The altitude-for-latitude disparity in the range retractions of woody species

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Increasing temperatures are driving rapid upward range shifts of species in mountains. An altitudinal range retreat of 10 m is predicted to translate into a ∼10-km latitudinal retreat based on the rate at which temperatures decline with increasing altitude and latitude, yet reports of latitudinal range retractions are sparse. Here, we examine potential climatic, biological, anthropogenic and methodological explanations for this disparity. We argue that the lack of reported latitudinal range retractions stems more from a lack of research effort, compounded by methodological difficulties, rather than from their absence. Given the predicted negative impacts of increasing temperatures on wide areas of the latitudinal distributions of species, the investigation of range retractions should become a priority in biogeographical research.

Climate change and shifting plant distribution

The geographical distribution of plants is strongly influenced by climate [1]. Minimum temperatures are particularly important in limiting the poleward (see Glossary) expansion of plant species, whereas limited water availability interacts with high temperatures to exert a direct climatic limitation on their expansion in the opposite, or equatorial, direction in many regions [1–7]. Changes in climate are, therefore, predicted to alter the geographic distribution of plant species at global to local scales.

Contemporary plant range shifts are most frequently reported from mountain regions, with elevational shifts of the mountain treeline being the most commonly documented response to increasing temperatures [8–12]. The distributions of species in mountain regions are typically restricted to relatively narrow and well-delineated altitudinal bands, in comparison with often broad and poorly defined latitudinal distributions in the lowlands. This strong altitudinal zonation of mountain vegetation, and its climatic sensitivity [13], makes mountains ideal 'natural laboratories' and favoured locations for the study of climate change impacts worldwide [13–15].

The altitudinal compression of montane vegetation zones is due to a rapid decrease in temperature with increasing elevation (∼5–6.5 °C per 1000 m) [3,14], which contrasts with a similar temperature decline occurring over ∼1000 km of latitude (6.9 °C at 45° N or S) [3]. An implication of this altitude-for-latitude temperature model

is that general biogeographical patterns resulting from the climatic limitations imposed on plants in mountains should also be observed in neighbouring lowland regions with similar temperature and moisture regimes. Distributional shifts already observed in mountain plants [8,16–18] should, therefore, be mirrored by lowland range changes occurring over distances that are several orders of magnitude larger (Figure 1).

Here, we discuss the implications of the altitude-for-latitude model for shifts in plant distributions and examine why lowland range shifts, particularly range retractions, are rarely reported. We discuss potential climatic, ecological and anthropogenic explanations for this disparity. Our focus is on woody plants, given that most data are available for these species, and because of the pivotal role that they have in global carbon and hydrological cycles [19–21]. We argue that greater emphasis should be placed on investigating lowland range changes, particularly at the trailing edge of the distribution of woody species, where increasing
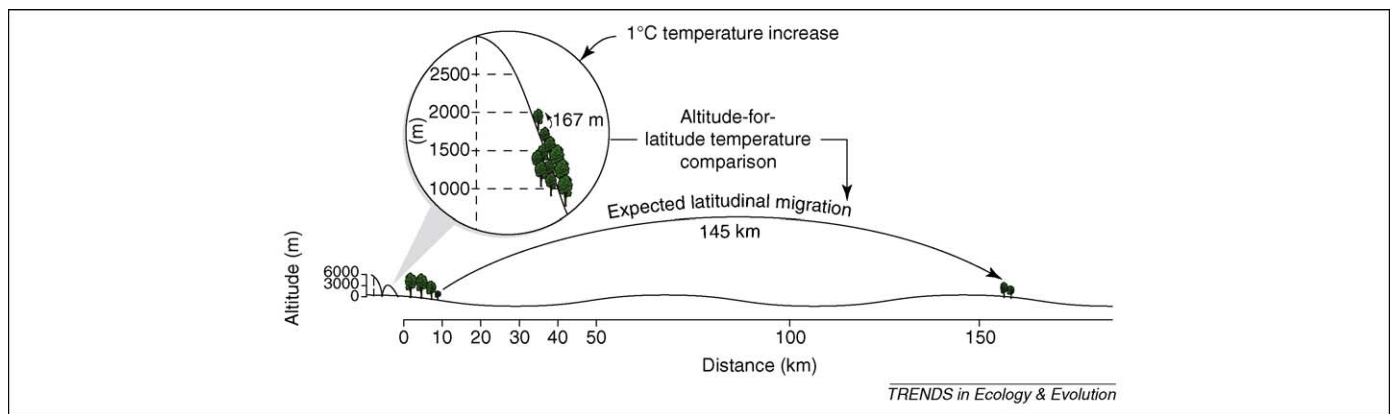
Figure 1. Equivalent migrations in lowland and mountain regions predicted based on an altitude-for-latitude model of temperature similarity. A 1 °C increase in mean annual temperature results in a range change of ~167 m in altitude but ~145 km in latitude (based on a temperature lapse rate of -6 °C km^{-1} altitude and -6.9 °C 1000 km^{-1} latitude from data in Refs [3,14]). Trees are not to scale.

