slopes presented physical barriers to human exploitation[9]. As such, most forest exploitation occurred in more accessible lowland areas for a variety of activities including logging and agriculture[10-12]. However, since the turn of the 21st century, mountain forests have been increasingly exploited for timber and wood products, as well as to support emerging agricultural systems, such as boom crops and tree-based plantations, for example in Southeast Asia[13-15]. These activities have reshaped montane forests, potentially reducing the size and number of refuge areas, increasing the risk of extinction of forest dwelling species[16], and weakening the ability of forests to store carbon[13] and regulate climate[17]. Elsewhere, such as in the Andes, there is reported evidence of an overall net gain in woody vegetation, the dynamics of which vary with elevation[18]. There, mountain forest losses dominated vegetation change at lower elevations (1,000–1,499 m) from 2011 to 2014, but forest gains occurred at higher elevations above 1,500 m[18]. Regional reports[13-18] that are often based on a diverse array of locally derived data and varying analytical approaches, may not necessarily contribute to the determination of clear and generalized trends in mountain forest loss at a global scale, leading to difficulties in assessing the impact of forest loss over mountain regions. Thus, a wider global analysis—with a common analytical framework—conducted in the 21st century when there is evidence of the frontier of forest loss encroaching into mountains, is required to accurately understand mountain forest loss patterns, trends, drivers and impacts worldwide. This information is essential for developing effective biodiversity conservation and forest management strategies in the future.

Here, we conducted a comprehensive assessment of global mountain forest loss during the first two decades of the 21st century. We first assessed forest loss patterns across global mountains and determined the proportion of areas showing signs of regrowth. Second, we determined the extent of mountain forest loss within biodiversity hotspots across a range of elevation gradients, as elevation regulates biophysical climate impacts[17] and therefore potentially reshapes expected species responses to climate change[19]. Third, we estimated the fraction of mountain forest loss within mountain biodiversity hotspots in and around protected areas (PAs). We also examined the drivers of mountain forest loss by comparing our mountain forest loss maps and statistics with other recently developed land-use maps[20]. We find that annual forest loss accelerated significantly across global mountains during the first two decades of the 21st century. Unfortunately, many of areas with the greatest mountain forest loss overlap with critical tropical biodiversity hotspots. Forestry caused the greatest mountain forest loss at the global scale. However, within biodiversity hotspots, commodity agriculture was the main driver of mountain forest loss in Southeast Asia and shifting cultivation was preeminent in tropical Africa and South America. Our results also emphasize the significance of protected areas in conserving forest-dependent biodiversity in mountains and provide a strong foundation for creating region-specific conservation recommendations aimed at preserving forests and the biodiversity they harbour.

## RESULTS

### *Patterns and drivers of mountain forest change*

Mountain forests covered 1,100 million hectares (Mha) globally in 2000 (Table 1). Approximately 78.1 Mha of forest loss occurred in mountain regions between 2001 and 2018, which constitutes a relative gross loss of 7.1% worldwide since 2000 (Table S1). Mean annual gross loss was 4.3 Mha $yr^{-1}$, equivalent to 0.39% $yr^{-1}$ (Table 1). We found that mountain forest loss was significantly accelerating worldwide, with a rate at 0.202 Mha $yr^{-2}$ ($p < 0.01$). Importantly, there was a striking difference in mountain forest loss rate between periods before and after 2010. Annual forest loss in mountains increased more than 1.5 fold from <3.5 Mha $yr^{-1}$ during 2001 to 2009 to 5.2 Mha $yr^{-1}$ during the period 2010 to 2018. Tropical mountains experienced the most rapid acceleration, with the annual loss after 2010 being twice that before 2010. This transition was probably related to the rapid expansion of agriculture into highland areas, for example in mainland Southeast Asia[14,15], as well as increased exploitation of mountain forest products as lowland forests became depleted or were the focus of greater forest protection.

Between 2001 and 2018, global mountain forest loss reached a prominent peak in 2016 (about 65% higher than in the previous year). This surge was mainly driven by forest loss in Asian mountains (Fig. 1A). Compared with the 2016 peak, annual mountain forest loss decreased in 2017 and 2018, but the annual loss in these two years (mean of 6.5 Mha $yr^{-1}$) remained high compared with the earlier years of the 21st century. The key activities associated with mountain forest loss were commercial forestry (42%), followed by wildfires (29%), shifting cultivation (15%) and commodity agriculture (10%; Fig. 3A). These drivers starkly contrast with the activities reported recently for global forest loss[20]. While our focus was forest loss, we note that substantial gains in mountain forests have also occurred worldwide. Using a sample-based method[21,22], we found that 23.14% (1,157 of 5,000 pixels) of the forest loss areas at some point during 2001–2018 experienced some degree of tree cover regrowth by 2019 (Fig. S1; Supplementary Data S1). For the whole period 2000–2018, the annual net rate of mountain forest loss, accounting for both forest losses and gains, was 0.31% per year (Table 1).

Five of seven global regions (Asia, South America, Africa, Europe, and Australia) experienced significant acceleration in mountain forest loss during the period of observation, with North America and Oceania being exceptions (Fig. 1A; Table 1). Over the 18-year study period, the greatest loss of mountain forest area occurred in Asia (39.8 Mha), accounting for more than half of the global total (Table 1). This increase in mountain forest loss primarily occurred in southern Asia (≤30°N), where high population densities potentially have a negative effect on forest cover and integrity[23,24]. However, the trend in mountain forest loss in northern Asia was not significant (Table 1). We also find clear regional differences in the drivers of mountain forest loss and the proportion of forest gain within Asia (Tables 1 and S1). Mountain forest loss in northern Asia (>30°N) was primarily attributed to wildfire (e.g., Russia); and this region experienced only a small proportion of forest gain (~15%). By contrast, mountain forest loss in southern Asia was driven by commercial forestry (e.g., in southern China) and commodity agriculture (e.g., in Indonesia, Vietnam and Myanmar); and ~40% of loss areas showed signs of regrowth—in part, due to the maturation of plantation trees (Table S1; Fig. S1). North America had the second greatest mountain forest loss area (18.7 Mha; 24% of global mountain forest loss), with ~16% of forest gain (Table 1). This proportional gain was less than half that in South America (~33%) and thus the annual net rate of forest loss in North America (0.41%

yr$^{-1}$) was more than twice that of South America (0.19% yr$^{-1}$; Table 1). Africa experienced the greatest relative forest loss of 0.54% yr$^{-1}$ and had the smallest proportional forest gain of 15.4%. Therefore, the annual net rate of mountain forest loss in Africa was greater than that of any other region at 0.48% per year (Table 1).

Globally, substantial mountain forest losses occurred at elevations <1,000 m, where >70% of forest gain also occurred (Fig. S2). From the 2000s to 2010s, there was a large increase in forest loss at low-to-moderate elevations, particularly below 1,000 m (Fig. S3). This pattern of increased forest loss at low elevations might obscure the fact that forest loss is creeping upwards. Further, temporal patterns indicate increases in forest loss at higher elevations in Asia, South America, and particularly Africa (Fig. S4B,D,E). In Asia, the peak of forest loss in 2016 was primarily concentrated at 100–300 m, but extended up to 1,200 m, which largely followed the global pattern (Fig. S4A–B). In North America, most mountain forest loss was concentrated in 2004 and 2005 at elevations below 1,000 m (Fig. S4C). In South America, Africa, and Europe, mountain forest loss reached a peak in 2017 at elevations of about 250 m, 300 m, and 500 m elevation, respectively (Fig. S4D–F). In contrast, mountain forest loss in Australia did not follow a particular trend with respect to elevation, but there were specific years (in 2003, 2007, 2009, 2013, and 2016) with significant loss (Fig. S4G) that were linked to drought and bushfires[25-28].

