Journal of Environment Sciences (2026), **Volume XII**, 110-129
https://doi.org/10.3126/jesv12i1.96889

Climate Change Impacts on Alpine Vegetation: The Role of Microclimatic Variability

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Abstract

Global surface temperatures have increased by about 1.1°C relative to 1850–1900, with 2011–2020 being the warmest decade on record and accompanied by changing precipitation patterns. Warming is amplified in alpine regions such as the European Alps, where temperature increases have been roughly twice the northern hemispheric average since the late 19th century, alongside contrasting precipitation trends between northern (wetter) and south-eastern (drier) areas. Alpine ecosystems, defined as treeless zones above the tree line, are highly sensitive to climate change, exhibiting upward species shifts, phenological changes, vegetation restructuring, and local extinctions. However, strong microclimatic heterogeneity may buffer these impacts. This study presents a narrative literature review of microclimatic buffering in alpine vegetation. The evidence was synthesized showing how topography-driven radiation differences, wind-induced cold-air pooling, and snow dynamics generate fine-scale habitat variability. These processes create microhabitats that can reduce exposure to macroclimatic warming and support potential microrefugia for plant species. The study argues that microclimatic buffering is a key but still insufficiently understood mechanism shaping alpine vegetation responses to climate change. Improved understanding of its limits is essential for more accurate predictions of vegetation dynamics and for informing conservation strategies in mountain ecosystems.

Keywords: *Mountain region, microhabitat, upward mobility, vegetation dynamics*

1. Introduction

A human-caused global surface temperature rise of 1.1°C (2011-2020 compared to 1850-1900) and changing precipitation patterns were determined by the Intergovernmental Panel on Climate Change (IPCC) (Calvin et al., 2023). This increase is not uniform across the globe, but enhanced warming rates can be observed over land and in higher latitudes (Calvin et al., 2023). However, there is also a tendency of higher warming rates at high elevations (Pepin et al., 2022), which is especially pronounced in some alpine regions like the European Alps (Kuhn and Olefs, 2020). In the European Alps a temperature rise about twice as large as the northern-hemispheric average was observed from the end of the 19th until the end of the 20th century (Gobiet et al., 2014). Precipitation patterns, however, are changing less uniformly. Already when only considering one alpine region, like the European Alps, changes in the precipitation pattern strongly depend on the region and season. For example, an increase in precipitation was observed in the northern area of the Alps, especially during fall, while the south-eastern alps show a strong drying trend (Gobiet et al., 2014). Globally, these changes in precipitation patterns vary even stronger between different alpine regions.15% of the total land surface is covered by alpine environments (Inouye, 2020), treeless areas located above the tree line in mountains (Verrall & Pickering, 2020). They can be found from the equator to close to the poles, occurring at higher elevation at lower compared to high latitudes, since their occurrence is connected to the low temperatures resulting in the absence of trees (Körner, 2021). The alpine area can be divided into the alpine zone, bordered below by the tree line, and the nival zone, extending up to the height in which plant life is limited (Grabherr et al., 2010). The alpine zone is characterized by closed plant communities, while the nival zone is dominated by open vegetation (Grabherr et al., 2010). Low temperatures, short growing seasons and highly heterogeneous landscape morphology are characteristic for the alpine environment, which is giving home to alpine plants, highly specialized to cope with these harsh environmental conditions (Körner, 2023).

Climate change directly and indirectly alters the environment of these specialized alpine plants, resulting in various vegetation responses. Upward migration of plant species, phenological alterations, changes in vegetation structure, evolutionary adaptation as well as extinctions are important reactions of plants to climate change. However, the heterogeneous landscapes in alpine regions, resulting in a high diversity of microclimates and habitats complicate the observed trends and may even be able to buffer the negative effect of climate change.

While broad macroclimatic trends in alpine regions are well-documented, global vegetation models often fail to capture how small-scale topographic variations decouple local microclimates from regional warming. Furthermore, literature is frequently fragmented across separate discussions of individual species responses (such as phenology or migration) without synthesizing how these mechanisms interact to alter community structure, generate ecological mismatches, or accelerate extinction debts.

This review synthesizes current ecological literature to address three key questions:

(1) Topographic variation and plant–trait feedbacks shape alpine microclimates and their capacity to buffer macroclimatic warming;
(2) Climate-driven upward migration and phenological shifts affect species interactions at individual and community levels; and
(3) Encroachment (woody) and structural change alter alpine ecosystem function, and what constraints limit the adaptive capacity of alpine flora before reaching extinction thresholds.

2. Methods

In this review, a structured literature-based methodology was used to compile and synthesize the existing information on the consequences of climate change on alpine vegetation, focusing on the importance of microclimatic heterogeneity in moderating ecological changes. Peer-reviewed articles up to 2026 were identified via systematic database searches (Web of Science, Scopus, selected due to their broad scope of ecological, biogeographical and climate change research) using relevant search terms investigating climate-induced shifts in alpine vegetation dynamics. The search was designed to cover the major themes of this review: microclimatic buffering, changes in species distributions, phenological alterations, community reorganizations, and extinctions. Boolean combinations of search terms were used, with 'alpine vegetation' combined with terms such as 'microclimate', 'phenology', "upward migration" or "range shift", "extinction debt", as well as the interaction of topography, climatic velocity and change. Literature found through backward citation chasing (by examining references within key reviews and strongly-cited empirical works) were additionally incorporated to ensure that core conceptual work was included.

The geographical scope of the review is global, focusing on alpine, sub-nival, and nival ecosystems across major mountain systems. Studies from the Tibetan Plateau, Nepal Himalaya, and other Himalayan regions were also considered; however, the number of peer-reviewed studies meeting the inclusion criteria and suitable for synthesis was limited. All relevant and methodologically robust studies available from these regions were included to ensure representation within the constraints of the existing literature.

This review followed PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines for study identification, screening, eligibility assessment, and inclusion, and a PRISMA flow diagram (Figure 1) is used to document the selection process (Page et al., 2021).

