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# How will biotic interactions influence climate change–induced range shifts?

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**Biotic interactions present a challenge in determining whether species distributions will track climate change. Interactions with competitors, consumers, mutualists, and facilitators can strongly influence local species distributions, but few studies assess how and whether these interactions will impede or accelerate climate change–induced range shifts. In this paper, we explore how ecologists might move forward on this question. We first outline the conditions under which biotic interactions can result in range shifts that proceed faster or slower than climate velocity and result in ecological surprises. Next, we use our own work to demonstrate that experimental studies documenting the strength of biotic interactions across large environmental gradients are a critical first step for understanding whether they will influence climate change–induced range shifts. Further progress could be made by integrating results from these studies into modeling frameworks to predict how or generalize when biotic interactions mediate how changing climates influence range shifts. Finally, we argue that many more case studies like those described here are needed to explore the importance of biotic interactions during climate change–induced range shifts.**

**Keywords:** global change; global warming; invasion; migration; realized niches; range limits; space-for-time substitutions

## Introduction

What determines the range limits of species? There is overwhelming evidence that species' physiological tolerance to climatic factors like drought or frost strongly influences the geographic location of their range margins.[1] However, factors other than climate also influence species distributions. For example, interactions with competitors,[2–9] consumers,[10–16] mutualists,[17–19] and facilitators[20–22] have been found to influence species' performance at range limits, suggesting that their geographic distributions reflect realized rather than fundamental niches (Table 1). The large variability in the magnitude and even direction of range shifts occurring in response to recent warming[23–26] is consistent with the idea that factors other than climate, including biotic interactions, limited dispersal, long generation times, and adaptation, influence range limits.[27–30] Among nonclimatic factors potentially influencing range limits, biotic interactions represent a key unknown in climate change studies.

If biotic interactions influence the movement and establishment of new populations at poleward (upper) range limits, or the extinction of populations at equatorward (lower) range limits, they could also influence the rate of climate change–induced range shifts (Fig. 1). Unfortunately, our understanding of the circumstances under which biotic interactions will critically affect range shifts is limited. There are examples of species interactions influencing (or even determining) a range boundary (Table 1), but it is generally unclear how such interactions will play out in a warmer world, because only a small number of studies have examined the role of biotic interactions in climate change–induced range shifts (Table 2). This lack of empirical data means that we have little information with which to generalize the species, interactions, and circumstances in which biotic interactions will play a large role in driving

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**Table 1. Mechanisms by which competition, consumption, facilitation, or mutualism can drive range limits, and examples demonstrating such biotically mediated constraints (facilitation appears in both the +/– and +/+ sections because facilitative interactions involve one species benefiting with the other experiencing positive, negative, or no effects). Studies assessing the strength of biotic interactions across large spatial distances (e.g., across a large portion of altitudinal or latitudinal ranges) are indicated with an asterisk**

| | Range limit determinants | |
|---|---|---|
| Interaction | Mechanism by which the species interaction can influence range limits | Empirical studies suggestive of such controls |
| Competition (–/–) | A species may be excluded from an area it can climatically tolerate due to competitive exclusion or competitive preemption by another species, potentially establishing a range limit | Arctic fish,[6*] barnacles,[2] birds,[8*] plants (marsh perennials,[3] Midwestern annual[7*]), lichens,[4] lizards[5] |
| Consumption (disease, facilitation, herbivory, or predation) (+/–) | A species may not achieve positive population growth rates in an area it can climatically tolerate due to the negative impacts of a consumer, predator, herbivore, or disease agent, potentially establishing a range limit<br>A species may be prevented from colonizing an area it can climatically tolerate because its prey, host, or facilitator is not present there, potentially establishing a range limit | Alpine plants[10] (herbivory), butterflies (hosts,[13,15*] reduced parasitoids[16*]), mussels[14] (predation by starfish), tropical trees[11*] (seed predation), treeline conifer[12] (herbivory) |
| Mutualism/facilitation (+/+) | A species may be prevented from colonizing an area it can climatically tolerate because its mutualist (or facilitator) is not present there, potentially establishing a range limit | Annual plant (pollinators[18*]), arctic trees (facilitation by N-fixers,[20] facilitation by neighbors[22*]), trees at treeline[21] (facilitation by neighbors), tropical treelet[17*] (pollinators), tropical montane shrub[19*] (pollinators) |

the range shifts we expect under future climate change.[13,31]

In this paper, we demonstrate that observational and experimental studies spanning species' ranges hold great promise for better understanding how biotic interactions will influence climate change–induced range shifts. We do so in three steps: (1) first, we outline the conditions under which biotic interactions can critically influence range shifts in response to climate change; (2) next, we use our own work to show that environmental gradients can be utilized to understand how and whether biotic interactions influence range limits, which is critical for being able to assess whether they will influence climate change–induced range shifts (i.e., a space-for-time substitution); and (3) finally, we provide suggestions on how to expand on this space-for-time approach, including the integration of the results into modeling frameworks that allow for prediction or generalization and the accumulation of multiple case studies through collaborative ventures.