We found significant increases in mountain forest loss in tropical and temperate latitudes, but not at boreal latitudes (Fig. 1B). Tropical montane forests, which experienced the greatest loss (32.9 Mha; 42% of global mountain forest loss), also had the fastest acceleration of loss at 0.131 Mha yr$^{-2}$ (Fig. 1B; Table 1). Around 31.2% of these losses have shown signs of regrowth, which is higher than that of temperate and boreal regions (Table 1). Our results show that the dominant drivers of mountain forest loss in the tropics were shifting cultivation (44%), commodity agriculture (28%), and commercial forestry (24%; Fig. 3A). In Indonesia, the tropical country with the greatest loss of mountain forests at 3.97 Mha (relative loss of 7.1%), commodity agriculture was the dominant driver (Table S1). Forest loss in Laos (3.08 Mha; 16.4%) and Vietnam (2.81 Mha; 17.8%) was also substantial (Table S1). Parts of Laos, Vietnam and northern Thailand (1.29 Mha; 7.9%) form a cluster in mainland Southeast Asia where agriculture-driven deforestation has moved to higher elevations in recent decades[15,29]. The loss of forest in Myanmar (2.80 Mha; 8.8%), which was affected by both commercial forestry and commodity agriculture (Table S1), was likely related to its recent re-engagement with regional and global economies[30]. Malaysia was ranked number 10 worldwide in mountain forest loss (2.2 Mha; 16.4%) (Table S1), with the most loss occurring in Peninsular Malaysia, where oil palm expansion before 2010 was an important driver (Fig. 2A)[31]. These Southeast Asian countries were all also in the top 10 with respect to acceleration in mountain forest loss (Table S1; Fig. 2B). In those regions, the loss was primarily attributed to deforestation in mountains through permanent land-use change for commodity production (Table S1), for example, rubber, oil palm, and feed corn[20,32]; this process can also be validated by sample-based manual interpretation (Supplementary Data). Brazil has experienced well-publicized lowland forest loss in recent decades[33]. Our results show that Brazil also experienced 2.26 Mha (7.6%) of mountain forest loss driven largely by shifting cultivation (Table S1). This result highlights the different drivers of mountain versus lowland forest loss, for which the latter is widely reported to be caused by conversion for commodity agriculture (e.g., soy)[34] and grazing[35]. Also associated with shifting cultivation is the loss of montane forests in other South American countries (e.g., Colombia and Peru) and in Africa (e.g., Guinea and Madagascar), with a total loss of 4.99 Mha in these four countries (Table S1).

Temperate montane forests had the second greatest area of losses between 2001 and 2018 (27.9 Mha; 36% of the global total). The primary cause of these losses was commercial forestry, with more than 75% of the area lost being attributed to this sector (Fig. 3A). Despite the large area lost, temperate montane forests had the smallest annual decrease among all the forests studied, with a rate of 0.28% per year (Table 1). In the mountains of the United States, forest loss in the west was greater than in the east (Fig. 2A); the leading cause was commercial forestry, followed by wildfire (Table S1). Most mountain forest loss in temperate China occurred in the southern mountains with a fast pace of loss (Fig. 2B) and was primarily driven by commercial forestry (Table S1). Elsewhere, absolute losses of mountain forests were small in Europe, but countries like Portugal, Ireland, and the United Kingdom had substantial percentage losses relative to forest cover in 2000. Again, commercial forestry contributed to >90% of losses in these countries (Table S1).

Losses in boreal regions were comparatively small than at lower latitudes, but in some years montane forest losses at these high latitude locations rivalled those found in temperate areas, and were on the order of 1.6 to 2.1 Mha $yr^{-1}$ (Fig. 1B). The rate of acceleration in losses of boreal mountain forests was also very low (0.016 Mha $yr^{-2}$; Table 1). Russia and Canada experienced a large amount of mountain forest loss: 11.95 Mha (6.9%) and 5.57 Mha (7.4%), respectively (Table S1). Wildfire (69%) was the dominant disturbance to boreal montane forests (Fig. 3A). However, the lack of a significant trend in boreal mountain forest loss (Fig. 1B; Table 1) may suggest that the reported increase in boreal wildfires[36] only affects montane forests in particular years, and does not constitute a long-term threat. Mountain forest gain in boreal regions was the smallest observed (12.5%; Table 1). The annual net rate of forest loss was therefore greater than in tropical and temperate regions, at 0.39% per year (Table 1).

As tree plantations have expanded greatly worldwide over the last few decades[37], their removal contributes to forest loss rates reported here. To test what proportion of tree plantation removal accounted for mountain forest loss, we separated the forest loss into naturally regenerating forests and plantations using new data on global forest management[38]. We confirmed that nearly 70% of the global mountain forest loss occurred in naturally regenerating forests (Fig. 4). At the regional scale, we showed naturally regenerating forests in the boreal zone accounted for the largest proportion of the loss (74%), while in the tropics, one third of mountain forest loss occurred in plantations (Fig. 4). Crucially we found that the proportion of mountain forest loss occurring in plantations has not changed over the analysis period (Table S2), providing evidence that the expansion of plantation forests does not explain the large acceleration in mountain forest loss reported here. This independent analysis confirms that the majority of mountain forest loss is occurring in natural forests.

### *Forest loss within mountain biodiversity hotspots*

To map biodiversity hotspots, we focused on two species pools: one for all species of amphibians, birds, and mammals listed on the International Union for Conservation of Nature (IUCN) Red List and the second for threatened species only. We used two metrics: range-size rarity (RSR) and species richness (SR). RSR, a measure of endemicity[39,40], is a reliable indicator of mountain biodiversity as endemism is positively associated with elevational ranges[41]. SR represents the total number of species present. Our mapping of mountain biodiversity hotspots shows they are primarily concentrated in tropical regions although they vary somewhat by the species pool (all or threatened) and the metric of hotspot definition (RSR versus SR; Figs. S5 & S6). The distribution of RSR hotspots is similar for all species and threatened species, including in Sundaland, Wallacea, the Philippines, Madagascar, western Ecuador, tropical Andes, Brazil's Atlantic forest, and Mesoamerica (Fig. S5). By contrast, SR hotspots vary widely for all and threatened species (Fig. S6). SR hotspots for all species have a small range probably because the most abundant species tend to inhabit the lowlands, not mountain areas, while SR hotspots for threatened species are concentrated in mountainous areas in southwestern China and Southeast Asia that contain the world's largest number of endangered species.

Total forest loss in mountain biodiversity hotspots over the 18-year study period ranged from 1.4 to 14.4 Mha (or 3.8 to 6.2%), depending on the index used. The loss for mountain forests in the hotspots for threatened species was 11.0 to 14.4 Mha (5.5 to 6.2%). Importantly, relative forest loss was greater in mountain hotspots for threatened species than for all species under the same index (Table 2). Further, the acceleration of forest loss in mountain biodiversity hotspots (0.005–0.064 Mha $yr^{-2}$) was significant ($p < 0.01$; Table 2) regardless of the species pool and the metric of hotspot definition. RSR hotspots, for which such areas comprise a larger proportion of the global distribution of species[3], occur at all elevations from 0 to 3,500 m, with high RSR values located above 2,000 m (Fig. 5). At any elevation, RSR hotspots for threatened species experienced greater relative mountain forest loss than for all species. Mountain forest loss in RSR hotspots reached the peak at about 100 m, then decayed exponentially with increasing elevation, with half occurring at about 350 m (Fig. 5). Although the greatest RSR values were found higher than where most forest loss occurred, substantial forest loss did occur at those elevations (i.e., approximately 2,500-3,000 m) (Fig. 5; Table S3).