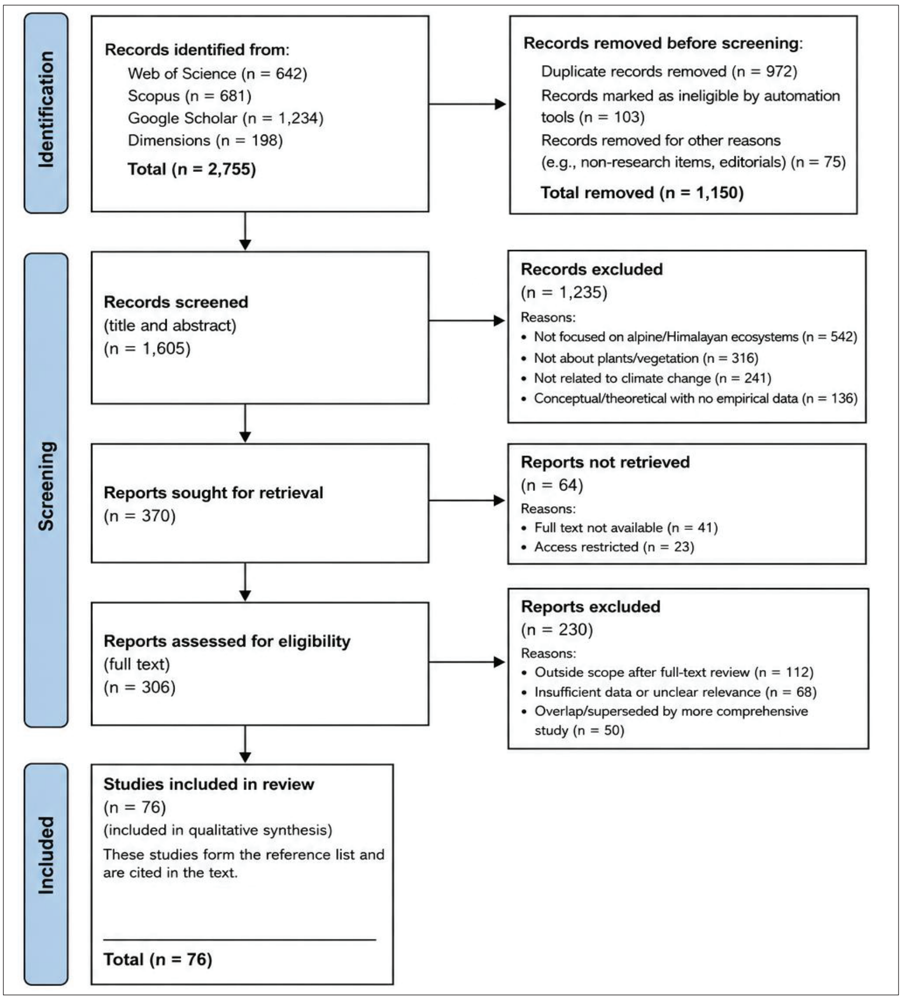

Figure 1: The flow diagram of PRISMA method used for the review of literature.

This review considered only studies from the alpine, sub-nival and nival regions that examine vegetation that is in direct contact with climate forcing agents at high elevation sites (expect for those needed for methodological or technical sense). High-resolution microclimatic measurements, empirical field studies of how vegetation is responding to climate change, and modelling studies that employed accepted species distribution models or a climate velocity approach were emphasized. Terrain-resolved climate data studies and long-term vegetation monitoring data were seen as most valuable because these provide information on interaction between global-scale climatic trends and local-level environmental variability. Vegetation studies outside alpine, sub-nival, and nival ecosystems were excluded to maintain focus on high-elevation climate–vegetation interactions, as were greenhouse or growth-chamber experiments which do not accurately reflect climate forcing of vegetation, nor controlled or greenhouse studies not validated in the field. Modelling studies were only included if supported by field validation, or if using well-accepted modeling frameworks.

The inclusion and exclusion criteria were explicitly defined to ensure consistency and reproducibility in study selection, including restriction to field-based or field-validated alpine studies addressing vegetation–climate interactions.

This collected literature was organized into three subject categories relating to the aims of this review,

(i) microclimatic buffers and ameliorating effects of landscape features such as topography and snow cover, as well as cold-air pooling,

(ii) range and compositional shifts of species populations and community turnover in response to climate, including thermophilisation and diversity shifts, and

(iii) plant phenological shifts and species interactions including changes in timing of flowering, response to snow melt and plant-pollinator interactions.

These categories allow a comparison of which mechanisms have received more attention within and among subalpine environments, as well as where knowledge gaps still exist. As this review found, studies that assess range and community-level climate response and which employ climate data studies that are resolved to the landscape-level are abundant, whereas studies that provide direct, quantitative estimates of the microclimatic buffering capacity of landscape features such as snow or cold-air pooling are scarce, although it is acknowledged that this mechanism can significantly mitigate impacts of climate warming (Körner, 2021; Pepin et al., 2022). Likewise, phenological responses to climate change are receiving increased interest, yet few of these studies specifically integrate how microclimate influences phenological synchrony among species and in relation to associated species.

A thematic synthesis approach was used to qualitatively group and compare studies across these three categories to identify dominant research trends and knowledge gaps.

These interaction mechanisms must be combined to have a coherent view of how macroclimatic change affects alpine vegetation via microclimatic buffering and ecological feedback. The conceptual framework, figure 2, outlines these processes.

Rising temperatures and altered precipitation regimes modify topographic, snow-related, and vegetation-driven microclimatic conditions, which in turn influence vegetation responses, including upward range shifts, phenological shifts, community turnover, and shrubification. These responses ultimately determine whether species persist through adaptation and occupation of microrefugia or experience increased extinction risk. Figure 2 illustrates the importance of microclimatic heterogeneity in shaping alpine ecosystem responses to climate change.

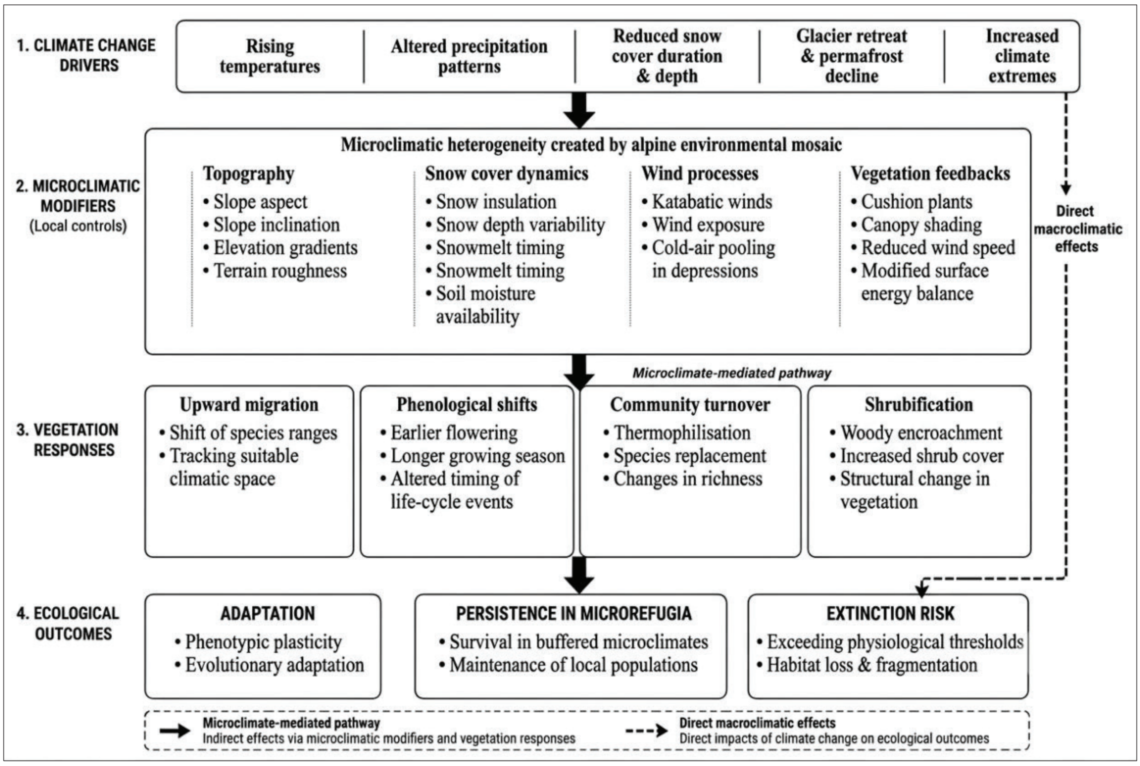

Figure 2: Conceptual framework illustrating how climate change influences alpine vegetation through both direct macroclimatic effects and indirect microclimate-mediated pathways.