## How and when do biotic interactions influence climate change–induced range shifts?

Although the performance of all species is strongly influenced by their competitors, predators, pathogens, prey, facilitators, and mutualists,[32–35] not all such interactions will influence how species distributions respond to climate change. A critical

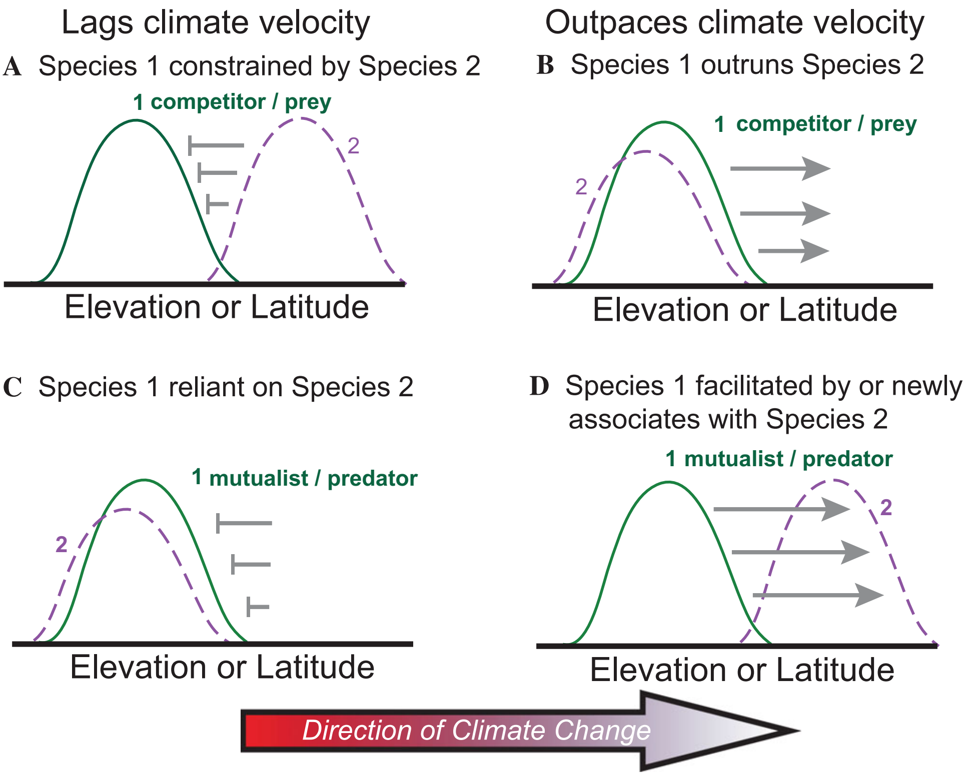

**Figure 1.** Scenarios in which negative interactions with competitors or predators (A and B) or positive interactions with prey or mutualists (C and D) can result in range shifts (of species 1) that lag (first column, gray inhibition t-bars) or, in the short term, outpace (second column, gray arrows) climate velocity due to their interactions with species 2. In each panel, the curves represent the abundance of species 1 (green solid line) and species 2 (purple dashed line) relative to a climatic gradient created by elevation or latitude (increasing to the right).

first question to consider is whether a biotic interaction influences the current range limit. If so, these interactions are likely to play roles during climate change–induced range shifts.[36] For example, decreased pollinator visitation and increased pollen limitation at the range edge of *Clarkia xantia* (a California endemic plant) strongly suggests that plant–pollinator dynamics play a role in establishing the range limit of this species,[18] and could therefore influence how that range boundary moves as climate changes (Fig. 1C). Studies on other interactions, including competition, facilitation, predation, herbivory, and disease provide similarly compelling (although correlative) evidence that biotic interactions constrain vital rates (like growth or survival) at range limits (Table 1). If these effects are strong enough to constrain population growth rates at range margins, range expansion or contraction for these species will depend not only on their direct physiological and demographic responses to changing climates, but also, indirectly, on the influence of climate change on their interactions with other species.[14,37,38]

However, range shifts of species with biotically determined range boundaries may still match climate change velocity (i.e., climate velocity—the speed and direction of climate displacement across a landscape[39,40]) if the relationship between climate and the strength of the biotic interaction is unchanged with warming and the migration ability of both interacting species matches (or exceeds) climate velocity. If not, range shifts may proceed at slower or even faster rates than would be expected from climate velocity. Specifically, species may be prevented from migrating into climatically suitable habitat by the presence of competitors, consumers, or the absence of suitable hosts (Fig. 1A and C, Table 2). For example, the lower intertidal limit of

**Table 2.** **Mechanisms by which competition, consumption, facilitation, or mutualism can result in ecological surprises during climate change–induced range shifts; that is, range shifts that are lagged relative to climate velocity or temporarily outpace climate velocity. Example studies documenting lagged or accelerated range shifts relative to climate velocity (not including studies documenting the potential for such dynamics) are noted in the third column. Facilitation appears in both sections because facilitative interactions involve one species benefiting, with the other experiencing positive, negative, or no effects**

| Interaction | Mechanisms | Examples |
|---|---|---|
| **Range shifts lagged relative to climate velocity** | | |
| Competition | Competitors prevent species from colonizing new habitat because of competition (priority effects) | ? |
| Consumption (disease, herbivory, facilitation, or predation) | Predators, consumers, or disease agents prevent species from expanding their ranges | The lower intertidal limits of mussels have not expanded downward in response to heat stress, because of a more stress-tolerant starfish predator[14] |
| Mutualism (or facilitation) | The absence of an important mutualist or facilitator prevents a species from expanding its range | ? |
| **Range shifts faster than climate velocity (in the short term)** | | |
| Competition | Species “outrun” their competitors | ? |
| Consumption (disease, herbivory, or predation) | Species “outrun” their consumers, or encounter a more desirable host, food source, or prey at their expanding range margins | Bark beetles encounter naive hosts at their expanding range edge, increasing population growth, and range expansion[34] |
| Mutualism (or facilitation) | Mutualists or facilitators allow species to overcome Allee effects; or species associate with a new host at their expanding range margins | A butterfly host shifts onto novel host with a more northerly range[33] |