Within RSR hotspots for threatened species, nearly half of forest loss was associated with shifting cultivation (47%); the other two major activities were commodity agriculture (23%) and commercial forestry (23%; Fig. 3B). The six countries with the greatest mountain forest loss within RSR (threatened) hotspots were Indonesia (1.62 Mha), Malaysia (0.95 Mha), Madagascar (0.75 Mha), Vietnam (0.71 Mha), Colombia (0.69 Mha), and Peru (0.62 Mha; Table S4). In the Southeast Asian countries, commodity agriculture was the main driver of mountain forest loss within the hotspots, whereas in tropical Africa and South America, shifting cultivation was preeminent (Tables S3). In terms of relative loss of montane forests in biodiversity hotspots, more than half of the top 10 countries were in Africa: South Africa (27.71%), Zimbabwe (27.64%), Guinea (24.79%), Côte d'Ivoire (22.55%), Madagascar (15.38%), and Mozambique (12.33%); the remaining four were in Chile (34.48%), Mongolia (30.10%), Canada (14.96%), and Malaysia (13.34; Table S4). The four countries with the greatest acceleration in montane forest loss in biodiversity hotspots were Indonesia, Madagascar, Vietnam, and Malaysia, ranging from ~3,200 to 4,850 ha $yr^{-2}$ (Table S4).

### *Mountain forest loss in protected areas within hotspots*

Protected area coverage (proportion of forest area within PAs) is the largest in the SR (all) biodiversity hotspots, with more than half of hotspot areas included within PAs (Table 2). In some cases, this coverage can approach 100% in areas with very high elevations above 3,500 m (Fig. S7). In RSR hotspots, only 30% of mountain forest within hotspots was included in PAs (Table 2), suggesting there is a large proportion of forest area with high rates of species endemism that is unprotected. At high elevations (>3,000 m), more than 35% of forest area within RSR hotspots is protected (Fig. 5; Table S3). However, there are some countries with low PA coverage for mountainous forests in biodiversity hotspots, particularly Angola and Papua New Guinea, where PA coverage is <1% (Table S5).

In all types of mountain biodiversity hotspots, relative forest loss inside PAs was much less than outside (Table 2), suggesting that PAs within mountain biodiversity hotspots may be effective in limiting forest loss (ratio of relative forest loss inside versus outside of PAs less than 1). However, the trends depend somewhat on the metric and pool of species considered. Relative forest loss within RSR hotspots in PAs was lower than outside of PAs at all elevations, albeit less so at high elevations (Fig. 5). In contrast, within SR hotspots, the distribution varied when all versus threatened species are considered. Relative mountain forest loss was less in PAs than outside at elevations up to 3,000 m for all species; but for threatened species, lower loss inside PAs only occurred for the elevation band ranging from 400 to 1,900 m (Fig. S7).

In the RSR (threatened) hotspots inside PAs the dominant drivers of forest loss were shifting cultivation (38.3%), commodity agriculture (33.1%) and commercial forestry (24.9%; Fig. 3B). The lowest relative forest loss ratio inside versus outside PAs was found in RSR hotspots where commodity agriculture was the dominant driver, while the highest ratio was observed in hotspots where shifting cultivation and commercial forestry were the main drivers (Fig. S8). In most countries, PAs were associated with reduced forest loss relative to their surrounding areas within hotspots (Table S5). For example, Brunei, Chile, Canada, and New Zealand have the lowest ratios of relative forest loss inside versus outside of PAs within hotspots (Table S5). However, in some countries, such as Côte d'Ivoire, Haiti and Nicaragua where shifting cultivation dominates, relative forest loss inside PAs is more than twice that outside (Table S5). The same is true for Russia where wildfire was the main cause of mountain forest loss.

## DISCUSSION

Our global analysis renders three important findings: (1) Mountain forest loss has accelerated significantly throughout most of the first two decades of the 21st century, encroaching upon areas of known high conservation value to terrestrial biodiversity; (2) Various types of shifting cultivation emerges as the most frequent driver of mountain forest loss in the tropics, but commodity agriculture and forestry activities are also key drivers; (3) Protected areas generally have been effective in curbing mountain forest loss within their boundaries inside biodiversity hotspots, particularly where commodity agriculture is the dominant deforestation driver. However, we find great variation on these three issues throughout the world.

About three quarters of the 129 countries we analysed experienced an acceleration of mountain forest loss (Table S1). Most of the countries with the greatest acceleration were within Southeast Asia. Parts of India and southern China also experienced substantial losses. These regions with large acceleration align with many of the world's most sensitive biodiversity hotspots for mammals, birds, and amphibians—thus substantial negative impacts to critical habitat have likely already occurred[42,43]. While we did not yet see a major upward shift in the elevation of forest loss at the global scale of analysis, this transition has been reported before for Southeast Asia[13]. Further, the history of the progression of forest loss in mountain areas suggests such a shift will likely unfold in locations with high forest pressure but limited capacity to protect forest lands from location-specific drivers, mostly related to agriculture expansion, forest product acquisition, and logging (including illegal). Increased encroachment resulting in forest loss into these sensitive areas directly increases the risk of species extinction and/or forces other species to migrate upward if possible.

Agricultural expansion is of concern worldwide with respect to forest loss[44]. The greatest acceleration of mountain forest loss occurred in countries where shifting cultivation or commodity agriculture were dominant (Table S6), highlighting the importance of agricultural expansion in mountain regions. Encroachment of shifting cultivation in highland forests is problematic to address in countries where this form of agriculture contributes to food and livelihood security of rural communities[45,46] and where intensification of cultivation can lead to negative consequences for biodiversity and climate[47,48]. Forest lands are often viewed as an ownerless public resource and are therefore utilized as needed by individuals for food and livelihood security[49]. A complicating issue is that contemporary protected area boundaries are often established in areas where people have lived and exploited the forest long before governments recognized the need to conserve and manage them, with varied impacts on human welfare[50]. In cases where profit-driven commodity agriculture is the driver of mountain forest loss, intervention can be effective when the will to enforce forest protection laws is strong. An example is found on the border areas of Thailand and Laos where maize cultivation on forested lands is being phased out by the Thai government, but in Laos the exploitation of forest for lucrative boom crops persists[51,52] (Fig. S9). This situation demonstrates the drastic outcome in forest loss patterns related to differing institutional efficiency and capacity to enforce existing forest conservation policies. Further, the economic situation in Laos and its geographical location in Southeast Asia make it susceptible to external investments that drive deforestation for agriculture, timber/wood products, and energy[53].

We recognize the importance of promoting the regeneration of converted forests both naturally and through forestation programs. While we find that much regrowth has occurred in the locations of mountain forest loss worldwide, two issues are critical within the scope of our analysis. Firstly, reforestation with native species is preferable over the establishment of mono-specific tree plantations, which by some definitions are considered a type of forest. Secondly, initial disturbance causing forest loss may critically damage the habitat of sensitive species to the extent that they may not recover when forests reappear. Another issue is that the wellbeing of other types of organisms that contribute to biodiversity should be considered. Regarding sensitive species in biodiversity hotspots, the critical issue extends beyond simply preventing forest loss to also maintaining the integrity of forests in large enough zones to allow natural movements and sufficient space for ranging species. Protected areas should be designed with this purpose in mind.