3. Results and Discussion

3.1 Microclimate in alpine environments

Some macroclimatic changes with elevation are present in all alpine areas. These include decreasing air pressures that are accompanied by decreasing CO_2 partial pressures, decreasing air temperature and moisture content and increasing solar radiation per area with higher elevations (Körner, 2021). Still, macroclimatic patterns vary strongly between different mountain regions. Seasonality, with its major impact on vegetation, for example differs dependent on latitude. But also, altitudinal patterns of precipitation and wind can differ significantly between alpine regions.

As important as these large-scale climate phenomena are, it is essential to consider microclimate in alpine regions, since this characterizes the actual habitats and climate that plants experience and live in.

Due to the highly heterogeneous topography, large microclimatic variation is typical for alpine regions. This includes small-scale differences in temperature, radiation, precipitation, winds and snow cover, which strongly impact the occurring vegetation communities. However, plants themselves can influence their microclimate. In the following we will briefly present important microclimatic phenomena which are common in alpine environments and then discuss how plants can impact their environment.

Topography has a considerable direct influence on solar radiation. In alpine regions the intensity of incoming radiation depends on the slope inclination. Areas where the slope inclination is perpendicular to the incoming solar radiation have the highest radiation per area. However, radiation is also dependent on the slope aspect (orientation of the slope), with essential differences between north and south facing slopes in their radiation budgets and consequently also in air temperatures. Also, in high and steep alpine regions a shadow effect can be observed, when the surrounding mountains cast a shadow on certain regions of the neighboring slope. Since solar radiation impacts vegetation directly but also indirectly through temperature differences, a complex terrain results in small-scale radiation and temperature differences, creating a variety of microhabitats for alpine plants (Weihs et al., 2016).

However, these effects on solar radiation can be more complicated, for example due to differing albedo with different ground covers. Dark soils, for example, that are fully exposed to sunlight were shown to heat up to temperatures around 80°C. Plants and seeds in these soils are strongly affected by these high temperatures and must be able to cope with these extreme conditions. Due to the differences in albedo, but also cloud cover patterns over the day, studies have shown that north-facing slopes can have slightly warmer soil temperatures than their south facing counterparts, especially on days with clear and sunny mornings and cloudy afternoons. This highlights the complexity of microclimatic patterns in alpine regions and how difficult they are to describe in detail for larger regions (Körner, 2021).

Alpine regions show typical wind patterns, with daily periodical changes of the wind direction. In a simplified way we can distinguish two types of wind: up-slope winds and down-slope winds. During the day the air close to the mountain slopes is warmed. It expands and rises, resulting in warm up-slope winds. In the night the air at higher altitudes cools down faster, starts sinking and moves down the slope, as cold down-slope winds (Seibert & Steinacker, 2016). Next to these radiation-based wind patterns, especially pronounced in clear weather periods, also foehn winds are typical for mountain regions. These are down-slope winds, where cool and dry air flows down the lee side of the mountains (Richner & Hächler, 2008). However, also smaller scale wind patterns can be observed, such as glacier winds on days with temperatures over 0°C (Seibert & Steinacker, 2016). Since the air above the glacier is cooler than the surrounding air under these conditions, air moves from the glacier outward in the lowest two to three meters of the atmosphere (Seibert & Steinacker, 2016).

One consequence of the daily changing wind patterns, that strongly shapes microhabitats, is the formation of cold-air pools. On a straight slope with an open valley the cold air that cooled down during the night in high elevations of the mountain can flow down the slope and valley. However, complex topography with troughs, basins, dolines but also other obstacles can prevent the cold air from flowing down the slope. Cold air consequently collects in basins and can cool down further over the night. This leads to the formation of cold-air lakes that are characterized by extremely low temperature minima. For example, Dorninger et al. (2016) measured daily temperature changes of 29°C in summer and 30°C in winter in a doline in the alps compared to only 10°C daily temperature change in summer and 5°C in winter in the surrounding area. The magnitude as well as the duration of these temperature inversions is strongly dependent on the geometry and size of the structures and result in significant habitat differences for plants on a small scale (Dorninger et al., 2016; Rauchöcker et al., 2024).

Snow cover also strongly influences the distribution of different vegetation communities. Main reasons are its isolating effect and its impact on the length of the growing season, but snow also influences the water supply (Chersich et al., 2015; Inouye, 2020). The isolating effect of the snow cover can result in a decoupling of the soil temperatures from the surrounding air temperatures. Studies recording air temperatures and the temperature below the snow cover show that the temperatures beneath the snow cover can stay at around 0°C over the whole winter period, as long as a thick enough snow cover persists (Körner, 2021). This protects plants from cold winter air temperatures and can prevent them from freezing during the winter months. Snow cover patterns are complex in alpine regions. They are influenced by cloud dynamics, snow deposition patterns as well as transportation. Snow is not as uniformly deposited as rain. Due to the lower density of the snow particles their deposition depends on the wind strength and direction. Snow is mainly deposited in wind protected areas such as depressions, basins or vegetated areas and not on wind exposed slopes or ridges. After deposition it is again dependent on the presence of wind patterns if and how the snow is resuspended and transported further. Again, topography resulting in small-scale differences in snow cover and snow depth has a significant impact on microhabitats of vegetation (Lehning & Mott, 2016). Several studies in alpine regions showed that the melting patterns of snow are quite constant over the years although the amount of snow as well as the snow-melt timing change considerably over the years. Also, close correlations were found between the boundaries of snow melt patterns and vegetation patterns. This indicates that vegetation communities are strongly dependent on the duration of the snow cover due to its effects on their microclimatic (Körner, 2021).

Plants, however, are not solely dependent on a favorable climate surrounding them but can influence the temperatures they are experiencing. Many studies have shown that plants highly specialized and adapted to the alpine environment can decouple from the air-temperatures surrounding them (Körner, 2021). The plant stature, height and leaf arrangements are essential in this context. While high growing life forms, like trees, are aerodynamically coupled to the atmosphere due to convective heat transfer, low growing plants can reduce this head convection, and solar heat is trapped in the plant (Körner, 2021). Cushion plants for example are good at trapping heat. Gauslaa (1984) found a difference up to 24.5 °C between air temperature and temperature in cushion plants in Norway. However, this is a rather extreme example that can occur on sunny days during the warm seasons. But also, the more often occurring only slightly warmer plant temperatures are important for the plants growing abilities, as they can enable better metabolism and growth rates (Körner, 2021).