mussels (*Mytilus californianus*) did not shift downward in response to increased warming and desiccation stress (even while its upper intertidal limit did), because the starfish predator *Pisaster ochraceus* did not similarly shift its distribution downward[14] (Fig. 1A). By contrast, range shifts that proceed, in the short term, faster than climate velocity could occur if species escape their slower moving predators and competitors or encounter a previously inaccessible host beyond the edge of their range (Fig. 1B and D, Table 2). For example, a British butterfly has expanded its range northward at a faster rate than climate velocity because of a warming-induced host shift to a more northerly distributed plant species (and potentially, reduced parasitism),[15] resulting in an altered relationship between climatic gradients and host availability[37] (Fig. 1D).

In short, biotic interactions can have no effect, impede, or even temporarily increase the rate of range shifts over those expected from climate velocity (Fig. 1, Table 2). Range shifts that match climate velocity, even if mediated by species interactions, may still allow for management, but those that are faster or slower than expected represent ecological surprises that are likely to be particularly challenging. Short of actually observing such rapid or lagged range shifts (e.g., Table 2), when might we expect that biotic interactions will lead to such ecological surprises? Our literature review suggests we need to understand (1) whether the interaction drives current range limits; (2) whether the relationship between climate and the strength of the interaction (i.e., the context dependence of the interaction) might be influenced by climate change; (3) how the relative migration abilities of the interacting species compare to climate velocity; and (4) whether a species will encounter a novel interactor that could impede or facilitate its movement.

We submit that experiments and observations conducted across large environmental gradients (i.e., space-for-time substitutions) are a critical first step to assessing how biotic interactions affect range shifts, despite important limitations (e.g., confounding nonclimatic factors that also vary spatially, the difficulty of inferring climate change–induced alterations to gene flow and disturbance from such gradients). Other approaches, including time series of population sizes of interacting species relative to climatic variability[41,42] and experiments documenting the impact of climate on species interactions,[27,43,44] are also valuable for understanding climate change effects on species interactions, but are more resource intensive or require longer periods of time to gather.

## Using environmental gradients to understand how biotic interactions influence range limits

Documenting the importance of biotic interactions on performance across species ranges is a powerful way to establish that the interaction in question affects the position of a range limit and, thus, might influence climate change–induced range shifts. Several experimental design elements are critical. First, such studies should be established across large environmental gradients that cover focal species' range limits and, ideally, match the direction of projected climate change. These gradients could be created by latitude,[22] longitude,[18] or elevation,[8–10,21] but may also include smaller scale gradients generated by depth,[2,14] microtopography, or urbanization.[45] Second, quantifying multiple climatic variables across this environmental gradient is important because climate change will influence more than just mean temperature (e.g., precipitation, snowmelt, extreme temperatures), and also because range position (or latitude or elevation) is not always an accurate surrogate for the many climatic variables that vary enormously over small spatial scales.[46–48] Finally, experimental manipulations, when feasible, are especially powerful. This is because unequivocally establishing that a species interaction constrains performance at a range limit may not be possible without experimental transplants of individuals beyond their range limits,[2] in combination with the manipulation of the biotic interaction in question.[14]

### *Example study system: Mt. Rainier National Park*

Mt. Rainier, located in the western Cascade Mountains of Washington State, is a 4,392-m high volcano designated as a National Park in 1899. Strong climatic gradients exist across this large elevation gradient, with cooler temperatures and greater precipitation (primarily snow) at higher elevations (Fig. S1). Dense coniferous forests prevail at lower elevations (reaching elevations of 1500 m), transitioning to subalpine parklands—mixtures of tree patches and meadows with high diversity of herbaceous flowering plants (1500–1900 m)—finally giving way to alpine vegetation, bare ground, and ice.

Mt. Rainier National Park presents an excellent model system for determining how biotic interactions vary across range limits and with climate. Large climatic gradients exist within a small area (Fig. S1). Importantly, the park contains the upper elevation range limits of virtually all species occurring within it (also of two biomes, coniferous forests, and subalpine/alpine meadows) and the lower elevation range limits of many species. Furthermore, limited direct human influence since the park's founding in 1899 means that the effects of climate and species interactions on distributions can more easily be inferred. We have taken advantage of this study system with detailed observations of species performance relative to experimental manipulations of species interactions and microclimate across an elevation gradient on the south side of Mt. Rainier.

