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Will plant movements keep up with climate change?

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In the face of anthropogenic climate change, species must acclimate, adapt, move, or die. Although some species are moving already, their ability to keep up with the faster changes expected in the future is unclear. 'Migration lag' is a particular concern with plants, because it could threaten both biodiversity and carbon storage. Plant movements are not realistically represented in models currently used to predict future vegetation and carbon-cycle feedbacks, so there is an urgent need to understand how much of a problem failure to track climate change is likely to be. Therefore, in this review, we compare how fast plants need to move with how fast they can move; that is, the velocity of climate change with the velocity of plant movement.

Plants on the move

Each population of a species has a limited range of tolerance to climatic variables: its climate envelope. As climate changes, this envelope moves across the surface of the Earth and populations must shift their ranges to stay within it. Although individual plants are immobile for most of their life cycle, plant populations move when seeds are dispersed and establish beyond the current range at the leading edge, while the plants at the trailing edge fail to regenerate. The cumulative effect of these individual movements and mortality leads to the displacement of populations, and these population movements in turn result in changes in the overall distribution of the species. Species that cannot track regions of suitable climate across the landscape are doomed to eventual extinction.

Paleoecological studies show that movement was a near universal response to past changes in climate [1] and many species have moved in recent decades [2] in response to rates of climate change that are apparently unprecedented in the Holocene [3]. However, some plant species failed to keep up with the generally slower warming at the end of last glacial period [4] and most plant populations have tracked recent warming only partly or not at all [2,5–8]. Failure to track climate change is expected to have a large impact on growth and survival, leading to plant extinctions and a reduction in the strength of the terrestrial carbon sink [9]. Delays in plant movements may also slow the movements of animals that depend on them for food or

habitat. The need for plant movements, however, is not currently included in global vegetation models, which only estimate the potential future vegetation, assuming there are no limitations on plant movements (Box 1). In this review, we assess the ability of plants to keep up with climate change, explore the consequences of their not doing so, and discuss possible management responses.

The velocity of climate change

The velocity of climate change is the velocity at which something must move over the surface of the Earth to maintain constant climatic conditions. Estimated global mean velocities of change for mean annual temperature and rainfall from 2000 to 2100 are 0.42 and 0.22 km year^{-1}, respectively, but the range of variation for both variables covers four orders of magnitude [10]. In the equatorial lowlands, shallow temperature gradients result in velocities of temperature change that can exceed 10 km year^{-1}, whereas on steep slopes, they may be less than 10 m year^{-1}. For comparison, the global mean velocity of temperature change between the last glacial maximum and the present day was only 5.9 m year^{-1}, although this long interval undoubtedly included periods with significantly higher velocities than this [11]. In practice, however, plant distributions are probably rarely controlled directly by mean annual temperature or rainfall, but by idiosyncratic combinations of other climatic and nonclimatic variables [12]. The relevant velocity of climate change will thus be species specific. Moreover, climate velocities are vectors, with both magnitude and direction, and the directions of the key variables may diverge. A modeling study of montane vertebrates found that the risks of extinction from warming alone (when a species is 'pushed off the top' of a mountain by rising temperature) were <5%, but these increased tenfold when the often divergent changes in precipitation were also considered [13]. Recent declines in the Haleakalā silversword in Hawaii may be a plant example of this phenomenon [14].

Do plants need to keep up?

The velocity of climate change is a measure of the climate-change exposure of a species, not necessarily of the impact, which will depend also on its climate sensitivity and its capacity for acclimation and adaptation. Current range limits are not necessarily set by climate; non-climatic factors (topography, soils, and biotic influences) are often

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Box 1. Plant movements in global vegetation models

The dynamic global vegetation models (DGVMs) used to simulate the effects of climate change on vegetation must handle approximately 1 trillion trees of 100 000 species [80], so they take short-cuts. One is to reduce plant diversity to a dozen or so plant functional types (PFTs), based largely on physiology. These simplifications render them useless for predicting species extinctions [81] and, coupled with the low spatial resolution of global models, make it impossible to account realistically for plant movements, so all locations are assumed to be accessible to all PFTs. Even for simple carbon accounting, this assumption is problematic. As this review shows, most species will not move fast enough, so when climate change velocities are high, invading PFTs will likely be represented by, at best, a well-dispersed subset of the species pool. Mid- and late-successional tree species will probably lag more than will early successional species, with their shorter generation times and longer dispersal distances, resulting in future forests dominated, at least initially, by smaller trees with lower density wood and, thus, less carbon [44]. Moreover, plant (or trait) diversity itself promotes carbon fixation [82], so the number of species matters.