The ongoing climate change is not only a large-scale phenomenon but also impacts these microclimatic conditions. In alpine regions rising temperatures and changes in precipitation result in decreasing expanses of glaciers and permafrost with many consequences such as changes in the water budget, soil properties or slope stability (Tamme, 2012; Chersich et al., 2015). Also, the extent and time of snow cover decreases and the lower boundary over which precipitation falls as snow rises (Chersich et al., 2015; Giaccone et al., 2019). However, although major changes are expected in alpine areas microclimate does not always follow macroclimate in a direct way. Especially the high microclimatic variability described above that is creating various habitats in close proximity to each other, may even have the ability to buffer the negative effects of climate change on alpine vegetation communities (Inouye, 2020; Ohler et al., 2020), since it allows species to find suitable habitats close by and reduces the need of upward migration (Ohler et al., 2020). Still, more research is needed to understand to what extent microclimates can buffer climate change in alpine regions (Jiménez-Alfaro et al., 2024).

3.2. Vegetation Responses to Climate Change

The observed and projected climate changes show a range of responses from alpine vegetation, displaying primarily through upward migration of species, alterations in phenology, shifts in vegetation structure, and, in some cases, the threat of extinction for highly specialized species.

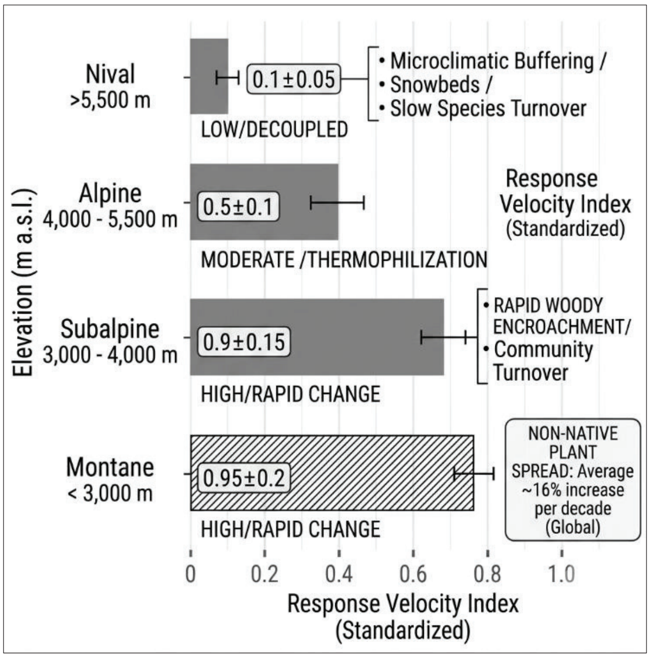

Figure 3: Standardized Response Velocity Index across elevational gradients illustrating the varying intensity of vegetation responses to climate warming, showing a transition from low-sensitivity/buffered nival zones (dominated by microclimatic refugia) to high-sensitivity/rapid change in subalpine and montane zones (characterized by woody encroachment and non-native plant spread) (Dullinger et al., 2012; Rosbakh et al., 2014; Lembrechts et al., 2020; IUCN, 2023, own illustration)

3.2.1. Upward Migration

With the rise in mountain temperatures, many plant species are seen to move to higher elevations to find conditions that are better suitable for their needs. In subalpine areas, while some existing plants seem to be adapted to the current climate, most species tend to shift uphill to stay within their ideal level of temperature and moisture (Körner, 2021). However, the entire plant communities are rarely seen to move together. Instead, each species tends to shift individually, finding small areas (microhabitats) that have become suitable. For plants to grow successfully at higher elevations they are dependent on several things such as open space, the soil types, and soil microbes. Species that have very specific temperature needs or can't spread their seeds far are especially at risk of falling behind as the climate changes.

Many studies across the European Alps provide compelling evidence of these shifts. Research shows a general increase in species richness at mountain summits and in high alpine zones over recent decades (Lamprecht et al., 2018). However, this increase in species richness should not be interpreted as an improvement in biodiversity or ecosystem health. Instead, it reflects a process of thermophilisation, where cold-adapted alpine species are gradually replaced or outcompeted by more generalist, warm-adapted species migrating upward from lower elevations (Lenoir et al., 2008; Lamprecht et al., 2018).

This trend is driven by the upward migration of species from lower elevations, which are now able to colonize previously too-cold habitats. At the same time, there is a continuing loss of cold-adapted alpine species from their historical ranges. The rising temperatures reduce the cold limitations that previously restricted warmer-adapted species to lower altitudes, allowing their expansion into higher zones. This often leads to increased overlap between expanding generalist species and narrow-range alpine specialists, resulting in competition and potential displacement of cold-specialist alpine plants. Consequently, the observed increase in species richness often represents a species turnover rather than a net gain in biodiversity, where pioneer species from lower elevations increase in abundance while characteristic subnival and nival zone species decline. This leads to biotic homogenization and a loss of endemic alpine biodiversity (Lenoir et al., 2008; Lamprecht et al., 2018).

Importantly, these compositional changes occur under a strong mismatch between species migration rates and the velocity of climate warming. Empirical evidence from the European Alps indicates that warming-induced isotherms have shifted upslope at approximately 62–71 m decade{ ^{1} since 1970, whereas woody plant communities have migrated at only about 32.7 m decade{ ^{1} (Figure 2). This disparity creates a climatic debt, whereby vegetation distributions lag behind the pace of changing climatic conditions. As a result, many alpine species may be unable to fully track their climatic niches, increasing the risk of habitat contraction, community reorganization, and local extinction of cold-adapted specialists (Vitasse et al., 2021).

As a consequence of these dynamics, there is an increasing loss of cold-adapted alpine species from their historical ranges. The rising temperatures reduce the climatic constraints that previously restricted warmer-adapted species to lower elevations, allowing their expansion into higher zones. This can intensify competition with specialist alpine taxa that are adapted to narrow thermal niches. Consequently, the observed increase in species richness often reflects a species turnover rather than a net gain in biodiversity. In many cases, this results in biotic homogenization, where widespread generalist species increase in abundance while endemic, cold-specialist flora decline, ultimately leading to a reduction in unique alpine biodiversity (Lenoir et al., 2008; Lamprecht et al., 2018).