### *Case study 1: the role of competitive interactions (–/–) in establishing range limits*

What are the relative roles of climate and competition in establishing range limits of conifer trees in the forests of Mt. Rainier? Studies, including our own, have shown that climate constrains tree growth at their upper range limits,[49–52] but the role of competitive interactions remains unknown. Because several studies suggest that the importance of biotic interactions such as competition increases as abiotic conditions become less stressful,[3,53,54] we hypothesized that competitive interactions might limit performance at lower range limits. However, in a recent study, we found that although competition influenced tree and sapling growth, it did so equally across species' ranges, suggesting competitive interactions at these two life-history stages do not influence the position of their range limits.[55] Thus,

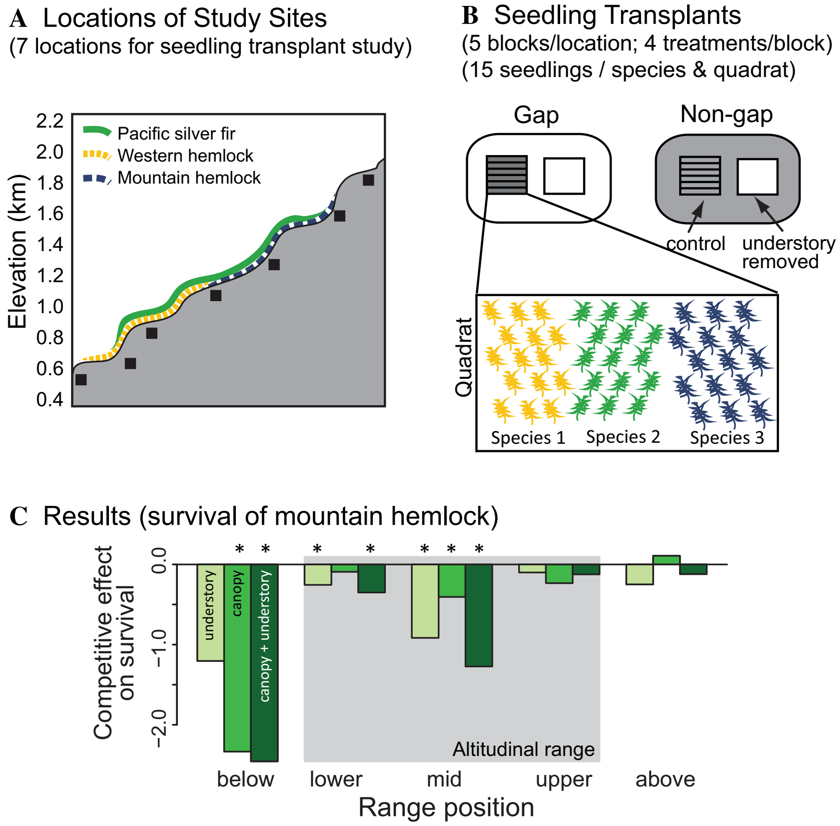

**Figure 2.** We used seedling transplants to assess the importance of competition at early life-history stages on the range limits of Pacific silver fir (*Abies amabilis*), western hemlock (*Tsuga heterophylla*), and mountain hemlock (*Tsuga mertensiana*), three dominant conifers occurring in Mt. Rainier National Park. To quantify climatic and competitive impacts on juvenile stages, we transplanted seedlings within and beyond their range limits (A), in four competitive environments per location (B). These competitive environments consisted of canopy gaps or nongaps, crossed with an understory removal treatment. We found that the influence of competitive interactions on seedling survival of mountain hemlock (over one year, 2010–2011) was greatest below its lower range limit (C). Bars represent the factor by which competitive interactions reduce survival after one growing season, calculated by dividing survival with competition (understory, canopy, or both—light, middle, and dark green) by survival without competition (on a log scale). Asterisks indicate bars where competitive effects alter survival significantly (from that experienced in the canopy control), assessed using mixed-effects models with a binomial error distribution.

we established a manipulative seedling transplant experiment to investigate the possibility that competitive interactions at seedling stages might instead influence the performance of three conifer species at range limits (Fig. 2A–B). Few studies have investigated the impacts of competitive interactions across range limits for these species, and indeed for plant species in general[1] (but see a recent study by Stanton-Geddes *et al.*[7]).

Overall, experimental results support the idea that competitive interactions at early life-history stages, rather than climatic constraints, influence performance at and below lower range limits. For example, the survival of mountain hemlock (*Tsuga mertensiana*) declined strongly in more competitive neighborhoods (i.e., under closed canopy with dense understory), but only at or below lower elevation range limits (Fig. 2C). Results were similar for Pacific silver fir (not shown), the only other focal species for which we could assess competitive interactions at lower range limits (western hemlock, our other focal species, does not have a lower range limit within the park). It is therefore possible that gap dynamics or interactions with understory plants, rather than direct responses to warmer (or drier) climates, constrain population growth of these species at lower range limits. In contrast to adult and sapling growth,[52,55] seedling survival of all three focal species did not appear sensitive to climate, with overall survival beyond both lower and upper range limits similar to that within species ranges (results not shown). Thus, the direct effect of climate on performance is strongest at upper range limits, but only for adults and saplings (not seedlings).

In all, our work provides the first step to understanding how biotic interactions may affect range shifts. Our studies suggest that competition plays a strong role at lower range limits, but not at upper range limits of focal conifers at Mt. Rainier (Fig. 2C). We speculate that range contractions at the lower range limit will lag with future warming, despite the possibility that competitive effects on focal conifer seedlings will increase with warming at lower range limits (Fig. 2C). This is because adult mortality rates are low (less than 1% annually),[56] implying that eventual displacement of focal species by warmer-adapted tree species will be slow, although this of course also depends on competitors' responses to climate change and biotic interactions. Climate change may increase mortality rates,[57] but these rates would have to increase considerably for focal conifers (which are very abundant) to disappear in step with the climate velocity. Moreover, the migration rates of warmer-adapted tree species displacing our focal conifers may also be slow.[30] Thus, we believe that range shifts of focal conifers are unlikely to keep pace with climate velocity at lower range limits (Fig. 1B), due to the interacting effects of competition and long generation times, unless fire begins to play a much more important role in these systems with warming.[58]