Although species-specific parameterization of vegetation models is currently impractical, except on a local scale, hybrid models of intermediate complexity can allow the major drivers of species distributions, including dispersal, to be represented in a more realistic way [81]. A recent regional study included a simplified representation of dispersal, using the same dispersal kernel for all species [83]. The challenge is to develop the global-scale vegetation models needed to provide the carbon-cycle feedbacks for global climate models, while retaining the spatial and biological resolution necessary for the realistic modeling of plant movements and other key vegetation processes [80]. The easiest approach conceptually is to add more PFTs, with some representing the capacity for movement [80,83]. A recent study in the French Alps distinguished seven dispersal classes on the basis of plant traits [84]. This approach could be scaled up, although information on dispersal traits is sparse for many vegetation types. Alternative approaches include using a widely available variable, plant height, as a proxy for mean dispersal distance [25], or adding dispersal traits to PFTs based on other, correlated, traits, such as those associated with the pioneer–climax axis [85].

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increasingly influential at finer scales [15]. Therefore, populations restricted by nonclimatic factors to ranges well within their potential climatic limits might not need to move. The capacity of individual plants for acclimation to climate change during their lifetime is largely unknown, although data from tree provenance trials suggest that this capacity varies both within and between species [16,17]. Rapid evolution *in situ* might also be possible in populations of short-lived species that have existing genetic variation in relevant traits, that experience high levels of gene flow from better-adapted populations [18], or that gain better-adapted genotypes through mutation [19]. Theoretical arguments for the potential importance of rapid evolution, however, must be set against the evidence from the paleoecological record of range shifts and local extinctions, that climate niches are conservative and that plants are more likely to move than adapt in response to even gradual climate change [1,20].

The potential velocities of plant movements

The maximum distance a population can move over a given time period depends on both the number of dispersal events in that time period and the distance covered by each event. The number of dispersal events is determined by the time from seed to first reproduction, which is 1–30 years in most plant species [21]. Recent reviews suggest that most seeds are dispersed within 10–1500 m of the parent plant, with a relatively small proportion of plant species regularly dispersing seeds further [22–26]. Routine dispersal distances significantly more than 1500 m are most likely in species with small, wind-dispersed seeds, and those moved by large birds, Old World fruit bats, megaherbivores, or humans [23,27].

Assessing the importance of rare (<2–10%), long-distance dispersal (LDD) events is problematic, because direct evidence for these movements is usually lacking. Mechanistic models of seed dispersal that include LDD events are best developed for species dispersed by wind [28], whereas models for animal dispersal are usually vector specific [29]. The likelihood that a small proportion of LDD events will translate into a high velocity depends on both the total number of seeds dispersed and the proportion of these that survive to reproduce [30,31]. High fecundity, high plant densities near the range margin, and high seed-to-adult survival probabilities are all expected to increase the velocity by making proportionately rare events significant in absolute terms. Models suggest that the abundance of seeds at a given distance and, thus, the potential velocity, tends to scale directly with fecundity as the tail of the dispersal kernel flattens [32]. Indeed, in woody plants, where fecundity (and, for wind-dispersed species, release height) increases with age, the minimum time to reproduction might be less important than the age at which they make their maximum contribution to range expansion [33].

Modeling studies suggest that dispersal distances are the dominant influence on velocities of plant movement, with the importance of other drivers being context dependent [34]. Time to maturity becomes increasingly important in longer-lived species, and both fecundity and seed-to-adult survival can have a significant impact in certain circumstances [34,35]. Combining routine maximum dispersal distances (50–1500 m) with typical times to maturity (1–30 years), the most important and best quantified variables, suggests that the normal velocities of plant movement in unfragmented habitats without interactions with other species will be in the range of 1.7–1500 m year^{-1}. However, the positive relation between dispersal distance and plant height [25] suggests that the combination of long dispersal distance and short time to maturity that is needed for the highest velocities in this range will be rare, with most species spreading less than a kilometer a year and many much less than this.