Regionally distinctive drivers of mountain forest loss mean that efforts to curb the acceleration of mountain forest loss will require regionally appropriate interventions. In regions where shifting cultivation is a strong driver, like in Brazil, Colombia and Peru, efforts should be made to ensure agriculture does not impact frontier (intact or primary) forests where possible. Rather, it would be better to preserver biodiversity to establish new agriculture ventures where forests are already disturbed or land has been recently cleared[54]. Whereas in regions where commodity production is more prevalent (e.g., Indonesia, Vietnam, and Malaysia), increased commitment is needed urgently to halt commodity-driven forest loss and safeguard mountain forest biodiversity. Given that human population pressure has also been a major cause of biodiversity loss in PAs in the past few decades[55], we recommend that relevant strategies should consider balancing economic development, biodiversity conservation and sustainable livelihoods especially within and surrounding PAs.

We see examples where the existence of PAs has significantly reduced forest loss, compared with the areas surrounding them. Recent studies have also demonstrated the role of PAs worldwide in preventing forest loss[56,57]. Largely in agreement, we find that of the 78 countries with data pertaining to PAs in montane areas, about half were effective in keeping forest loss to be less than half of the loss experienced outside of PAs (Table S5). Unfortunately, in 12 countries the forest loss inside the PAs was greater than or equivalent to that outside. Drivers of mountain forest loss inside PAs tend to vary, with shifting cultivation, commercial forestry and commodity agriculture being important in a variety of locations. The strategic expansion and development of new PAs are thus promising avenues to improving mountain forest conservation for biodiversity now and into the future, especially in countries where PA coverage is low[58,59]. Many countries have only marginally effective PAs because, even in areas where forests are protected, there are destructive anthropogenic activities (e.g., logging) taking place that tax sensitive organisms. In these places, there is ample opportunity for improved PA management, and more adequate resourcing, and stricter enforcement of laws and regulations designed to protect forests.

As alluded to above, any new measures to protect mountain forests should be adapted to local conditions and contexts[60], and they should reconcile the need for enhanced forest protection with ensuring food production and human wellbeing[61]. More integrated socio-ecological research is needed to improve our understanding of biodiversity and ecosystem functioning in complex and sensitive mountain ecosystems, especially at the interface between social and natural systems. Such knowledge should boost awareness of the importance of preserving forest integrity whilst maintaining or enhancing human wellbeing, and, hopefully, help change attitudes regarding the reliance on destructive food production and energy generation systems.

In closing, our global analysis of mountain forest loss identifies an alarming acceleration in mountain forest lost worldwide over the last two decades. Important drivers have been various types of agriculture, forestry, and wildfire, with regional differences. These global results provide a foundation for further regional and local studies to examine nuanced differences more closely. Our analysis also highlights the importance of appropriately managed protected areas in preserving mountain forest biodiversity in the face of increasing human pressures for food production and a changing climate. By providing a clear understanding of the current trends and drivers of mountain forest loss, we hope to this analysis will inform and support conservation efforts aimed at preserving critical montane forest ecosystems for future generations.

## EXPERIMENTAL PROCEDURES

### *Resource Availability*

### *Lead Contact*

Requests for further information should be directed to and will be fulfilled by the lead contact, Zhenzhong Zeng (zengzz@sustech.edu.cn).

### *Materials Availability*

This study did not generate new unique materials.

### *Data and Code Availability*

The original data generated during this study are available at Mendeley Data, https://data.mendeley.com/datasets/myym96xcdy/1 and https://data.mendeley.com/datasets/t67hc9k7gd/1. Code used to analyse and plot data have been deposited at https://github.com/hexinyue33/mountain_forests. Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request.

### *Data sources*

*Global forest change data and visual interpretation for forest gain*

We used a Global Forest Change (GFC) dataset from 2000 to 2018 (version 1.6, available at https://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.6.html)[62] to analyse forest loss over mountains during the 21st century. This dataset uses Landsat satellite images to detect annual forest cover loss at a 1 arc-second resolution (~30 meters at the equator), spanning latitudes from 80°N–50°S. The global dataset is divided into 10° × 10° tiles (each containing 40,000 by 40,000 pixels). Trees are defined as "all vegetation taller than 5 m in height"[62]. Forest loss is "stand-replacement disturbance"[62], which includes both permanent loss (conversion to another land use) and temporary loss (e.g., loss from a forest fire). We first created a baseline forest cover map in 2000 from the percent tree cover layer using the criteria of Hansen et al.[63] that forest cover comprises at least 25% tree canopy cover at the pixel scale (30 × 30 m), which is an appropriate threshold for multispectral imagery to unambiguously identify tall woody vegetation. To investigate the degree to which our results were sensitive to the choice of threshold, we also used a tree-cover threshold of 50% to define forests for comparison (Fig. S10). Then, we mapped forest loss for all years in the 2001 to 2018 period from the forest loss layer at the pixel level. Forest loss area is the sum of all pixel areas where forest loss occurred. To distinguish the change of pixels with latitude, we calculated the pixel area as a function of latitude: pixel area = cos(latitude) × pixel area at the equator.

To check whether there was subsequent regrowth around 2019 where the forest was lost during the study period 2001-2018, we performed an independent assessment of forest gain using a sample-based approach following recommendations from Global Forest Watch[21] and good practice guidance of Olofsson et al.[22]. We randomly sampled 5,000 pixels that experienced forest loss (Supplementary Data) using random number generation, and visually interpreted forest gain using very-high-resolution imagery from Google Earth and Planet Explorer. We started with Google Earth for visual interpretation because it has a very high resolution (ranging from 15 m to even 15 cm); if there was no clear satellite image in 2019, we expanded the time range to the two years before and after, i.e., 2017-2020, but the image is at least a year after forest loss occurred. For the remaining points that have no images in Google Earth, we changed to Planet Explorer at a resolution of ~3.7 m for interpretation using daily or monthly imagery.

### *Drivers of forest loss*

We determined drivers of forest loss using the dataset generated by Curtis et al.[20]. This dataset shows the dominant driver of forest loss at each 10 km grid cell. There are five categories of drivers of forest loss, including commodity-driven deforestation which is defined as permanent and/or long-term clearing of trees to other land uses (e.g., commodity agriculture), shifting cultivation, forestry (a combination of logging, plantations and other forestry operations with visible forest regrowth in subsequent years), wildfire, and urbanization. The grids that were marked as zero or minor loss in the driver dataset are categorized as "other". We resampled data from 10 km resolution to 30 m using the nearest neighbour method, to match the scale of global forest cover change data. We then reported the proportion of each driver of mountain forest loss for each country.

### *Topography data*

A digital elevation model and global mountain polygons were applied to quantify the topographic pattern of forest loss. We used a high-resolution (30-m) elevation dataset from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM, version 3, available at https://earthdata.nasa.gov/)[64] to quantify the elevational gradients of mountain forest loss. The ASTER GDEM was generated by stacking the observed cloud-masked and non-cloud-masked scene DEMs, spanning latitudes from 83°N – 83°S[65-67]. Each tile of data has a dimension of 3,601 × 3,601 pixels, or a 1° latitude by 1° longitude area[23]. As the tile size of ASTER GDEM differs slightly from that of the forest change data, we first resampled each 1° x 1° DEM tile to 4,000 × 4,000 by using the cubic convolution method and then merged it into a tile of 10° latitude by 10° longitude pixels as in the forest change dataset (i.e., 40,000 × 40,000 pixels).