### *Case study 2: the role of facilitation (+/–) in establishing range limits*

How will subalpine and alpine herbs and shrubs influence the upward expansion of trees into meadow habitats with warming? The high-elevation ecotone between forest and meadows is known to be sensitive to climatic constraints: treelines globally follow a narrow range in mean growing season temperatures,[59] and upward shifts in treeline position are strongly associated with the magnitude of warming.[25] Though this suggests that the treeline at Mt. Rainier will move upwards with continued warming, biotic interactions may strongly modulate the recruitment of tree seedlings into subalpine and alpine meadows, where facilitation has been found to influence the performance of many plant species.[12,22,35,60,61] We used a manipulative experiment to determine the relative importance of snow duration (which strongly limits growing-season length in high snowfall mountains such as Mt. Rainier) and indirect facilitation via soil development (meadow soil versus bare ground) on the performance of the dominant species forming treeline, subalpine fir (*Abies lasiocarpa,* Fig. 3A–B). Although other studies suggest that facilitative effects in stressful treeline environments are mediated by tree density,[22,60] less attention has been paid to the importance of soil development, which is influenced by meadow plant cover (but see a recent study by Henne *et al.*[62] who address this issue with a vegetation modeling approach). Soil development by meadow vegetation can aid the establishment of trees that may eventually exclude meadow species, creating an antagonistic facilitative interaction between meadow and tree species.

In total, our results add to the studies suggesting that both climate and species interactions influence the performance of tree seedlings at treeline.[51,63] Specifically, we found that subalpine fir seedling growth was lower as snow duration increased, implying that performance is depressed at higher elevations where snow remains on the ground well into the summer. Such direct climatic effects on growth can potentially limit the successful establishment of subalpine fir in high-elevation meadows (since larger seedlings generally have higher survival), and may prevent expansion beyond its current upper range limit. However, seedling growth was also higher in meadow soils, indicating a facilitative effect of meadow plants on subalpine fir through soil development. Successful establishment of subalpine fir at higher elevations is thus more likely where meadow plants are present. Since the density of meadow plants (and associated soil characteristics such as deep soils and high water-holding capacity) declines at higher elevations,[48] this facilitative interaction may ultimately also influence the position of subalpine fir's upper range limits.

How might these facilitative effects influence the upward movement of treeline as climate warms? Our results lead us to speculate that in the short term, species interactions may accelerate the displacement of meadow plants by trees (Fig. 1D).

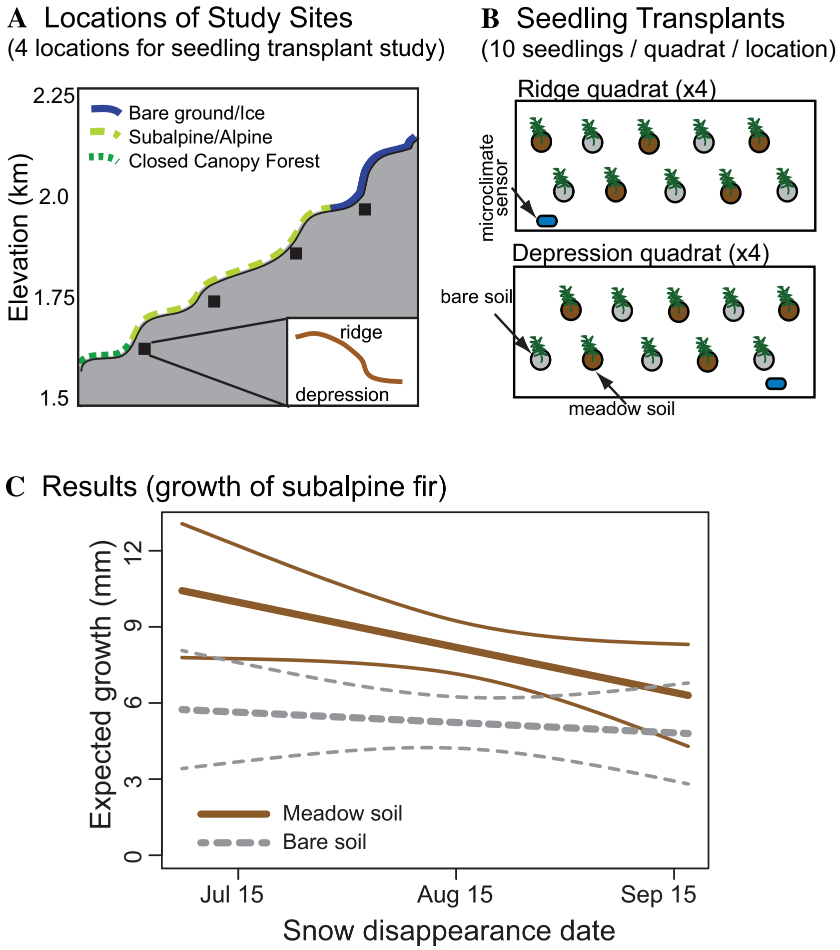

**Figure 3.** We assessed the importance of climate versus edaphic conditions (soil type) on subalpine fir (*Abies lasiocarpa*), the dominant tree forming treeline on Mt. Rainier, by placing study locations across a broad elevation gradient spanning the upper and lower range limits of subalpine fir (A). To quantify climatic and facilitative impacts on seedling growth, we transplanted 10 subalpine fir seedlings into soils collected either from meadows or bare ground in eight quadrats at each location B. Quadrats were located on ridges and in depressions, which resulted in additional variability in snow duration (beyond that driven by elevation) that we captured with microclimate sensors (B). We found that seedling growth of subalpine fir over one growing season (2010–2011) was influenced by snow duration (as measured by snow disappearance date), soil type (brown lines = meadow soil and gray lines = bare soil), and an interaction between the two (C). Expected growth (thick line) was calculated using a linear mixed-effects model, with quadrat as a random effect; the thin lines show the standard error.