3.2.2. Phenological Alterations and Mismatches

Temperature is the main determinant of phenology for alpine plant species (Ohler et al., 2020), but snowmelt timing has a big impact on the beginning of the growing season (Inouye, 2020). With ongoing climate change, the average beginning of the growing season was predicted to be 17 days earlier by the end of the century compared to the period 1971-2000 (Inouye, 2020). But these changes in phenology differ between different species and can result in phenological mismatches, when interacting species´ phenology changes at different rates. This can result for example in the prevention of existing interactions between plant and pollinator

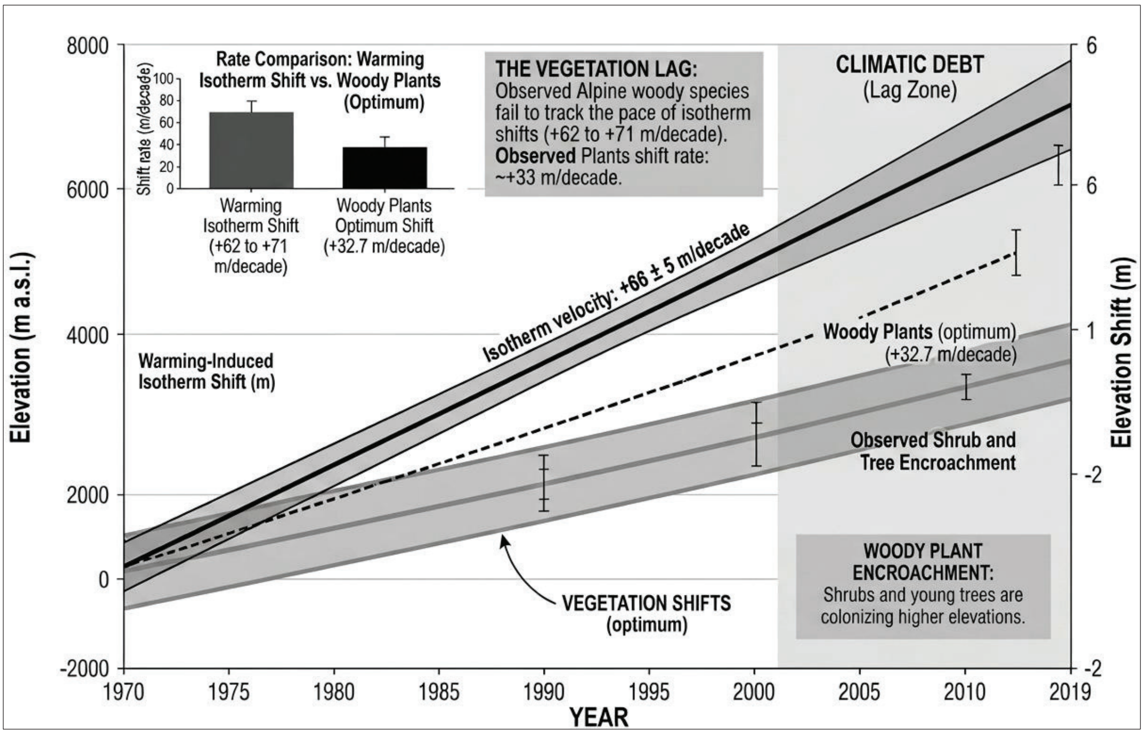

Figure 4: Empirical evidence of vegetation lag under climate warming

Source: (Vitasse et al., 2021; Snell et al., 2022, own illustration) species, but it can also create possibilities for new interspecific interactions and competition (Inouye, 2020). These phenological mismatches as well as a decreasing connectivity of pollinator populations can result in decreasing visitation rates, seed production, pollen limitation and therefore also a decreasing stability of the plant community (Parmesan, 2006; Inouye, 2020).

This is especially true for snowmelt trackers, species with a phenology dependent on their ambient conditions that flower at approximately the same time after snowmelt, independent of when snowmelt occurred within the year. However, there are also many plant species with a phenology controlled by the photoperiod, the length of the days, and therefore flower at the same time each year, mostly independent of the yearly weather conditions (Körner, 2021). With an earlier snowmelt and warmer temperatures earlier in the season, mainly plant species independent of the photoperiod may benefit from the longer growing season, while plants with a phenology connected to the photoperiod may be disadvantaged due to higher competition when their flowering period starts (Körner, 2021). However, climate change may also enhance late frosts after warm spells earlier in the season. Plants with a phenology connected to the photoperiod may be protected against more of these freezing events than snow tracker species, due to their later flowering, independent of warm spells early on in the season (Körner, 2021).

To understand the ecological consequences of these asynchronous dynamics, it is necessary to consider empirical evidence from both experimental and long-term observational studies. Field experiments show that earlier snowmelt can create temporal mismatches between subalpine plants and their pollinators, leading to reduced interaction success. For instance, in *Delphinium nuttallianum*, shifts in flowering phenology ahead of the emergence of early-season bumblebee queens have been associated with reduced visitation rates and significant declines in per-capsule seed set due to pollen limitation (Inouye, 2020).

Similarly, long-term alpine monitoring studies indicate that phenological responses to climate warming are often uneven across trophic levels. Across multi-decade datasets, subalpine and alpine plants have generally advanced their flowering times more rapidly than the emergence periods of their primary solitary bee pollinators, resulting in increasing temporal decoupling between interacting species (Parmesan, 2006). This growing asynchrony highlights how climate-driven shifts can disrupt mutualistic interactions even when both plants and pollinators are responding to the same environmental signal.

Overall, changes in phenology are species specific and an overall trend of phenological changes with climate change across alpine vegetation is difficult to predict. Also, due to the topographic complexity in alpine regions the growing season can vary over short spatial scales and this may be able to buffer phenological mismatches and their negative effect on vegetation communities (Inouye, 2020). This microclimate-buffering hypothesis has been directly validated by empirical studies testing plant-pollinator networks across complex alpine terrains. Specifically, field research by Scherrer and Körner (2011) showed that small-scale alpine topographies create detailed thermal mosaics where soil temperatures can differ by up to 10°C over distances of just a few meters. This fine-scale variation allows individuals within the same plant population to experience completely different snowmelt timelines. Field observations demonstrate that high aspect and slope variation create adjacent microhabitats where identical plant species flower up to 30 days apart, thereby preserving overall regional landscape connectivity and providing continuous forage resources that buffer temporary temporal mismatches (Ohler et al., 2020).

Furthermore, CaraDonna et al. (2014) provided long-term evidence showing that while broader regional warming tends to compress the overall community flowering season, complex topography acts as an important spatial buffer. By spreading out the flowering windows of different micro-populations across ridges, depressions and snow beds, the landscape prevents everything from happening at the exact same time. This keeps a continuous supply of floral resources open for pollinators throughout the summer season.

Fine-scale microclimatic logging confirms that heterogeneous terrain allows interacting species to adjust spatially rather than temporally, reducing the selective pressure of macroclimatic warming on mutualistic links (Jiménez-Alfaro et al., 2024). Climate change and the consequence of phenological alterations will lead to the creation of new vegetation community compositions and changing species-species interaction (Körner, 2021), the resulting vegetation communities and their distribution are however difficult to predict.