We used the Global Mountain Biodiversity Assessment (GMBA) definition (version 1.2, available at www.mountainbiodiversity.org, https://ilias.unibe.ch/goto_ilias3_unibe_cat_1000515.html)[68] to identify mountain regions, which adopts a ruggedness threshold indicating that the geometrical slope between the lowest and the highest point within a 2.5′ pixel must exceed 200 m[69]. The GMBA mountain definitions have the advantage of excluding some unstructured terrain such as large plateaus and expansive valleys or basins, while also not limiting mountains to particular elevations. Based on this definition, the world's mountainous terrain occupies about 1.64 billion ha and accounts for 12.3% of the total land area. It uses the GMBA definition along with expert delineations to provide a worldwide inventory of 1048 distinct mountain systems as vector polygons. Mountain regions are divided into eight mega-regions (mostly continents): Asia, Africa, Europe, Australia, North America, South America, Oceania, and Greenland[68]. Although mountain areas in Greenland occupy 4.3% of the total land area in the region, these mountains contain no tree cover and so are not considered here. In the analysis, we also examined forest loss in tropical (24°S to 24°N), boreal (≥50°N) and temperate (residual) regions.

### *Biodiversity hotspots*

We identified biodiversity hotspots for amphibians, birds, and mammals (as they have been the most comprehensively assessed and thus polygon maps are available) based on two species pools: (1) all accessed species belonging to any International Union for Conservation of Nature (IUCN) Red List category; and (2) threatened species listed as CR (Critically Endangered), EN (Endangered) and VU (Vulnerable) on the IUCN Red List. Thus, the second pool is a subset of the first. Note that the dataset used a filtering process that eliminates records of Extinct (EX) and Extinct in the wild (EW) from the start. For each of the two species pools, we used existing maps of range-size rarity (RSR) and species richness (SR) based on the raw IUCN ranges (available at https://www.iucnredlist.org/resources/other-spatial-downloads). RSR within each pixel is calculated as the pixel area divided by the total distribution area of each species that occurs within this pixel and then summed across all these species to determine the aggregate importance of each pixel. SR represents the total number of species potentially occurring in each pixel (including the possibility of presence and the uncertainty of seasonal occurrence of a species). We therefore used four raster layers consisting of all combinations of the two biodiversity indicators (RSR and SR) and the two species pools (all and threatened). The resolution of these rasters is about 5 km at the equator, but we resampled them to ~30 m to match global forest change data for calculation in our analysis.

In this dataset, RSR values range from 0 to ~0.72 (for all species) and from 0 to ~0.29 (for threatened species); SR values range from 1 to 912 (for all species) and from 1 to 59 (for threatened species). For each raster, we defined biodiversity hotspots as the upper 2.5% of land cells with the highest RSR or SR values as done previously[70] and clipped it to the boundaries of the mountain range delineations. The four biodiversity hotspot criteria are referred to as: (1) RSR (all); (2) RSR (threatened); (3) SR (all); and (4) SR (threatened). In each type of biodiversity hotspot within the mountain extent, RSR values range from 0.00073 to ~0.19 (for all species) and from 0.00012 to ~0.29 (for threatened species); SR values range from 675 to 847 (for all species), and from 24 to 59 (for threatened species) respectively; these ranges were calculated based on the upper 2.5% the land area.

### *Protected areas*

To investigate how much of the area of forest loss within biodiversity hotspots has been protected, we used polygon delineations of PAs from the World Database on Protected Areas (WDPA; available at https://www.protectedplanet.net/en/thematic-areas/wdpa?tab=WDPA). We did not include PAs represented by points, as forest loss calculations required areas. Due to the large size of the database, the data were divided into three shapefile layers. We clipped these layers to the extents of our mountain range boundaries separately and then merged them into one layer. A total of 30,515 PA polygons within the mountain range delineations was obtained. All pre-processing was performed in ArcMap 10.6.

## ***Data analysis***

We assessed temporal, spatial, and elevational patterns of forest loss across global mountains and within mountain biodiversity hotspots. We estimated annual forest loss area occurring in years between 2001 and 2018, beginning from the reference year 2000. Relative forest loss is based on forest cover in the baseline year 2000, calculated as the amount of forest lost in the region relative to the amount of forest that was there (relative forest loss = forest loss area/forest cover in 2000), providing information about rates of forest loss. We evaluated the temporal trend in annual forest loss (i.e., acceleration) using a non-parametric Theil-Sen estimator regression method[71] due to its robustness for trend detection and insensitivity to outliers, which has been widely used in previous research, including in forest cover trend analysis[72,73]. We then assessed the significance of the trends using the Mann-Kendall (MK) test[74]. To make our results more comparable among different regions or climate zones, we used a standardized annual rate of forest loss proposed by Puyravaud[75], calculated as: $r = (1/(t_2-t_1)) \times \ln(A_2/A_1)$ where $A_1$ and $A_2$ are the forest cover at time $t_1$ and $t_2$. In our analysis, $A_1$ is forest cover in the baseline year 2000 (obtained by the existing tree cover layer as mentioned above) and $A_2$ is forest cover in 2018 (= forest cover in 2000 – forest loss 2001 to 2018 + forest gain).

To visualize mountain forest loss area occurring at different elevations, we grouped elevation into 50 m bins within 0.5° grid cells. In mountain biodiversity hotspots, we calculated mean RSR (and overall SR) patterns within each elevation bin to represent the potential impacts of elevation-specific forest loss on biodiversity. We then compared the amount of forest loss in mountain hotspots of all species with those associated with threatened species to reveal the differences between various species pools affected by mountain forest loss. Finally, we specifically calculated each country's mountain forest loss for the RSR biodiversity hotspot with threatened species.

To assess the elevation-specific patterns of PA protection, we calculated PA coverage (i.e., fraction of forest in PAs) as the ratio of mountain forest within PAs in hotspots versus mountain forest in the corresponding hotspots. We also compare mountain forest loss within biodiversity hotspots inside PAs and outside of PAs at different elevations. In this study, we use the ratio of relative mountain forest loss within biodiversity hotspots inside versus outside of PAs to assess forest loss in the context of PAs (i.e., when the ratio <1, PAs experienced less forest loss than unprotected areas).

### *Uncertainties and limitations*

The GFC product we used, does not distinguish between natural forests and tree plantations[76,77]. Forest loss estimates therefore include forestry activities within tree plantations. Another difficulty we encountered was distinguishing forest (tree) loss from selective logging, which tends to degrade forests rather than resulting in a transition to another type of land cover. Not only permanent forest loss poses direct threats to montane forest biodiversity, but other forms of temporary loss (including partial tree removal) and forest degradation at large spatial scales are threatening to biodiversity, particularly in sensitive habitats like cloud forests, wetlands mountain patches in valleys, etc. Although forestry is an important driver of mountain forest loss as we reported, our independent analysis of forest loss and plantation loss confirms that the majority of loss occurs in natural forests, with less than 20% occurring in plantations (Fig. 4). Thus, the forest loss estimates presented in this study are likely to be conservative.