Several factors are likely to reduce normal velocities in real landscapes below these theoretical estimates. Many plant populations have nonclimatic local adaptations that may negatively affect their growth and survival in new areas [36]. Moreover, the densities of most species decline near range margins, which will reduce velocities by reducing propagule pressure [37]. Landscape heterogeneity also reduces velocities in models and in observations of invasive species, but becomes less important as dispersal distances increase relative to the size of the gaps in favorable habitat [38–40]. Velocities approaching the theoretical predictions thus seem most likely for well-dispersed generalists with

good colonizing ability, such as many ruderal and pioneer species.

If seed movements dominate gene flow, natural selection will tend to favor the evolution of increased movement rates at the margins, because populations established in new areas will be dominated by plants with traits favoring fast movement [41], but it is not clear how often this will be significant. Moreover, although seeds are the only means by which species can invade previously unoccupied habitat, pollen flow from existing populations to newly established individuals could subsequently help or hinder further range expansion, depending on what genes it brings. Beneficial effects have been predicted to dominate at the leading edge of forest tree populations, because these pollen flows can replenish the genetic variance needed for adaptive evolution [16]. By contrast, if individual plants are locally adapted, then gene flow from contrasting habitat patches might have a negative impact by reducing adaptation to the local environment [42].

Interactions with other species

Plants will not move through a vacuum. Interspecific competition is expected to reduce velocities significantly because habitats that are newly available as a result of climate change are usually already occupied by resident species [43,44]. Even if the current residents are poorly adapted to the new climate, they might have better local adaptations to nonclimatic factors [37] and they start with a numerical advantage [8]; thus, they might take a long time to weaken and die, freeing up space, light, and nutrients for the invaders [45]. Local disturbance events (e.g., fires or storms) can reduce competition [45] and strong competitors (e.g., trees invading grassland) and highly fecund or well-dispersed species will be slowed less than will weaker competitors and less fecund or poorly dispersed species. Conversely, plant–plant facilitation could increase velocities by increasing seed–adult survival probabilities. Although facilitation is usually described from stressful environments [46], it can also be important for sensitive juvenile plants under milder conditions [15]. The need for facilitation in tree establishment above altitudinal treelines might explain the lack of response to recent warming at some sites [47].

Velocity could be decreased if plants out-run their mutualists. Seed dispersal agents are typically mobile generalists, but some, such as many primates, might be unable to track climate change, particularly in the tropical lowlands and human-modified landscapes [48], which could slow the spread of plants that depend on them for dispersal. Pollinators are often more specialized than are seed-dispersal agents and have the more difficult task of locating a conspecific stigma. This could lead to Allee effects from mate limitation at the low-density leading edge of a spreading population [49]. There is also evidence for one group of pollinators, butterflies, that they are not tracking climate change at northern latitudes, which could in turn be related to limited movements of their larval host plants [50]. Somewhat surprisingly, the ants in the obligately ant-inhabited species of *Macaranga* appear to be less well dispersed than their plant partners and may limit their rate of spread [51]. The most widespread plant mutualisms

are mycorrhizae, but poor dispersal of fungal partners will limit plant velocity only if the fungi are also host specific [52]. This combination of high host specificity and low dispersal seems to be most likely in ectomycorrhizal fungi with underground (hypogeous) fruiting bodies.

Janzen–Connell effects could increase velocities if host-specific natural enemies (i.e., invertebrates and pathogens) are less mobile than the seeds, so that they do not locate seeds, seedlings, or adults that are established far from the parent plant [53]. Janzen–Connell effects on growth and survival in woody plants have been recorded from seeds into adulthood and can have a large impact on the seed to sapling transition [54]. However, most studies showing these effects have been on relatively small spatial scales (<100 m), with impacts leveling off at longer distances from adults, whereas dispersal distances will normally need to exceed this range if plant species are going to track climate range. On a much larger spatial scale (typically >500 km from the existing native range), release from natural enemies might favor plant invaders, but there is currently little evidence for this [55]. Conversely, resident generalist enemies can slow invasion by reducing establishment and fecundity [30].

Differences between species in their velocities of movement will lead to future interactions between plant, animal, and microbe species with no shared coevolutionary history [56]. The consequences of these novel interactions will be as varied as those considered above, but negative impacts would be expected to predominate in the absence of coevolution. Novel interactions with invasive aliens will also increase over the next century, with climate change possibly accelerating this process [57]. Again, negative interactions are expected to predominate, although aliens might also increase velocities by any of the mechanisms considered above, particularly in highly modified landscapes with reduced native diversity.