temperatures are expected to have a negative impact on the structure and function of forest ecosystems [4,5,22–25].

Range shifts and growth decline in altitudinal distributions

Shifts in the geographic ranges of plant species occur as a consequence of a combination of population expansion at the leading edge of their distribution and retraction at the trailing edge. Recent changes in the distribution of plant species in mountains have been reported for various plant species, from tropical epiphytes [3], alpine plant species [17] and forest understory plants [18], to shrubs and trees [3,4,12,26,27]. Mountain treelines have shifted upwards, commonly by up to 130 m, over the past 50 years [8].

Investigation of mountain range shifts has been biased towards woody plants and the upward or leading edge of the distribution of species [8,16]. However, an increasing number of reports demonstrate that retraction of the trailing edge of the distribution of various woody species is now underway in mountains worldwide [3,4,12,26–29]. Tree species, including the European beech (*Fagus sylvatica*) [12,29], trembling aspen (*Populus tremuloides*) [28], Ponderosa pine (*Pinus ponderosa*) [4] and red spruce (*Picea rubens*) [26] are declining at their lower range limits, driven by elevated mortality and reproductive decline, linked to increasing temperatures and drought stress [12,30,31]. The few studies that quantify altitudinal range retractions or entire range shifts indicate range retractions of up to 140 m in species ranging from boreal forest trees to drought-tolerant evergreen shrubs during the past 50 years [26,27].

Predicted and observed lowland range shifts

The frequent reports of ongoing range shifts driven by rising temperatures in mountain regions imply that extensive shifts in the latitudinal distribution of species should be expected (Figure 1). For example, a temperature decline of ~6 °C occurs with an increase in elevation of 1000 m [3,14] but with a latitudinal increase of ~1000 km (6.9 °C at 45° N or S) [3]. Consequently, the observed upward elevational shifts of species should translate into latitudinal shifts of tens to hundreds of kilometres based on this altitude-for-latitude model. This expectation is further supported by analyses of common garden experiments (Box 1) [32–36], species-specific process and niche-based models [37–39], and the responses of species to past climatic changes [40,41].

Significant changes in distribution are occurring at the leading edges of lowland plant ranges in response to current climatic changes. In Canada, an increase in the density of black spruce (*Picea mariana*) has occurred at the Arctic treeline [42]. In Alaska, an increase in the density and latitudinal position of shrubs and trees such as green alder (*Alnus crispa*) and white spruce (*Picea glauca*) has been reported from Arctic treelines [43,44], leading to an estimated expansion of forest across ~11 600 km^2 of tundra over the past 50 years [45]. However, despite the theoretical predictions outlined above, reports of latitudinal range retractions remain rare.