We acknowledge that our results are based on vertebrate (amphibians, birds, and mammals) distributions only, and that a more thorough investigation of the impacts of forest loss on other taxonomic groups such as plants, fungi, protists, and other types of wildlife (e.g., fish, insects) is needed. As the realm of most organisms (e.g., freshwater protists, fungi and other soil community members including bacteria, protozoa, nematodes, arthropods) is largely unknown, potentially important services offered by entire mountain forest ecosystems may soon be lost, or at least degraded following forest removal[78].

Finally, some geographic mountainous areas of known forest loss were not detected in our analysis (e.g., the islands of Timor-Leste and Dominica[79]). The reason for the omission of these countries, and possibly others, is the definition of mountains following the GMBA definition[68]. Although regrettable, as this paper is a global analysis, we used a standard global definition of mountains.

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## Author contributions

Conceptualization, X.H., Z.Z., D.V.S. and J.H.; methodology, X.H.; investigation, X.H; writing – original draft, X.H.; writing – review & editing, A.D.Z., P.R.E., Y.F., J.C.A.B., S.L., J.H., D.V.S., and Z.Z.; supervision, Z.Z., D.V.S. and J.H.

## Declaration of interests

The authors declare no competing interests.

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**Table 1. Mountain forest cover change in different regions/climates (2000 to 2018).** Mountain forests in 2000 is the area of mountain forest based on the tree cover threshold of 25% in the year 2000 (Mha). Total mountain forest loss 2001–2018 is the total loss during the period (Mha). Annual relative forest loss (gross) is the mean of relative forest loss (= mountain forest loss/mountain forest cover in 2000) over the 18 years in the region (%). Mountain forest loss acceleration is the gradient in mountain forest loss with time in the region (Mha $yr^{-2}$), determined from the regression of annual loss (dependent variable, which is a rate in ha $yr^{-1}$) and year (independent) using Theil-Sen estimator, thus, the units of Mha $yr^{-2}$. Mountain forest gain proportion is independently estimated by forest gain divided by the total sample size in the region (%). Annual net rate of mountain forest loss is calculated by a standardized method proposed by Puyravaud[55], by comparing forest cover in the same region in 2000 and 2018 (% per year). Asia was separated into northern and southern Asia, with a boundary of 30°N.

| **Region** | **Mountain forest area in 2000 (Mha)** | **Total mountain forest loss 2001–2018 (Mha)** | **Annual relative mountain forest loss (%)** | **Mountain forest loss acceleration ($10^{-2}$ Mha $yr^{-2}$)** | **Mountain forest gain proportion (%)** | **Annual net rate of mountain forest loss (% per year)** |
|---|---|---|---|---|---|---|
| Asia | 560.5 | 39.8 | 0.39 | 12.2 (*) | 27.0 | 0.30 |
| Northern Asia | 255.8 | 14.1 | 0.31 | 1.0 | 14.9 | 0.27 |
| Southern Asia | 304.7 | 25.7 | 0.47 | 11.4 (*) | 39.9 | 0.29 |
| North America[τ] | 220.5 | 18.7 | 0.47 | 1.5 | 15.9 | 0.41 |
| South America | 158.9 | 8.3 | 0.29 | 1.4 (*) | 33.2 | 0.19 |
| Africa | 66.0 | 6.4 | 0.54 | 2.8 (*) | 15.4 | 0.48 |
| Europe | 71.9 | 3.4 | 0.26 | 0.9 (*) | 16.4 | 0.22 |
| Australia | 15.0 | 1.0 | 0.38 | 0.2 | 47.4 | 0.20 |
| Oceania | 7.2 | 0.4 | 0.32 | 0.1 (*) | 46.7 | 0.17 |
| **Global** | **1100.0** | **78.0** | **0.39** | **20.2 (*)** | **23.2** | **0.31** |
| Tropical | 436.1 | 32.9 | 0.42 | 13.1 (*) | 31.2 | 0.30 |
| Temperate | 419.9 | 27.9 | 0.37 | 4.6 (*) | 27.3 | 0.28 |
| Boreal | 244.0 | 17.2 | 0.39 | 1.6 | 12.5 | 0.35 |

* indicates a significant trend at 95% confidence interval (Mann-Kendall test).

[τ] North America includes Mexico, central American countries (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, and Panama) and nearby island countries of Cuba, Jamaica, Haiti, Dominican Republic, and Trinidad and Tobago.

**Table 2. Comparison of mountain forest loss within different types of biodiversity hotspots.** Proportion of forest (or loss) within protected areas (PAs) is the forest (or loss) area within PAs divided by the forest (loss) area in the corresponding hotspots. Relative forest loss inside (or outside of) PAs is percent forest loss relative to forest cover in the baseline year 2000 inside (or outside of) PAs within hotspots.

| **Hotspot Types** | **Forest area in 2000 (Mha)** | **Total forest loss 2001–2018 (Mha)** | **Relative forest loss 2001–2018 (%)** | **Forest loss acceleration ($10^{-2}$ Mha yr$^{-2}$)** | **Proportion of forest area within PA (%)** | **Proportion of forest loss within PA (%)** | **Relative forest loss inside PA (%)** | **Relative forest loss outside of PA (%)** |
|---|---|---|---|---|---|---|---|---|
| RSR (all) | 223.32 | 12.98 | 5.81 | 4.10 (*) | 28.32 | 15.07 | 3.09 | 6.89 |
| RSR (threatened) | 177.62 | 11.03 | 6.21 | 3.66 (*) | 29.79 | 16.75 | 3.49 | 7.36 |
| SR (all) | 37.49 | 1.43 | 3.81 | 0.48 (*) | 58.98 | 21.95 | 1.42 | 7.26 |
| SR (threatened) | 260.15 | 14.41 | 5.54 | 6.40 (*) | 13.14 | 9.02 | 3.80 | 5.80 |

* indicates a significant trend at 95% confidence interval (Mann-Kendall test).

RSR: range-size rarity; SR: species richness.