3.2.3. Community Turnover and Extinction Risk

The response of vegetation communities to climatic shifts is mostly characterized by a time lag, that current plant distributions may not fully reflect the altered climatic conditions, which complicates future projections (Alexander et al., 2018). The speed and extent of alpine plant community turnover can depend on several factors like, the dispersal rates of species moving upwards, their successful establishment and competitive ability in new habitats, the rate of population growth in these newly colonized areas, and, crucially, the extinction rates of existing resident alpine species. Some of the specialized alpine plants are particularly vulnerable. For example, species like the glacier buttercup (*Ranunculus glacialis*), purple saxifrage (*Saxifraga oppositifolia*), and creeping avens (*Geum reptans*) are at significant risk of extinction as their unique glacier-adjacent habitats rapidly retreat due to global warming (Losapio et al., 2021). Importantly, however, climate-driven extinction vulnerability is not restricted to these glacier-adjacent pioneers; broader subnival specialists and alpine meadow endemics that lack direct associations with glacial ice sheets face equivalent long-term threats from upslope competitive exclusion, severe microclimatic soil aridification, and physiological thermal stress as lower-elevation generalist flora ascend into historical alpine refugia (Dullinger et al., 2012; Grytnes et al., 2014). Research utilizing detailed ecological and trait-based models on 117 alpine plant species found in Italian Alps glacier forelands indicates substantial threats to their long-term survival due to the direct and indirect impacts of glacier melt (Losapio et al., 2021). These examples highlight the severe consequences of climate change for the unique and often endemic flora of alpine regions.

3.3. Changes in Vegetation Structure

3.3.1. Drivers and Dynamics of Woody Encroachment in Alpine Systems

Climate change has significantly altered alpine vegetation structure by driving widespread functional and compositional shifts across elevational gradients. One of the most prominent expressions of this transformation is the expansion of woody vegetation, including dwarf shrubs and small trees, into alpine and subalpine ecosystems where such growth forms were historically limited (Harsch et al., 2009; Elmendorf et al., 2012).

This process, commonly termed woody encroachment or shrubification, is primarily driven by rising temperatures, reduced duration and depth of snow cover, lengthened growing seasons, and increased frequency of freeze–thaw cycles, all of which enhance establishment conditions for woody species (Myers-Smith et al., 2020). In European mountain systems, land-use change, particularly grazing abandonment, further reinforces this trend by reducing herbivory pressure and enabling shrub establishment and persistence (Snell et al., 2022).

Comparable and, in some cases, more rapid transitions are occurring across high-elevation systems in South Asia. On the Qinghai–Tibetan Plateau and in the Eastern Himalayas, coupled climate warming and shifts in pastoral land use have triggered a large-scale regime shift in ecosystem structure. Since the late twentieth century, this process has resulted in the conversion of approximately 39% of historical alpine meadow systems into shrub-dominated communities primarily composed of Rhododendron, Caragana, and Dasiphora species as these ecosystems have lost their historical resilience to woody encroachment (Brandt et al., 2013).

In the European Alps, shrub cover has been reported to increase at rates of up to 16% annually in localized regions, with average increases of approximately 5.6% per decade (Snell et al., 2022). This structural reconfiguration increases vegetation vertical complexity by replacing low-stature herbaceous and graminoid communities with woody canopies, thereby modifying microclimatic regimes, light availability, and snow accumulation patterns (Camac et al., 2017).

3.3.2. Elevational Controls on Vegetation Structure and Canopy Complexity

Vegetation responses to shrubification are strongly modulated by elevation. In lower alpine belts, increased temperature and reduced grazing intensity often enhance primary productivity and vegetation cover, particularly among tall herbs and shrub species. In contrast, upper alpine and nival zones frequently experience the decline of cold-adapted cushion plant communities, leading to structural simplification, reduced surface roughness, and altered snow retention dynamics, with cascading effects on hydrological processes (Lamprecht et al., 2018).

These structural changes also influence soil thermal regimes. Shrubs exert contrasting seasonal thermal effects by insulating soils during winter while reducing soil temperatures in summer, thereby altering permafrost stability and subsurface energy exchange processes (Myers-Smith et al., 2020).

In addition, high-elevation systems such as the Tibetan Plateau exhibit complex structural vegetation shifts under warming. Rather than keeping pace with rapid thermal changes, long-term tracking shows that shifts in the upper limit of alpine grasslands drastically lag behind climate warming across the region. This substantial distributional delay is highly influenced by localized environmental constraints, including severe water scarcity, poor soil development, and a lack of stable physical substrates beyond existing boundaries (Liu et al., 2026).

3.3.3. Biotic Interactions and Functional Disruption under Shrub Expansion

Shrub expansion exerts strong controls on ecological interactions and ecosystem functioning. Mod and Luoto (2016) demonstrated that shrubification in Arctic systems modifies community composition and regulates the response of tundra vegetation to warming, with effects that may either buffer or amplify climate impacts depending on shrub density and spatial configuration.

In alpine meadow systems of Colorado, Kettenbach et al. (2017) showed that willow encroachment into subalpine meadows altered pollinator visitation dynamics. Co-flowering shrubs attracted pollinators away from *Polemonium viscosum,* reducing visitation rates and negatively affecting reproductive success of the focal species, thereby demonstrating how shrub expansion can restructure plant–pollinator networks.

Comparable disruptions have been observed in monsoon-influenced alpine ecosystems of the Western Himalayas, where upward expansion of broad-leaved shrubs into subnival meadows has compressed foraging ranges of alpine bumblebees (Bombus spp.). This has intensified interspecific competition and disrupted long-established plant–pollinator synchrony, with significant implications for the reproductive success of endemic high-elevation forbs (Singh et al., 2024).

3.3.4. Below-ground Biogeochemical Processes and Soil Microbial Feedbacks

Below-ground, woody encroachment induces substantial shifts in soil microbial communities and nutrient cycling processes. Soil microbial diversity and activity are strongly influenced by vegetation functional traits, soil pH, and carbon-to-nitrogen ratios (Collins et al., 2020). Nitrogen-fixing shrubs can enhance fungal diversity and modify nitrogen availability, while ericoid shrubs exert strong control over bacterial community composition and soil biogeochemistry.

Vegetation change can also disrupt seasonal coupling between plant nutrient uptake and microbial activity, leading to decoupling of established plant–soil feedback loops. In high-altitude permafrost systems across the Himalayan–Tibetan region, woody root expansion accelerates thawing of previously frozen organic carbon pools, triggering enhanced nitrogen release that favors fast-growing generalist species over slow-growing endemic alpine specialists (Yun et al., 2023).

Although shrub expansion may increase aboveground biomass and carbon storage in certain contexts, it may simultaneously accelerate soil organic matter decomposition, resulting in uncertain net ecosystem carbon balance outcomes (Collins et al., 2020).

Projected vegetation trajectories indicate that continued warming and land-use change will likely intensify shrub expansion and associated biodiversity loss unless actively managed. Management interventions such as controlled grazing and targeted shrub removal are increasingly being explored to maintain herb-dominated alpine systems and slow structural transitions (Snell et al., 2022). Overall, woody encroachment represents a major driver of long-term ecosystem transformation in alpine environments.