Box 1. Evidence and implications from common garden experiments

Common garden experiments have a long tradition in forest research. So-called 'provenance trials' were (and are) widely established to identify and select populations with particular growth traits sought by growers. Data collected from these trials have resulted in important insights into the field of evolutionary ecology; for example, on the pattern and processes of adaptation of quantitative traits reviewed in Refs [88,89]. Provenance trials also provide a powerful tool for studying climate tolerance and response [90]. Observed changes in growth, phenology or vitality in a provenance in response to climatic changes experienced over a latitudinal transect can be interpreted as simulations of its response to future changes in climate predicted to occur in its native population as a result of global climate change.

Common garden trials of many tree species indicate that populations are frequently genetically adapted to their local climate [33–35,91]. For example, if introduced to more arid conditions than those of the population origin, populations typically react with declines in growth and health. In extreme cases, total mortality indicates that the genetically determined tolerance limits of the population have been exceeded. By contrast, transfer into cooler environments with lower water stress often results in growth acceleration, highlighting the tradeoffs in local adaptation to lower water availability. This pattern has been observed for various tree species tested close to the drought-linked edge of their distribution, including Scots pine (*Pinus sylvestris*) and larch (*Larix spp.*) [91], white spruce (*Picea glauca*) [34], and lodgepole pine (*Pinus contorta*) [35].

Forest dieback in lowland regions

Recent studies have documented large-scale dieback events affecting hundreds or thousands of square kilometres of forest within the lowland distribution of various North American trees, including yellow cedar (*Chamaecyparis nootkatentis*) [46], yellow birch (*Betula alleghaniensis*) [47], the pinyon pine (*Pinus edulis*) [5] and trembling aspen [48,49] (Figure 2). Comparable dieback events are reported in Chilean cedar (*Austrocedrus chilensis*) at the forest-steppe ecotone in Northern Patagonia [50] and from European beech in Northern Eurasia [51], eucalypts in northeast Australia [52] and various trees and shrubs in the Mediterranean [53]. Furthermore, a recent review of such dieback events reports that they are occurring with increasing frequency [54].

A common factor inducing these dieback events is elevated temperature, which acts during the summer to exacerbate drought [5,24,33,48–51,53,55] or during winter to cause a premature start to growth and subsequent winter injury [24,46,47]. Elevated temperature and drought can directly elevate mortality [4,27,30,31,48,53,55,56], increase the

Figure 2. Dieback in lowland forests. **(a)** Aerial view of severe dieback of trembling aspen taken in 2004 following the 2001–2002 drought [48] in the aspen parkland zone of Saskatchewan, Canada, and **(b)** the impact on the aspen canopy still visible in 2006. Understory vegetation includes *Prunus virginiana*, *Amelanchier alnifolia*, *Rosa* spp. and *Salix* spp. with only limited vegetative regeneration of aspen (T. Hogg, personal communication). Reproduced with permission from Michael Michaelian (a) and Ted Hogg (b).

susceptibility of species to attack by pests and pathogens [5,28,49,57], or favour outcompetition owing to reduced reproduction and relative competitive ability [12,26,29,55].

Disparity between altitudinal and latitudinal range shifts

The studies cited above [5,46–53,58] provide compelling evidence of increased mortality within the lowland distribution of various woody species, in some cases at subcontinental scales [5,47,48]. These mortality events are linked directly or indirectly to increasing temperatures, yet observed regional mass mortality remains poorly linked with the range retractions predicted to accompany current and future global temperature changes. Consequently, there is an apparent contradiction between predicted impacts of increasing temperatures on the distribution of species and those impacts that are reported from lowland regions. Therefore, it is important to determine if lowland range retractions are occurring, and if they are going undetected or unreported. Here, we summarise potential explanations for this disparity.