Overall, it seems likely that interspecific interactions will usually slow plant movements in response to climate change. The most negative impacts are expected for slow-growing, mature-phase species with specialized mutualisms, and the least negative for pioneer species moving into open, but not barren, habitats. However, interspecific interactions are highly idiosyncratic, so these generalizations should be treated with caution.

Human impacts on velocities of plant movement

Most modern plant species survived periods of rapid climate change during the glacial–interglacial transition, but paleoecological records of plant spread reflect a very different situation from that faced by the same species today [1]. Human activities have reduced and fragmented most natural habitats, while extending and increasing the continuity of others. In general, fragmentation of suitable habitat is expected to substantially reduce velocities of plant movement [44,58–61], although land abandonment could have a positive impact on velocities of some species by providing patches with low competition from existing plants [44]. Human activities have also impacted seed dispersal. Size-selective hunting has extirpated or drastically reduced the populations of the birds and mammals responsible for the longest natural dispersal distances,

including the species most likely to cross large habitat gaps [62], whereas logging removes the largest and most fecund trees, reducing crop size and LDD [39]. By contrast, human movements themselves provide effectively unlimited dispersal opportunities for the minority of plant species able to take advantage of them [25,26,31] and human-introduced animal species can sometimes substitute for extirpated native dispersal agents [63].

Anthropogenic climate change and elevated CO_2 levels could affect most of the variables that influence the velocity of plant movements, including seed dispersal by wind [64], fecundity, time to maturity [28,32], competition, other species interactions [56], and the frequency and extent of disturbances, such as fire [32]. Although it is possible to pick combinations of variables that would significantly accelerate plant movements (higher fecundity, quicker maturation, longer dispersal, reduced competition, and increased establishment in disturbed areas), or the opposite, responses to climate change are likely to be nonlinear (e.g., fecundity could increase initially and then decrease subsequently as thermal tolerances are exceeded) and to vary greatly between species and locations. Overall, human impacts on plant movements are likely to favor some species and slow others, but 'losers' are likely to outnumber 'winners' greatly, particularly in the most human-dominated landscapes.

Can plants track climate change?

Most plant populations studied have tracked recent warming partly or not at all, with more complete tracking upslope than latitudinally [2,5–8,65] and by better-dispersed species [66]. It is not clear if these lags reflect a lack of need for movement, after only a small increase in temperature, or a lack of ability. A time lag in the response to warming is another possibility, although the paleoecological record suggests that this must be less than 50–100 years [67]. The lack of response to warming could also reflect the influence of other climate variables, such as water availability, with divergent movement vectors [12,68].

Whichever explanation for recent migration lags is correct, the evidence presented above suggests that many plant species will be unable to keep up with the higher velocities of climate change expected for the remainder of the 21st century. The ranges for predicted climate-change and plant-movement velocities broadly overlap, but most plant-movement velocities are likely to be at the lower end of the range and will be exceeded by climate-change velocities in many areas. Nonfragmented habitats in steep topography, where the velocities required are relatively low, may be an exception, but even in mountainous areas, topographic and edaphic heterogeneity, competition from existing plant communities, anthropogenic habitat fragmentation, loss of dispersal agents, and declining area with altitude will cause many species to lag behind climate change. Unless we are greatly underestimating plant movement capabilities, unaided survival of many species will depend on their ability to acclimate, adapt, or move to microrefuges within dispersal range (Box 2), with a great deal of uncertainty about the likelihood of all three options.

Box 2. Climate change refugia

In *The Origin of the British Flora*, the 19th-century paleobotanist Clement Reid pointed out that oaks could not have reached northern Britain from their presumed glacial refuge in southern Europe through normal dispersal processes and suggested that some unknown means of LDD must have been involved. An alternative explanation for 'Reid's Paradox' is that these species persisted through the glacial maximum at much higher latitudes in 'cryptic refugia' or 'microrefugia' with locally favorable climates, from which they expanded when conditions allowed [86]. Although not confirmed for British oaks, the existence of high-latitude refugia for many species has received support from phylogeography and macrofossils, with LDD still required to explain the spread of plants into areas that were entirely covered by ice [67]. Could the same combination of refugia and LDD help avoid the mass extinctions threatened by the inability of most plant populations to track the predicted velocities of climate change?