3.4. Adaptation

3.4.1. Mechanisms of Physiological, Phenotypic, and Evolutionary Adaptation

Adaptation in alpine plants arises through both evolutionary change in heritable traits and phenotypic plasticity. While evolutionary processes can contribute to increased thermal tolerance, most documented responses remain constrained within existing species ranges (Parmesan, 2006). Current evidence suggests that evolutionary adaptation alone is unlikely to offset the magnitude and pace of contemporary climate change, indicating that ecological and plastic responses will remain critical for persistence (Parmesan, 2006).

For example, Wahlenbergia ceracea exhibits potential for evolutionary response to climate warming; however, observed rapid responses are primarily mediated through phenotypic plasticity and epigenetic variation rather than genetic change (Arnold et al., 2024).

Alpine plants display a wide suite of morphological and physiological adaptations to extreme environments. These include compact growth forms such as cushion and rosette structures, slow growth rates, and evergreen leaf traits, which optimize resource use during short growing seasons and enhance resistance to frost, high radiation, and nutrient limitation (Körner, 2021). Many species also maintain photosynthetic activity at low temperatures, enabling persistence under frequent freezing conditions.

Phenological adjustment represents another key adaptive mechanism. However, these responses often lag behind climatic change. Temporal mismatches between environmental conditions and biological timing are widely documented, indicating incomplete adjustment of growth and reproductive cycles in many alpine plant communities (Alexander et al., 2018). Such mismatches can disrupt synchrony with pollinators and reduce reproductive success (Hegland et al., 2009). In the Central Himalayas, this decoupling is particularly pronounced, where earlier spring conditions have led to severe seasonal pollination limitations for Primula species, forcing early-flowering cohorts to rely on evolved compensatory mechanisms to offset the severe drop in pollinator synchrony (Yin-Mei et al., 2026).

3.4.2. Spatial Adaptation Strategies: Range Shifts and Microclimatic Refugia

Upslope migration is a primary spatial response to warming, with alpine species shifting distributions toward higher elevations in search of suitable climatic conditions. Telwala et al. (2013) documented significant elevational range shifts in the Himalayas, accompanied by increased species richness at higher elevations. However, such shifts are constrained by topography and interspecific competition, often resulting in crowding and increased extinction risk at upper elevational limits (Dullinger et al., 2012).

Long-term monitoring in the Kashmir Himalaya further indicates strong thermophilisation trends, where generalist species from lower elevations increasingly dominate summit communities, leading to displacement and fragmentation of endemic subnival flora into isolated and highly vulnerable populations (Hamid et al., 2020).

Vegetation responses also vary spatially along elevation gradients. Rosbakh et al. (2014) observed that lower alpine sites in the Bavarian Alps responded strongly to warming, whereas higher elevations exhibited weaker or decoupled responses, likely due to microclimatic buffering and ecological inertia. Similarly, Gottfried et al. (2012) reported continent-wide vegetation change but emphasized strong spatial heterogeneity in alpine responses.

Microclimatic refugia play a critical role in moderating exposure to regional climate warming. Features such as north-facing slopes, snow beds, and cloud-influenced microsites create locally stable thermal conditions that allow cold-adapted species to persist beyond macroclimatic expectations (Lembrechts et al., 2020). Jiménez-Alfaro et al. (2024) further demonstrate that such refugia support long-term persistence of relict alpine plant communities under ongoing climatic change.

Tree line dynamics provide additional evidence of spatial adaptation processes. In the central Himalayas, upward shifts in tree line position have been documented in response to rising temperatures, resulting in structural reorganization of mountain vegetation belts (Gaire et al., 2014). Similar patterns across the Himalayas highlight the combined influence of climate warming and anthropogenic disturbance on tree line dynamics (Schickhoff, 2005).

3.4.3. Socio-Ecological Constraints and Anthropogenic Limits to Adaptive Capacity

Alpine ecosystems are also embedded within socio-ecological systems in which indigenous knowledge contributes to long-term environmental observation and adaptive resource use. Salick et al. (2014) highlight that Himalayan communities have historically adjusted land-use and harvesting practices in response to observed ecological change, reflecting an important dimension of human–ecosystem adaptation.

However, adaptive capacity is increasingly constrained by anthropogenic landscape modification. Deforestation, land degradation, and habitat fragmentation reduce ecological connectivity and limit gene flow, thereby constraining species' ability to track shifting climatic niches (Chaudhary et al., 2011; Holderegger & Di Giulio, 2010). In highly fragmented mountain systems such as the Hengduan Mountains, infrastructure development and mining activities have disrupted migration corridors, effectively isolating alpine populations within topographically constrained habitats and severely limiting upslope dispersal opportunities (Li et al., 2024).

3.5. Extinction

The accelerating pace of climate change poses a significant threat to alpine plant species, particularly those characterized by narrow environmental tolerances, slow reproductive rates, and limited dispersal capacity. Alpine ecosystems are composed of a high proportion of specialist taxa adapted to narrow thermal regimes, short growing seasons, and edaphic constraints, which collectively limit their capacity to respond rapidly to environmental change. As a result, many of these species exhibit reduced adaptive potential under contemporary warming trajectories (Dirnböck et al., 2011).

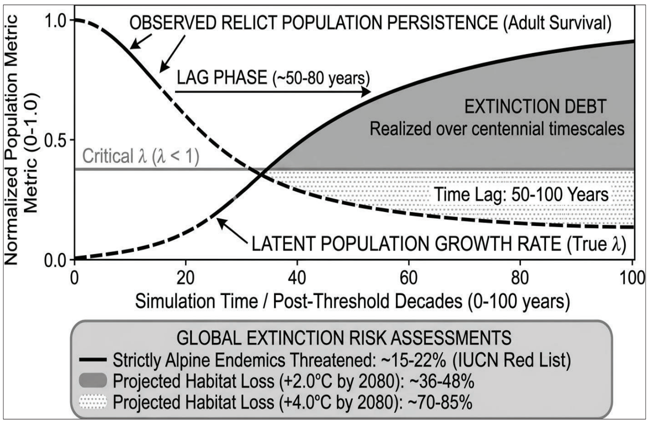

Figure 4: Demographic simulation model illustrating the multi-decadal time lag (extinction debt) in high-mountain perennial flora. The curves isolate the divergence between observed population persistence (sustained by adult clonal survival and slow biomass turnover) and the latent collapse of the true population growth rate induced by climate warming. The figure also contextualizes these demographic shifts within broader global extinction risk assessments, highlighting projected habitat loss for alpine endemics under different warming scenarios. (Dullinger et al., 2012;Rosbakh et al., 2014; Lembrechts et al., 2020; IUCN, 2023;Nomoto et al., 2021, own illustration)

Species restricted to the highest elevations, particularly within alpine and nival zones, are at greatest risk due to the absence of further upslope habitat, a condition often described as a "climatic cul-de-sac" (Loarie et al., 2009). As temperatures rise, thermophilic species expand upward, increasing biotic pressure on cold-adapted assemblages through habitat compression and competitive displacement. This phenomenon has been widely documented across mountain systems, including the European Alps and the Himalayas, where consistent upward range shifts and contraction of cold-adapted species have been observed (Klanderud, 2004; Pauli et al., 2012).