Climatic explanations

Several climatic and/or physical factors that are relevant here present a differing pattern with latitude than with altitude. In addition to the altitudinal reduction of land area, four primary atmospheric changes are associated with altitude rather than with latitude: (i) decreasing total atmospheric pressure and partial pressure of all atmospheric gases, including CO_2; (ii) increasing radiation when the sky is cloudless; (iii) a higher fraction of UV-B radiation; and (iv) steep gradients in temperature and ambient humidity, occurring over distances of metres (as opposed to similar changes occurring over kilometres along latitudinal transects) [59]. Moreover, altitudinal gradients are not subject to the variation in seasonal changes in photoperiod that occurs across latitudes. In principle, these factors could enhance plant responses to warming in mountain regions. However, physiological adjustments, such as increased CO_2 fixation efficiency, can negate or substantially reduce the impacts of change (i), whereas increased cloud and fog at higher altitudes might negate changes (ii) and (iii) [59]. A mismatch between altitudinal and latitudinal climatic and/or physical gradients is insufficient to explain the observed disparity because temperature has a key role in determining species distributions in mountain and lowland regions. Range retractions might, however, be exacerbated in mountains because, on average, sites at low elevations and latitudes are warming less rapidly than at high elevations and latitudes [60].

Ecological explanations

Whereas plant range expansion occurs via migration (i.e. dispersal and establishment of individuals), range retraction occurs ultimately via declining vitality and death. In woody species, recruitment typically occurs more rapidly than tree death, which can take several decades [12,61–63]. However, successful recruitment is contingent upon favourable conditions for seed production, germination and subsequent seedling establishment [63]. Thus, recruitment depends on favourable climatic events in addition to mean climatic conditions [56].
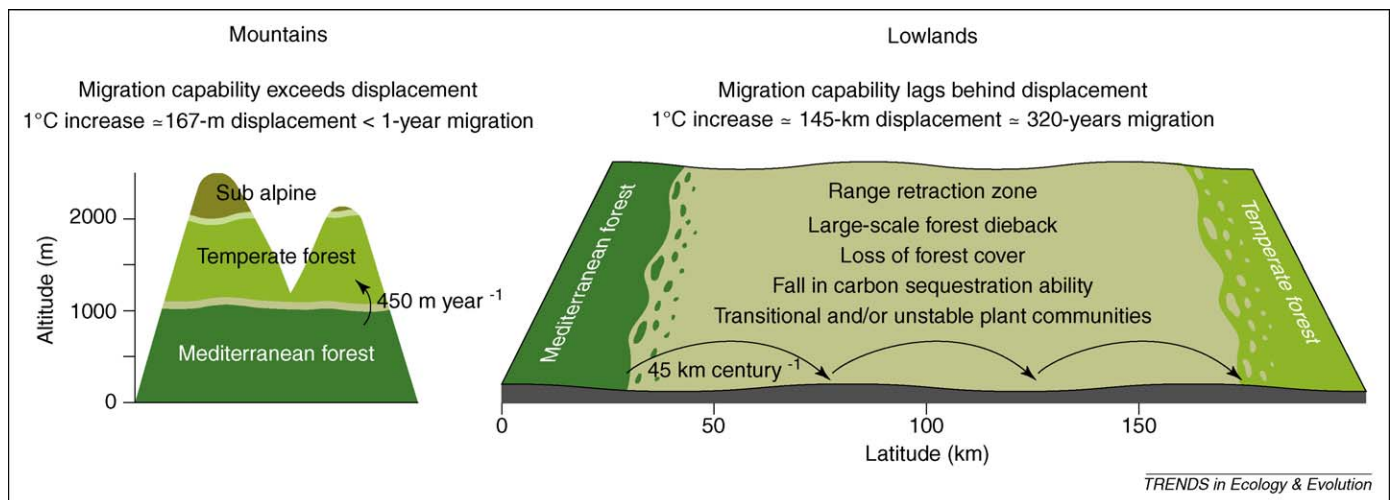
Figure 3. Contrasting consequences of increasing temperatures for range retractions in lowland and mountain regions. A more extensive range retraction zone (grey–green) occurs in lowland than in mountain regions during the hypothetical range retraction of the temperate forest biome, resulting from a 1 °C increase in mean annual temperature (as Figure 1). Potential implications for the range retraction zone are based on a mean tree dispersal capability of 450 m year⁻¹ (45 km century⁻¹) (based on maximum rates reported in Refs [40,41]). Scale differs between mountains and lowlands for clarity of the figure.