Refugia could help reduce the velocities required for survival in two ways (Figure I). Firstly, outlying populations or individual plants might currently survive in front of the main range of the species, reducing the movement velocities required to track future climate change [65]. For example, rainforest outliers near water bodies in tropical savanna regions could facilitate the spread of rainforest if rainfall were to increase [87]. Range outliers can not only occur naturally as relicts of past climates (e.g., spruce outposts beyond the modern tree line in Russia [88]), but also result from planting by humans, although such plantings are more commonly a source of unwanted alien invasions [65]. Conversely, plant populations that failed to track climate change could persist in locally favorable refugia long after the regional climate becomes unfavorable. Locally moist sites could act as refugia in a drying climate and combinations of elevation, aspect, and slope could buffer rising temperatures [77,89]. More work is needed to understand which situations can act as refugia and how effective these will be in the longer term, but there is enough evidence already to

suggest that predictions from coarse-scaled climate-change data are unduly pessimistic about the ability of poorly dispersed plant species to persist into the future [89]. If we can identify these future climate refuges now, they could be prioritized for protection.
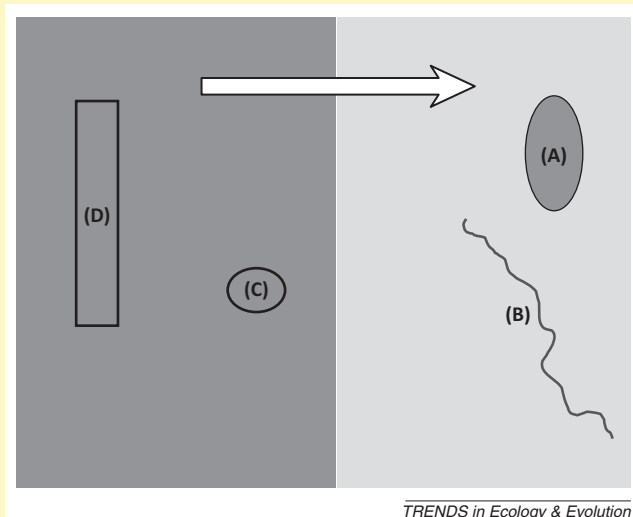

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Figure I. Microrefugia could reduce the velocities needed for plant survival. The dark gray area represents the current main range of a plant species and the white arrow the direction of climate change. **(A,B)** represent outlying populations in front of the main range that could reduce the dispersal distances required to track climate change. **(C,D)** represent future refugia in which the species could persist in locally favorable environments after the regional climate had become unfavorable.

What are the consequences of not keeping up?

Modeling studies predict large-scale extinctions as suitable habitats within dispersal range disappear [69], but in reality the process is likely to be untidy, idiosyncratic, unpredictable, and slow. Even if migration lag leads to loss of fitness, an absence of better-adapted competitors might allow persistence [70] and populations might be able to 'catch up' if the climate velocity declines subsequently. Even partial tracking of climate change should reduce extinction risk. Moreover, extinction in a changing climate will depend on the balance between range expansion, considered here, and range retraction at the trailing edge, determined by very different factors and processes [71,72].

No plant extinctions have so far been attributed to recent climate change and only one species, the previously widespread *Picea critchfieldii*, is known to have become globally extinct during the Late Pleistocene from natural climate change [2,73]. In vertebrates, however, the strong association between low rates of local endemism and high velocities of climate change since the last glacial maximum is most easily explained by increased extinctions when species fail to track climate change [11]. Moreover, the association is strongest in amphibians, the most poorly dispersed group, and weakest in the relatively mobile birds. Although there has not yet been a similar study for plants, these results suggest that we are underestimating the number of species lost to natural climate change and, thus, the importance of movement velocity in buffering against extinction.

Changes in carbon storage are easier to predict than are extinctions. Species that fail to track climate are likely to grow more slowly and eventually die [72]. They will probably also be more sensitive to insect or pathogen outbreaks and, where declining or more seasonal rainfall is an issue, to fire [74]. Moreover, differential movement capacities are likely to lead to replacement forests with less carbon (Box 1).

What can we do about it?

Given the uncertainties outlined above, a first priority is to monitor enough plant populations to assess the extent, causes, and consequences of migration lag. This monitoring needs to go beyond the naive assumption that plant distributions are mechanistically controlled by simple climate variables, such as mean annual temperature, and recognize the role of complex and often divergent climate-change vectors as well as nonclimatic factors [12]. Among recent global initiatives, the Essential Biodiversity Variables approach being developed for the Group on Earth Observations Biodiversity Observation Network (GEO BON) seems ideally suited to monitoring on the required spatial and temporal scales [75]. The involvement of government agencies, nongovernmental organizations, and citizen-science networks will be essential, given the focus of academic science on novelty.