In the Third Pole region, high-elevation ecosystems of the Himalaya–Hengduan Mountains exhibit strong evidence of climate-driven vegetation change, including shifts in species distributions and restructuring of alpine communities. These changes reflect ongoing redistribution of plant assemblages along elevational gradients under warming conditions, with associated impacts on cold-adapted vegetation (Kumar & Khanduri, 2024; Xie et al., 2025). When assessed against global conservation frameworks, these patterns translate into substantial extinction risk. Macroecological models and regional applications of IUCN Red List criteria indicate that narrow-range, high-mountain flora face severe range contractions, with a substantial proportion of strictly alpine endemic plant species currently classified as threatened due to climate-driven habitat loss, restricted population sizes, and competitive disadvantage under changing environmental conditions (Dullinger et al., 2012; Geppert et al., 2023). Regional modelling in the Hindu Kush–Himalaya similarly indicates substantial vulnerability among narrow-range alpine taxa, with projected habitat reductions under future climate scenarios driven by limited dispersal capacity and strong climatic sensitivity (Shrestha et al., 2026). Bioclimatic modelling further indicates that these risks are likely to intensify under future warming scenarios. Under future warming trajectories, macroecological models suggest severe reductions in alpine bioclimatic zones by the end of the century. High-resolution projections indicate that 36–55% of alpine plant species across major mountain ranges face losing more than 80% of their suitable habitat space by 2070–2100 (Engler et al., 2011), while severe, high-emission scenarios could leave up to 60% of the mountain flora functionally vulnerable to local extinction (Thuiller et al., 2005). Given the topographic isolation of alpine systems, such reductions in habitat availability are strongly associated with elevated risks of local and regional extinction.

A central concept in explaining delayed species loss is extinction debt, whereby species persist temporarily in environments that have already become unsuitable, but are ultimately committed to decline in the absence of mitigating processes (Alexander et al., 2015). This phenomenon is particularly pronounced in alpine ecosystems due to the life-history characteristics of many resident species, which are often long-lived perennials with slow demographic turnover and strong clonal persistence (Körner, 2021). In high-mountain regions such as the Eastern Himalayas and Southwest China, such demographic inertia can result in the continued presence of relict populations even after environmental conditions have surpassed thresholds for successful regeneration (Dullinger et al., 2012; Han et al., 2023).

This delayed response is further reinforced by demographic lag effects, where populations may appear stable due to vegetative persistence despite reduced reproductive success under changing climatic conditions. As a result, declines in population viability may remain undetected until mature individuals senesce without sufficient recruitment (Jackson et al., 2009). Empirical and modelling studies suggest that ongoing climatic shifts have already exceeded the physiological and demographic thresholds of numerous high-elevation endemics, resulting in populations with negative growth trajectories ($\lambda < 1$) that persist as relictual assemblages (Nomoto et al., 2021). These extinction debts are expected to be realized over centennial timescales, typically within 50–100 years, as reduced recruitment, reproductive failure, and cohort senescence lead to progressive population collapse (Dullinger et al., 2012). Such lagged responses may obscure the full magnitude of biodiversity loss, thereby complicating conservation planning and risk assessment.

In addition to direct climatic effects, disruptions to biotic interactions further amplify extinction vulnerability. Many alpine plant species depend on tightly coupled mutualisms, including specialized pollination systems and mycorrhizal associations, which are sensitive to phenological and environmental mismatches. Climate-induced shifts can therefore decouple plant–pollinator synchrony and alter below-ground microbial communities, reducing reproductive success and nutrient acquisition even under otherwise suitable abiotic conditions (Hegland et al., 2009; Collins et al., 2020). These pressures are compounded by anthropogenic habitat fragmentation associated with tourism, infrastructure development, and land-use change, which further restricts gene flow and reduces adaptive capacity across isolated populations (Holderegger & Di Giulio, 2010).

Empirical observations support these projected dynamics. Cold-adapted species such as Ranunculus glacialis and Silene acaulis have already exhibited measurable range contractions and declines in abundance associated with warming temperatures and altered snow regimes (Lamprecht et al., 2018; Steinbauer et al., 2018). While some generalist and pioneer species expand into newly available niches, these taxa do not typically compensate for the ecological functions of lost specialists, leading to altered community composition and potential degradation of ecosystem processes.

Climate change represents a multifaceted threat to alpine plant diversity through habitat compression, disruption of ecological interactions, and increasing population isolation. Addressing these challenges requires integrated conservation strategies that prioritize habitat connectivity, protection of mutualistic networks, and explicit incorporation of extinction debt dynamics into long-term management frameworks.

4. Conclusions

Climate change is driving consistent and well-documented shifts in alpine vegetation worldwide, including upward range shifts, altered phenology, changes in community composition, and increased vulnerability of cold-adapted specialist species. Although alpine plants exhibit a range of adaptive responses, these are often constrained by dispersal limitations, biotic interactions, and the progressive reduction of suitable habitat under continued warming (Körner, 2021). Microclimatic heterogeneity plays a key role in moderating these impacts by creating fine-scale refugia that can buffer species against regional climate warming. However, these effects are likely temporary under sustained climatic trends and may only delay, rather than prevent, long-term biodiversity losses. In addition, the expansion of woody vegetation into alpine zones is altering microclimatic conditions and ecosystem functioning, introducing further uncertainty in carbon cycling and ecosystem stability (Pepin et al., 2022).

Despite significant progress, this review highlights the need for improved integration of macroclimatic and microclimatic processes to enhance predictive understanding of alpine ecosystem responses. Such integration is essential for developing effective conservation and management strategies, including interventions such as grazing regulation or shrub management aimed at maintaining herb-rich alpine habitats.

Future research should address three major gaps. Methodologically, there is a need to combine high-resolution microclimatic sensor networks with terrain-aware modelling and LiDAR-based topographic data to better resolve microclimatic variability beyond coarse-scale climate grids (Lembrechts et al., 2020; Zellweger et al., 2020). Geographically, monitoring remains unevenly distributed, with strong representation in the European Alps and parts of North America, particularly through long-term networks such as GLORIA (Pauli et al., 2012), while substantial gaps persist in high-mountain regions of Asia, including the Himalaya and other under-monitored systems (Schickhoff et al., 2016). Moreover, observations remain biased toward subalpine and tree line zones, whereas upper alpine, subnival, and nival ecosystems remain underrepresented despite their importance for understanding ecological limits under extreme conditions (Körner, 2021). Functionally, important uncertainties remain regarding non-vascular and cryptogamic components of alpine ecosystems, including bryophytes, lichens, and biological soil crusts, which play critical roles in soil stability, nutrient cycling, and hydrological regulation but remain poorly understood in terms of climate sensitivity (Signori et al., 2023).

Overall, advancing multi-scale integration across climate, terrain, and biological processes is essential for improving predictions of alpine ecosystem resilience under ongoing global environmental change.

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