First, the facilitative effects of meadow soils on tree seedlings are likely to amplify with warming, since meadow soils have a stronger positive effect on seedling growth when snow duration declines (Fig. 3C). Second, subalpine fir recruitment may also increase rapidly once adult densities increase (an Allee effect driven by positive canopy effects on recruitment),[64] creating an additional positive feedback between climate and treeline expansion driven by another kind of facilitation. Of course, range shift dynamics depend not just on these facilitative effects, but also on the dispersal and migration capacity of treeline species, which is unknown at our site. We speculate that the facilitative effects will dominate the upward movement of treeline in the short term, because meadow habitats at Mt. Rainier are relatively close to tree seed sources. Eventually, the upward migration of all plant species (both tree and herbaceous) will likely be limited by edaphic constraints as the habitat transitions to bare ground (and ice), where soils are shallow and rocky, but this constraint will first be experienced by higher-elevation meadow species. This potential imbalance in migration constraints could lead to the lower limits of meadow plant species contracting faster than their upper range limits expand, causing alpine and subalpine meadows to shrink.

### *Case study 3: the role of mutualisms (+/+) in establishing range limits*

How do pollinators influence the range limits of insect-pollinated meadow plants? Climatic constraints, particularly snow duration, likely influence the upper range limits of meadow species through effects on the growing season.[65] However, pollinator diversity, abundance, or foraging duration may also decline at colder temperatures,[66] raising the possibility that climatic effects on pollinators[18] provide an additional constraint on upper elevation range limits. To assess the role that plant–pollinator interactions play in determining range limits, we quantified the influence of pollinator access to flowers and pollen load on fruit production across the range of an early blooming subalpine wildflower, avalanche lily (*Erythronium montanum,* Fig. 4A–B). Although the importance of mutualisms for plant seed production is well known,[67] there have been surprisingly few studies on the role of this biotic interaction in determining range limits[1] (but see three recent studies[17–19]).

Our results suggest a complex interplay between abiotic and biotic factors influencing fruit production and, potentially, the distribution of avalanche lily. Fruit production of avalanche lily was highest at mid-elevations, in keeping with expectations that plant performance is highest in the core of the distribution[68] (Fig. 4C). Pollinators were critical for seed production, with only one of the 49 plants without pollinator access (flowers covered by mesh bags) setting fruit. However, pollinators seemed to play a differentially important role at the lower, middle, and upper range positions. At lower range limits, the probability of fruit setting was low and only slightly increased by experimental pollen addition, suggesting that seed production is constrained by factors besides pollen loads (Fig. 4C). We speculate that resource limitation, particularly competition for light (due to higher tree cover at lower elevations), is responsible. By contrast, fruit production at the upper range limit was pollen limited (Fig. 4C), although this trend was not statistically significant.

Plant–pollinator dynamics clearly influence fruit production of avalanche lily (Fig. 4C) and may additionally constrain population growth at the upper range limit of this species, but will this mutualism influence the ability of wildflowers to shift their ranges in response to warming? We expect that plant–pollinator dynamics will only weakly limit the upward range expansion of avalanche lily and other subalpine and alpine wildflowers in response to warming (Fig. 1D), if at all. Most high-elevation wildflowers on Mt. Rainier are pollinated by a suite of generalists, which have broad distributions and the ability to forage over large distances, suggesting that the upslope migration of the plants will not be limited by the dispersal ability of their pollinators (although it might by their own dispersal). However, if pollen limitation at upper range limits (Fig. 3C) is driven by low pollinator visitation due to sparse floral resources at the range limit (for example), upward range shifts of meadow plants may lag in warming climates due to fecundity-driven Allee effects. Only additional information on the factors influencing population growth at upper range limits can fully address this question.

### *Implications for our understanding of climate change–induced range shifts at Mt. Rainier*

The space-for-time substitution approach we have taken has increased our understanding of how climate influences biotic interactions (i.e., the context dependence of the interaction) and helped us identify biotic interactions that likely influence range limits (Figs. 2–4, Table 1). However, assessing how and whether these biotic interactions will affect range shifts in a warming world is more challenging (Fig. 1, Table 2). For example, we suspect that range contractions of trees in closed-canopy forests will depend on their slow competitive displacement by more thermally tolerant tree species (Fig. 2C), but without additional information on population dynamics and dispersal of both focal species and their low elevation competitors, as well as potential changes to disturbance regimes (fire), we do not know how rapidly this will occur. Similarly, we expect that turnover and change at treeline will be relatively fast, because facilitation driven by the soil type (Fig. 3C) reinforces the strong positive effects of