At the leading edge of the distribution of a species, the impact of climatic warming can, therefore, be rapidly reflected in the establishment of young populations beyond the former range margins as periods favourable for reproduction become more frequent. However, as high temperatures and droughts become more frequent and more intense [60] at the trailing edge, the frequency of events that are favourable for recruitment is likely to decline. Regeneration thus becomes sparse, whereas a more resilient old generation persists [64]. These impacts are evident in the European beech, where trailing range-edge populations are threatened by increasingly rare recruitment and declining growth of remaining adult trees as temperatures increase [12,51,65,66].

The persistence of relict trees at the trailing edge of the distribution of a species can result in an asynchrony with climate at the trailing range edge of montane and lowland species [63]. The consequence of this asynchrony, potential widespread dieback, will be exacerbated in lowland regions, where it is likely to occur over a larger area (Figure 3). However, local variation in topography, microclimate, soils and hydrology can enable the local persistence of populations even if regional climatic conditions are unfavourable [3,67]. If such favourable microhabitats persist during a period of climatic change, reduced population density and range fragmentation will occur, rather than regional population extinction and an obvious shift of range boundaries [67]. Consequently, changes in trailing range edges are more likely to go undetected than at the leading edge of the distribution of a species because range limits might remain relatively similar, even though a retraction in the core area of the species distribution has occurred (Figure 4).

Genetic explanations

Pressure on trailing range-edge populations to adapt to climatic conditions beyond the present boundary of the species is intense, whether at the altitudinal or latitudinal limits of the species distribution. Climatically determined range limits, therefore, represent the limits to the ability of the species to adapt [6,33,61].

The altitudinal compression of the montane distributions of plant species creates a crucial difference from their lowland analogues in that the geographic distance between the leading and trailing edges of their distribution is much reduced. For example, to cross the same climatic zones experienced in a trip from humid upper montane tropical forest to a high glacier in the Andes (~5-km altitude), one
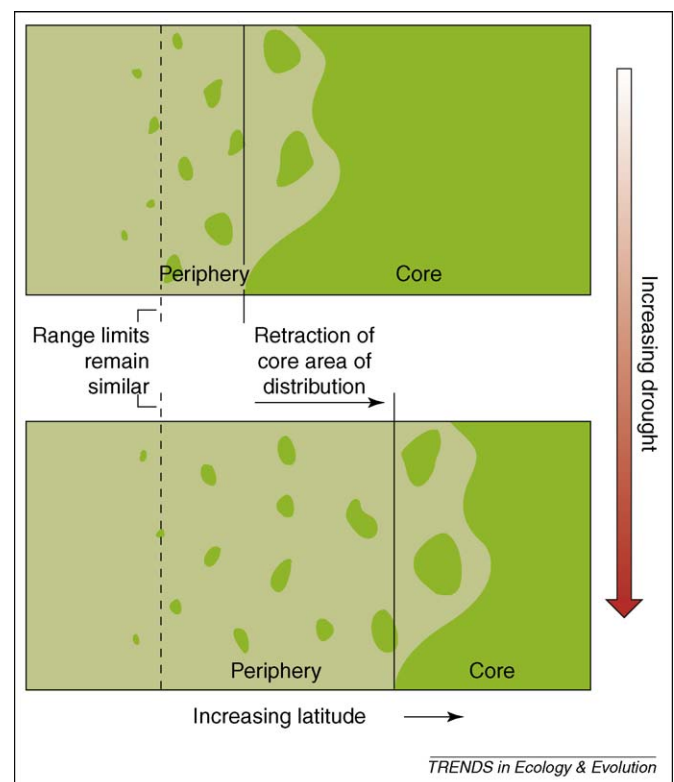
Figure 4. The difficulty in detecting range changes at the trailing edge of the distribution of a species. Local variation in topography, microclimate, soils and hydrology can enable the local persistence of populations even where regional climatic conditions are unfavourable. Reduced population density and range fragmentation result rather than regional extinction and an obvious range retraction [67]. In the figure, the absolute range limits remain similar following an increase in drought at the trailing edge of a species, even though a retraction in the core area of the species distribution has occurred.