If (and, indeed, while) migration lag is confirmed, plant movements could be facilitated by preserving or restoring habitat connectivity, although, in agreement with this review, modeling studies suggest that only the most mobile plant species will benefit from this if climate change velocities are high [76]. Only in steep topography is habitat continuity across climatic gradients likely to benefit most

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Box 3. Managed translocation

Managed translocation (also called assisted migration or assisted colonization) is the deliberate establishment of populations outside their natural range for conservation purposes: in this case, to reduce the risks of extinction from climate change [90]. It is a controversial idea that not only pits two widely accepted 'conservation rules' against each other (the duty to prevent extinction against the prohibition on introducing non-native species), but also reflects two opposing views of local communities, as coevolved assemblages or the result of 'ecological fitting' of species that are locally available, irrespective of their evolutionary history. The choices are not really as stark as this, however, because managed translocations of plants will normally be into similar communities near the edge of their natural ranges, reducing the risk of unpredictable impacts. Moreover, the traits that make a species likely to require translocation (e.g., poor dispersal, long life-cycle, or low competitive ability) are the opposite of those commonly associated with invasiveness [90], although invasion biology is a field where predictability is still low. Less controversial than translocation outside the current range would be moving plants within their range, from the core to the expanding margin, to increase gene flow [41,79]. By contrast, the proposed use of managed translocation to restore ecological processes in the recipient ecosystem, rather than simply to reduce the risk of extinction for the translocated species, is more controversial, because the aim in this case would be to have a substantial impact [91].

The most serious concerns are not with the philosophy, but with the practicality of moving large numbers of species in ways that minimize the risk:reward ratio. The risks that have received most attention in the literature are of translocated species becoming invasive [78] and locally adapted genotypes being disrupted [92], although neither seems likely to be a general problem. We are faced with a moving target, so there is also an additional risk of moving long-lived species too far or not far enough. Foresters suggest targeting the climate expected during the sensitive establishment phase [74], but this might not be the optimum for all species. Conservation laws, which almost everywhere ignore climate change, can also put legal barriers in the way of deliberate movements of plants outside their current ranges [90]. Managed translocation is still too new for formal, enforceable guidelines, but there is an urgent need for conservation agencies to develop guides to best, and worst, practice [90,93].

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plant species. Identifying and protecting climate-change refugia (Box 2) is another possible approach [77], particularly in areas of complex topography, although it is not clear how many landscapes have sufficient variance in the relevant climate parameters at the appropriate spatial scale for this to work. Given the disproportionate concentration of existing protected areas in steep and complex topography, however, the protection and, if necessary, strategic restoration of vegetation across altitudinal gradients in such landscapes should be a general recommendation. In less steep topography, managed translocation (Box 3) will probably be needed for many species. *Ex situ* conservation will also be critical as backup against the possibility of failure and to bridge temporal gaps between population loss and re-establishment [78]. The use of a formal decision framework linked to specific management interventions will help with decisions on individual species [79].

Concluding remarks

This review shows that movements by many plant species are likely to lag behind broad-scale patterns of climate change over the remainder of this century. There are significant gaps in our understanding of the processes involved in tracking climate (Box 4), but filling them is

Box 4. Outstanding questions

Plant movements are complex and idiosyncratic, but this review suggests several major areas where additional research could enhance our ability to predict migration lag and its consequences.

- Firstly, our ignorance of the factors that currently limit species ranges makes it difficult to predict how sensitive these will be to climate change [15].
- Secondly, despite the diversity of processes involved, the capacity of plant species for LDD appears to be the single most important unknown in predicting movement velocities [28].
- Thirdly, it is not clear to what extent competition from existing plant populations can slow or halt invasions by better-adapted species. Although such invasions have been observed in low-diversity montane vegetation (e.g., [45]), it is possible that 'biotic resistance' could be contributing to the apparent failures of tracking elsewhere.
- Fourthly, it is largely unknown to what extent plants can acclimate to climate change in situ, what the costs of this acclimation are, and how much the capacity varies among species [9].
- Finally, the capacity for adaptive evolution is also unknown, with no test so far of the common assumption that plant populations will find it impossible to adapt rapidly to completely novel climates for which there are no pre-adapted genotypes [9].

unlikely to change this general conclusion. Although several worthwhile adaptation measures have been suggested, it is clear that we must prioritize the global agreements needed to slow climate change.

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