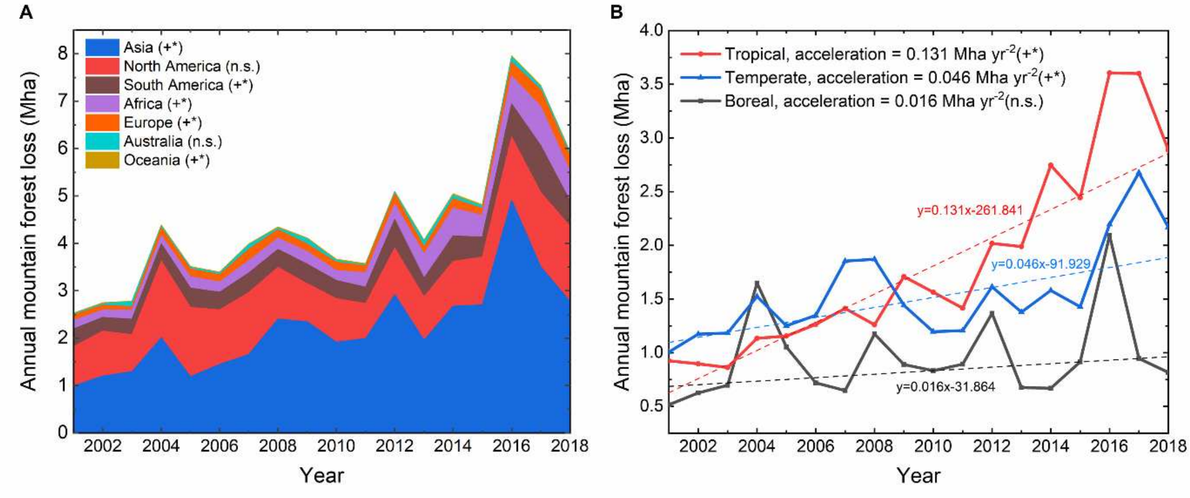

**Figure 1. Time series of annual mountain forest loss from 2001 to 2018.** (A) Annual mountain forest loss in different continents. The total area of all seven regions for each year represents global mountain forest loss since the baseline year 2000 (i.e., the area is stacked, not superimposed). A symbol (+*) after the region shows a significant positive trend in mountain forest loss at the 95% confidence interval; (n.s.) means no significant trend in mountain forest loss. Trends are determined for the entire 2001–2018 forest loss time series. The loss areas for Oceania are comparatively small, which appear as a black line. (B) Annual mountain forest loss in tropical (24°S to 24°N), boreal (⩾50°N), and temperate (residual) regions. Dashed lines are trend lines for annual mountain forest loss in tropical (red), temperate (blue), and boreal (black) regions, estimated by Theil-Sen estimator regression.

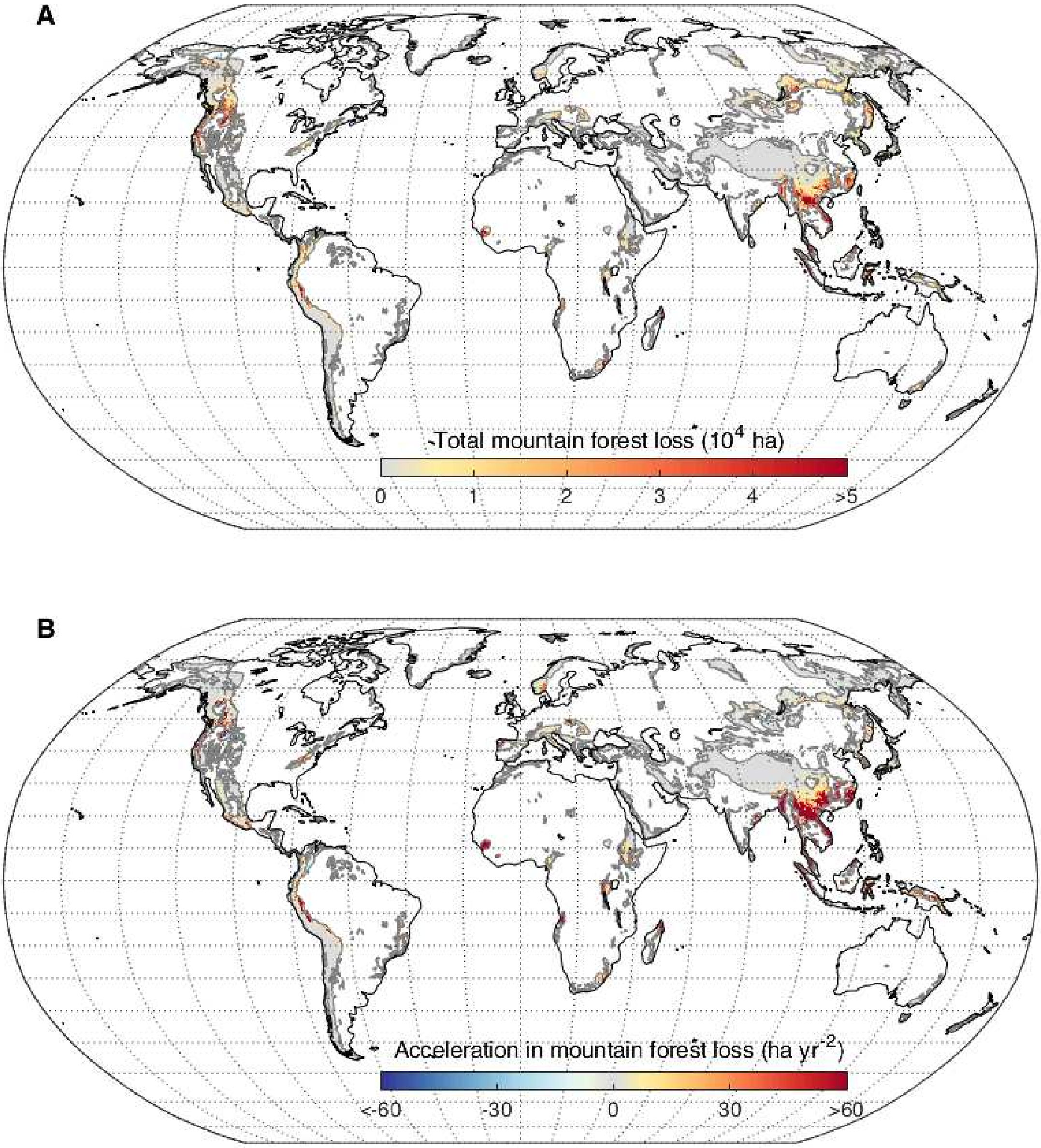

**Figure 2. Spatial pattern of mountain forest loss in the 21st century.** (A) Total mountain forest loss area. (B) Acceleration in mountain forest loss in 0.5° cells. Mountain regions in grey show mountains with either little forest loss area or no obvious change during the period.

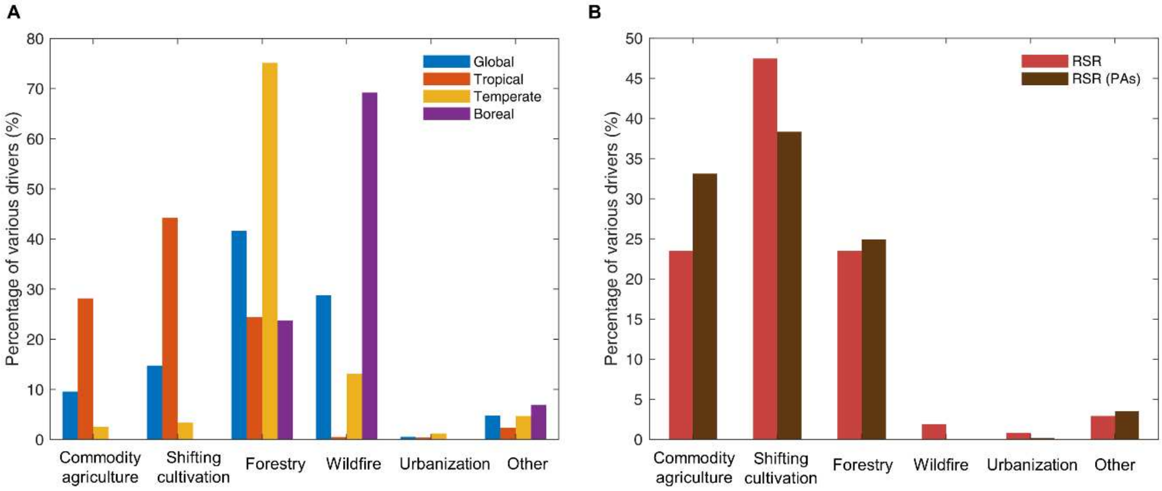

**Figure 3. Drivers of mountain forest loss.** (A) Comparison across all mountains (global), and in tropical, temperate, and boreal regions. (B) Comparison between the biodiversity hotspots based on range-size rarity for threatened species (RSR) and inside protected areas in the hotspots (RSR (PAs)).