would need to travel a latitudinal distance of some 7000 km, the distance between Central America and northern Alaska [15]. In mountains, this compression of the species distribution could prevent local adaptation at altitudinal range margins owing to extensive gene flow from core to peripheral populations [68]. Across the latitudinal distributions of species, the greater distance between core and periphery could prevent such 'swamping' gene flow from occurring, thus rendering local adaptation to climate at the range edge more probable.

Latitudinal range-edge populations might, therefore, be expected to be better able to tolerate climatic extremes than would their altitudinal counterparts. However, when previous climatic changes are considered, warm-adapted genotypes at the range edge might be least likely to survive cold climates during past glacial periods [3,61]; consequently, the trailing edge populations of the latitudinal distribution of a species would be unlikely to maintain a genetic advantage in the long term.

Anthropogenic alteration of range limits
Forest use could also explain why lowland range retractions, although predicted, remain unreported. Across Europe, lowland forests have typically been intensively managed throughout recent history. Natural forest stands close to trailing range edges were more likely to be subject to conversion to tree plantations or other land uses owing to the poor growth and unsatisfactory yield of the native trees [69]. Such exploitation could contribute to a time lag in observing range retractions because the observed limit of the distribution of a species might not match the limits of its potential natural distribution but already lie within them. Furthermore, regular forest management, such as artificially supported natural regeneration, can artificially maintain a species and suspend range shifts, thereby further contributing to any time lag in range retractions [64]. Additionally, suppression of wildfires can speed or slow range shifts by allowing stand density to increase across the range of many fire-prone species, but also increasing the risk that catastrophic wildfires will occur in particularly hot and/or dry years [22,70,71].

Methodological difficulties
The scale of latitudinal distributions makes them more difficult to study than distributions in mountains. Whereas one can cross the entire temperature range occupied by a species in mountain regions in a single day with ease, gathering data range-wide across latitudinal distributions can require covering much of a continent, and research coordinated across different nation states and institutions [14,16]. The investigation of the impacts of climate change on a species is thus more likely to take a regional focus within its latitudinal distribution, and less likely to form part of a study of the distribution of the species as a whole, owing to methodological and logistical difficulties inherent in conducting experimental research over such broad areas. The great potential for broad-scale integrated research into range changes is demonstrated by research in trembling aspen. In this species, a combination of techniques including long-term monitoring, dendroecological analyses, forest inventory data and modelling studies are being used to understand and predict range changes over broad regions of North America [7,28,48,49,72]. Remote-sensing techniques can help here, for example, with the use of indices such as the Normalized Difference Vegetation Index (NDVI), which is a good estimator of total green biomass [73]. Remote sensing might be particularly useful when the retraction is one of a whole ecosystem type, (i.e. from forest to shrubland or from shrubland to desert) but it is not fully capable of monitoring range shifts of particular species where the local distribution of the parent biome does not change [74].

Impacts of climatic changes at the trailing range edge
Ongoing increases in temperature linked to current climatic changes will increase drought stress if these are not matched by increasing precipitation. Plants can tolerate environmental changes *in situ* through a combination of phenotypic plasticity (Box 2) and genetic adaptation [75]; however, both are likely to be of limited effectiveness as temperatures continue to increase [60,75]. Populations at drought-linked trailing range edges will face intense selection pressure to adapt to increased drought. Range-edge populations might show some capacity to adapt via an increase in frequency of the most drought-tolerant genotypes already present within the population [24,55,76]; however, their failure to expand beyond their current limits demonstrates that their short-term adaptive potential has already been largely exhausted [61]. As a result, multiple ecological and evolutionary consequences are anticipated for trailing range-edge populations, as we discuss below.