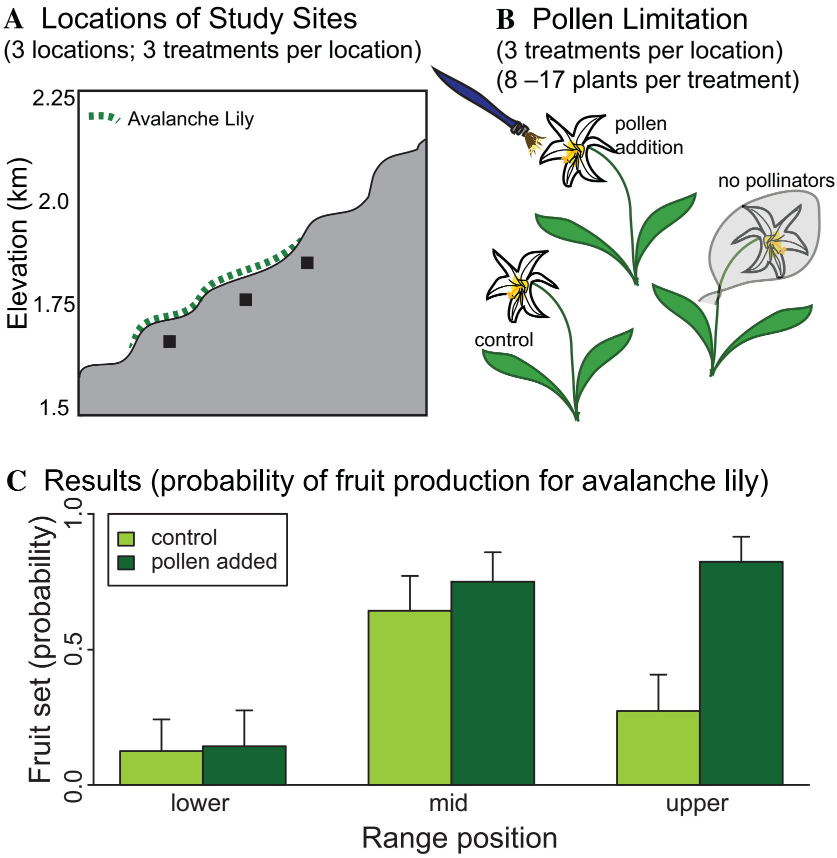

**Figure 4.** We assessed the importance of pollinators for reproductive performance of avalanche lily (*Erythronium montanum*) by manipulating pollen loads and pollinator access at three locations spanning its altitudinal range limits at Mt. Rainier National Park (A). To assess the importance of pollinators for fruit set, we quantified fruit production of individual plants subjected to three treatments at each location: (1) a control plant (to assess baseline levels of fruit production), (2) a plant with pollinators excluded with a mesh bag (to assess the importance of pollinators versus selfing for fruit production), and (3) a plant with pollen added to stigmas to quantify the degree of pollen limitation (B). We found that avalanche lily fruit production in 2011 required the presence of pollinators (results not shown) and varied by elevation (C). Although not significant ($P = 0.089$), potentially due to low sample size, there is a trend toward greater pollen limitation at higher elevations, suggesting that pollen limitation may constrain fruit production at upper range limits.

warming on tree growth at high elevations,[52] but this will also depend on the rate at which subalpine fir is able to disperse into meadows. Finally, although our work suggests that the upward expansion of avalanche lily may depend on how pollinators respond to warming (Fig. 4C), we cannot assume that other insect-pollinated subalpine and alpine plant species will show similar patterns. Thus, our ability to predict specifically whether biotic interactions will lead to ecological surprises at Mt. Rainier (Fig. 1), as well as to generalize our results to other species or systems, is limited. Fortunately, we believe that there are several ways in which these data can be expanded upon to move us closer to such predictability and generality.

## Recommendations for future work

Here, we describe two approaches for evaluating whether biotic interactions will result in ecological surprises during climate change–induced range shifts (Fig. 1), drawing on our own experience (Figs. 2–4), and similar studies (Tables 1 and 2) for insight. Both approaches require additional data and the integration of such data into modeling frameworks, but differ in their overarching goals (prediction versus generalization). However, we emphasize that both can increase our understanding of the role of biotic interactions in mediating species' responses to climate change.

### *Approach 1: forecasting biotically mediated range shifts under climate change*

Empirical data collected over large environmental gradients (e.g., Figs. 2–4) provide information on whether biotic interactions influence current range limits as well as how climate change might influence the strength of those interactions (e.g., Figs. 2–4, Table 1). However, rates of range expansion and contraction (i.e., range shifts) ultimately depend on population dynamics and dispersal. Several population dynamic models of spatio-temporal spread exist, most of which can be parameterized with data from experiments like the ones described above, when additional dispersal data and demographic information[69–73] are also available. Doing so may only be possible for species with extensive demographic and dispersal data available (e.g., some birds[72] and many plants[74]) and where such information exists for all members participating in the interaction (e.g., competitive interactions between tree species), but in such cases, predicting whether biotic interactions will impede (Fig. 1A and C) or even accelerate (Fig. 1B and D) climate change–induced range shifts for specific species may be possible. Because population spread models often do not include all factors influencing range shifts (e.g., adaptation over time, novel interactors encountered during range shifts, altered disturbance regimes), we cannot expect precise predictions (e.g., species X will move at rate Y due to the competitive effects of species Z). However, for well-studied systems, these models can still provide important insights on the species whose range shifts are most likely to be influenced by biotic interactions and the direction of such effects (i.e., resulting in lagged or accelerated range shifts relative to climate velocity [Fig. 1]).