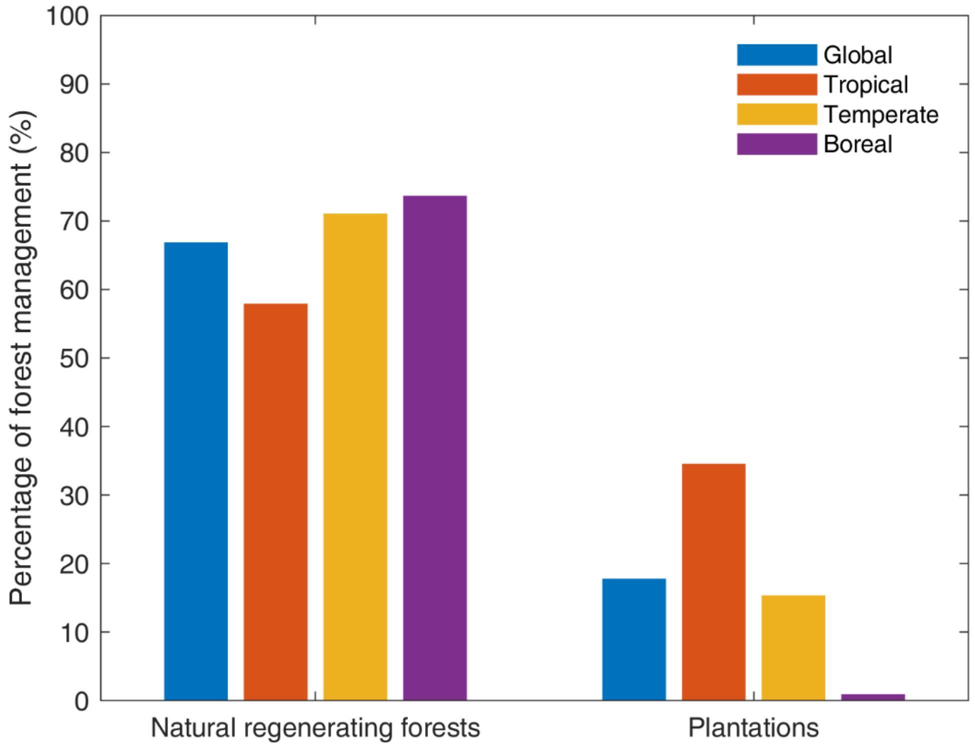

**Figure 4. Proportion of natural regenerating forests and plantations accounting for mountain forest loss.** Naturally regenerating forests include those without any signs of management (primary forests) and with signs of management (e.g., logging, clear cuts, etc.). Plantations include planted forests, plantation forests (rotation time up to 15 years), oil palm plantations and agroforestry.

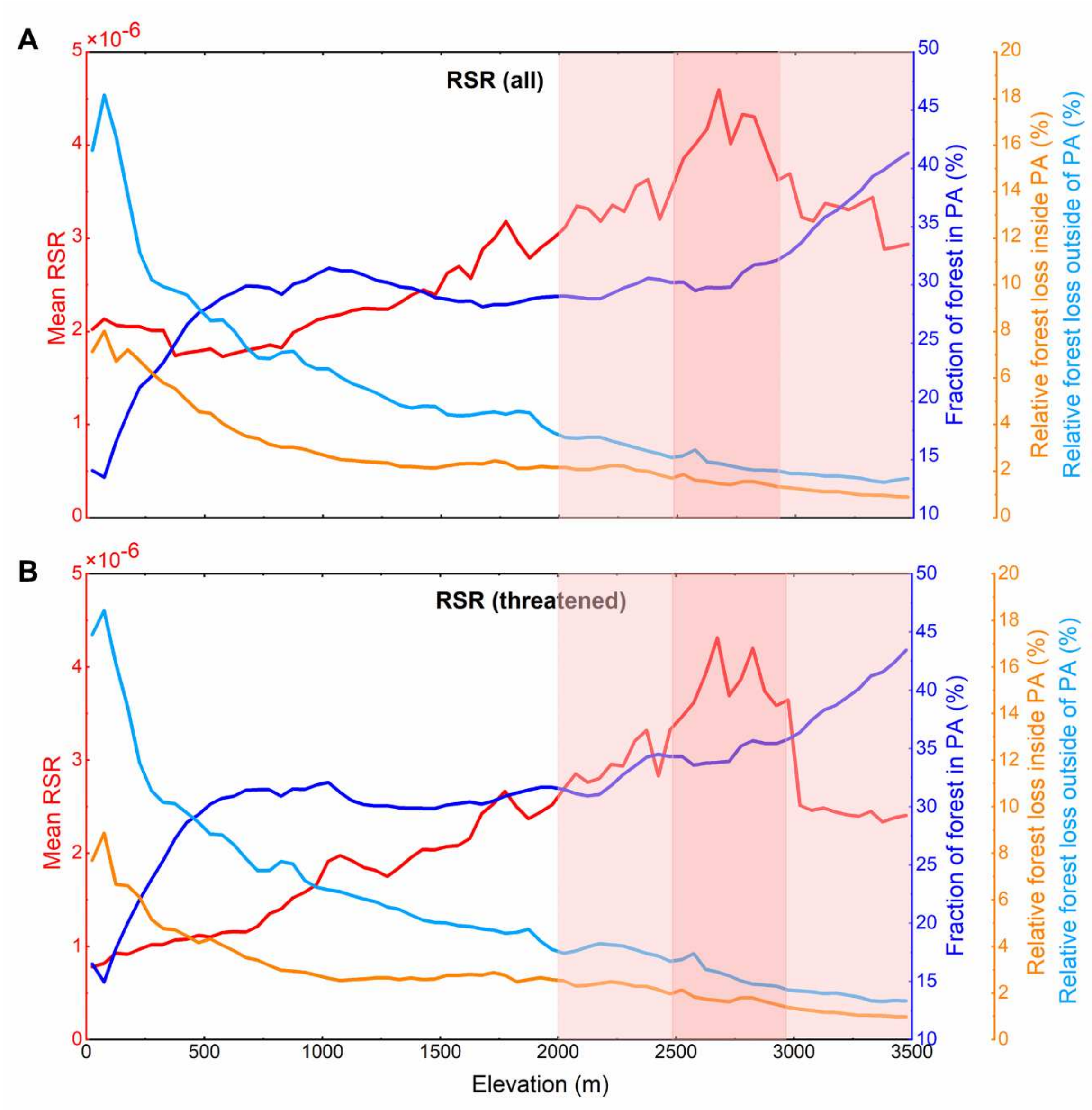

**Figure 5. Elevational gradients of biodiversity value, protected area (PA) coverage, and mountain forest loss inside and outside of PAs within biodiversity hotspots.** Biodiversity hotspots are based on range-size rarity (RSR) for all species (A) and threatened species (B). Mean RSR (red lines) is mean value of biodiversity metric of RSR at each elevation bin on the pixel of 30 m. PA coverage (fraction of forest in PAs) is the ratio of mountain forest within PAs in hotspots versus mountain forest in the corresponding hotspots. Relative forest loss is percent forest loss relative to forest cover in the baseline year 2000. Relative forest loss inside PAs and outside of PAs within hotspots are shown in orange and light blue lines, respectively. The background shading highlights occurrence of the highest levels of biodiversity (light and dark red).

**Supplemental Data S1. Visual interpretation of Landsat imagery at 5,000 forest loss pixels randomly selected from Hansen GFC product across all mountain regions.**