Increased susceptibility to pests and diseases
Declining vitality at trailing range edges can predispose populations to pest and pathogen outbreaks and can exacerbate the damage that such outbreaks cause [4,77].

Box 2. Extended adaptability through phenotypic plasticity

Phenotypic plasticity is the environmentally sensitive production of alternative phenotypes by given genotypes [75,92]. It maintains the fitness of the individual or population over a range of environmental conditions without genetic change, and sets the limits to the degree of environmental heterogeneity that a genotype can tolerate during its lifetime. Phenotypic plasticity is important for long-lived organisms such as trees, which must tolerate relatively broad fluctuations of environmental conditions throughout their lifetime if they are to survive.

Analyses of common garden trials of tree populations (Box 1) demonstrate a remarkable width of tolerance to changes in thermal environment and, to a lesser extent, in moisture supply, in large part owing to a plastic phenotypic response. However, the presence and magnitude of phenotypic plasticity is under genetic control and is not unlimited [75]. Evidence from provenance trials demonstrates significant within-species differences in plasticity, which have been linked to differences in selection pressure reducing plasticity at extreme sites, such as drought-linked range limits [33,93].

Given directional changes in mean climatic conditions such as increasing global temperature and increased frequency of extreme events, including droughts, heatwaves and severe storms [60], phenotypic plasticity is likely to be under strong directional selection at the range edge of a species [75]. In many cases, therefore, range limits mark the limits to genetic adaptation and phenotypic plasticity. This phenomenon explains the historically conservative adaptive response of tree species to climate change [41,94,95] and should caution against assuming that phenotypic plasticity will enable range-edge populations to tolerate substantial future environmental changes.

A frequent feature of the dieback events recorded in woody species is that elevated temperatures and drought often predispose tree populations to outbreaks of bark beetles, wood-boring insects [4,5,28,30,49,57] and fungal pathogens, including *Phytopthora* species and the canker-causing *Valsa sordida* [28,30,49,57], resulting in mass mortality. Given that increases in global temperature and increasing frequency of severe drought events are predicted to continue [60], future increases in the frequency, severity and spatial extent of pest and pathogen outbreaks are likely within trailing range-edge populations.

Carbon sequestration
Synchronous mortality might occur suddenly and over a large area in response to climate change [4] but the spatial pattern of drought-induced dieback often shows preferential mortality along the drier and lower fringes of tree species distributions [4,7,28–30,48,55]. The processes and rates of carbon sequestration are expected to vary as a consequence of the onset and duration of such forest dieback [21,24,78], with the effect of reduced uptake potentially being magnified by increases in carbon released from tree decomposition [31]. Carbon sequestration can be reduced even in the absence of mass mortality events via tree growth decline and elevated mortality rates, as reported recently at the southernmost range edge of beech distribution in Europe [65,66], and in temperate trees across the western USA [31]. Furthermore, such alterations to carbon economy are occurring despite the predicted enhancement of water-use efficiency by increasing CO_2 and its expected fertilization effect (higher atmospheric CO_2 concentrations leading to higher plant productivity) [79].

Genetic and evolutionary implications
The loss of peripheral populations from the trailing edge of the range of a species during a range shift might have important genetic and evolutionary implications. The peripheral populations at the equatorial range margins of a species might contain a disproportionate share of their genetic diversity owing to a combination of long-term isolation and genetic divergence and their proximity to the glacial refugia of the species, where genotypes have escaped extinction during past glacial periods [25]. Furthermore, these populations are likely to harbour individuals that are locally adapted to the climatic extremes of the range edge [25,55]. Population losses accompanying climate change could, therefore, result in losses of genetic diversity that are disproportionately large relative to the proportion of the range of a species that is lost. These populations represent a valuable genetic resource for conservation, biological exploitation and for the long-term evolutionary potential of the species [25].

Temporal consequences for forest communities
When mortality occurs at the trailing range edge of the montane distribution of a species, rapid replacement by a competitor is likely owing to the short migration distances that are a consequence of the altitudinal compression of the distributions of species. The result is a rapid shift in the boundary or ecotone between species or vegetation zones [4,12,26,29].

Where mass mortality occurs across extensive areas of the latitudinal range of a species, however, the leading edge of a replacement species is likely to be more distant (Figure 3). Consequently, where woody species die over large areas of their latitudinal range, rapid replacement by more drought tolerant species is unlikely without human intervention owing to the dispersal lag of the incoming species [8,24,80–84]. In such a scenario, recent studies demonstrate that, rather than observing ecotone shifts, ecotone expansions and rapid alterations to plant communities are likely to occur [4,5,8,41,46], including the formation of novel species assemblages driven by expansion of non-native species [8,85] or the absence of competitors [3]. Community shifts could be persistent and accompanied by changes in the properties and services of ecosystem [82], such as decreased soil stability and elevated erosion [4,5,23].

Future research
Given the potential severity of impacts that range from increased susceptibility to attack by pests and pathogens, to decreased carbon sequestration ability and altered ecosystem function, it is surprising that the trailing range edges of plant species have received so little attention in recent years [24,25,39,63]. As global temperatures continue to increase, there is an urgent need for research at trailing range edges to enable the impacts of changes to be predicted and conservation and adaptation strategies developed before they occur [24,25,30,55].

Improved methods for delineating the range edges of species that combine population presence with local and regional abundance will enable better detection of range changes where trailing latitudinal range edges are poorly defined (Figure 4). Distributional modelling studies need to consider explicitly ecological processes at the trailing edge and resulting population dynamics [25,39,86,87]. Forest inventory data can provide a valuable resource for modelling studies, as recent work assessing potential future range changes in trembling aspen demonstrates [7]. Monitoring must include sites across the range of a species while ensuring that trailing range-edge populations are monitored in sensitive as well as locally favourable sites. Monitoring data should be provided by remote sensing techniques, such as the NDVI [4,5], in combination with a network of local monitoring plots to ensure changes in NDVI can be correctly interpreted [74]. At the local level, tree establishment and vitality should be assessed using ecophysiological [24] and dendroecological methods [12,31,65,66], in addition to current monitoring of forest condition conducted by international programmes such as the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests, www.icp-forests.org). Trailing range-edge populations represent a potentially valuable resource for the future conservation and management of the species range-wide [25,55] (Box 1) and therefore strategies must be developed to conserve the genetic diversity they contain.

Conclusion
Global temperatures have increased rapidly over the past 50 years, accompanied by an increasing frequency of extreme weather events [60]. Altitude-for-latitude

temperature comparisons indicate that plant range retractions observed in mountains should be mirrored by lowland range retractions several orders of magnitude larger (Figure 1), yet these are not reported.

A lower rate of warming at low latitudes and potentially greater local adaptation to climatic extremes in lowland range-edge populations might partially explain this disparity. Furthermore, human intervention, such as tree planting and assisted reproduction, can artificially maintain populations and locally suspend range shifts in managed forests. The typically poor definition of trailing range edges [1] might confound the detection of range retractions where these are currently occurring (Figure 4). However, a lack of coordinated research into trailing range-edge populations [24,25,39,63], particularly in lowland distributions, is a more probable explanation for the lack of published reports of lowland range retractions.

Increasing global temperatures are already having a negative impact on woody species, with elevated mortality and declining reproduction leading to regional decline and dieback events worldwide [54], (Figure 2). Consequently, rapid lowland range retractions might be imminent, with large-scale dieback poised to occur on a sub-continental scale in some species, as recent reports from North America demonstrate [5,7,30,37,46,47,55,72]. Such impacts will result in significant changes to plant community composition and associated biodiversity, ecosystem function and carbon dynamics. Furthermore, potentially valuable genetic resources for the future conservation and management of species might be lost as populations die. Given the probable impacts of rapid range retractions in woody species, we should direct greater research effort at their trailing range edges, to enable us to identify changes that are already underway, predict those that are yet to occur, and develop appropriate adaptation and conservation strategies.

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