### *Approach 2: generalizing how and when biotic interactions mediate range shifts during climate change*

Phenomenological models that incorporate both the direct effects of climate change and indirect effects of climate change via interactions (e.g., community modules[36] or others[75,76]) could elucidate the context for ecological surprises (Fig. 1); essentially allowing us to generalize when, how, and which biotic interactions strongly influence climate change–induced range shifts. The insights gained from these models could be even more powerful if compared to studies like these (Figs. 2–4), especially given sufficient studies that cover a wide variety of taxa differing in their interactions, their taxonomy, their habitat, and their traits[36] (Tables 1 and 2). Multi-investigator studies and collaborative networks are more likely to be able to replicate experiments or observations of biotic interactions along environmental gradients, and in fact, have already contributed great insight to the importance of facilitation relative to climate as well as the impacts of warming on alpine and arctic plant communities.[35,77,78]

## Conclusion

There is no doubt that ongoing climate change will massively influence species distributions, and thus reshuffle communities.[75,76] Ecologists are increasingly recognizing that biotic interactions can mediate these responses in important and sometimes unexpected ways.[13,31] The challenge for ecologists is to develop predictive tools that better incorporate biotic interactions into forecasts of future species distributions under climate change and generalize how and when species interactions will play a large role during range shifts. This will require large amounts of data as well as the continued development (and application) of quantitative models. As our planet continues to warm, it is imperative that we invest the necessary resources to generalize and forecast changes, so that we may better manage the biological impacts of climate change.

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Figure S1**. The 4.3-km elevational gradient created by Mt. Rainier (A) generates large gradients in temperature (B), winter precipitation (C, falling primarily as snow), and summer precipitation (D). Picture© Michael Arthur Hill / Wikimedia Commons / CC-BY-SA-3.0. Data in B–D are smoothed from 800×800-m grid cell estimates of 30-year monthly temperature and precipitation averages (1971–2000) through the PRISM climate model.[79] Mean annual temperature is the average temperature across all months; winter precipitation, the sum of November–March values; and summer precipitation, the sum of May–September values.

## Conflicts of interest

The authors declare no conflicts of interest.

## References

1. Sexton, J.P. *et al.* 2009. Evolution and ecology of species range limits. *Ann. Rev. Ecol. Evol. Syst.* **40:** 415–436.
2. Connell, J.H. 1961. Influence of interspecific competition and other factors on distribution of barnacle *Chthamalus stellatus*. *Ecology* **42:** 710–723.
3. Bertness, M.D. 1991. Interspecific interactions among high marsh perennials in a New-England salt-marsh. *Ecology* **72:** 125–137.
4. Hestmark, G. *et al.* 2007. Early recruitment equals long-term relative abundance in an alpine saxicolous lichen guild. *Mycologia* **99:** 207–214.
5. Huey, R.B. *et al.* 2009. Why tropical forest lizards are vulnerable to climate warming. *Proc. R. Soc. B–Biol. Sci.* **276:** 1939–1948.
6. Helland, I.P. *et al.* 2011. Ice-cover effects on competitive interactions between two fish species. *J. Anim. Ecol.* **80:** 539–547.
7. Stanton–Geddes, J. *et al.* 2012. Role of climate and competitors in limiting fitness across range edges of an annual plant. *Ecology* **93:** 1604–1613.
8. Jankowski, J.E. *et al.* 2010. Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. *Ecology* **91:** 1877–1884.
9. Gifford, M.E. & K.H. Kozak. 2012. Islands in the sky or squeezed at the top? Ecological causes of elevational range limits in montane salamanders. *Ecography* **35:** 193–203.
10. Freeman, R. *et al.* 2003. Flowering phenology and compensation for herbivory in Ipomopsis aggregata. *Oecologia* **136:** 394–401.
11. Hillyer, R. & M.R. Silman. 2010. Changes in species interactions across a 2.5 km elevation gradient: effects on plant migration in response to climate change. *Global Change Biol.* **16:** 3205–3214.
12. Speed, J.D.M. *et al.* 2010. Experimental evidence for herbivore limitation of the treeline. *Ecology* **91:** 3414–3420.
13. Hellmann, J.J. *et al.* 2012. The influence of species interactions on geographic range change under climate change. *Year Ecol. Conserv. Biol.* **1249:** 18–28.
14. Harley, C.D.G. 2011. Climate change, keystone predation, and biodiversity loss. *Science* **334:** 1124–1127.
15. Merrill, R.M. *et al.* 2008. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *J. Anim. Ecol.* **77:** 145–155.
16. Menendez, R. *et al.* 2008. Escape from natural enemies during climate-driven range expansion: a case study. *Ecol. Entomol.* **33:** 413–421.
17. Chalcoff, V.R. *et al.* 2012. Erosion of a pollination mutualism along an environmental gradient in a south Andean treelet, Embothrium coccineum (Proteaceae). *Oikos* **121:** 471–480.
18. Moeller, D.A. *et al.* 2012. Reduced pollinator service and elevated pollen limitation at the geographic range limit of an annual plant. *Ecology* **93:** 1036–1048.
19. Stone, J.L. & E.G. Jenkins. 2008. Pollinator abundance and pollen limitation of a solanaceous shrub at premontane and lower montane sites. *Biotropica* **40:** 55–61.
20. Chapin, F.S. *et al.* 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecol. Monogr.* **64:** 149–175.
21. Bader, M.Y. *et al.* 2007. High solar radiation hinders tree regeneration above the alpine treeline in northern Ecuador. *Plant Ecol.* **191:** 33–45.
22. Stueve, K.M. *et al.* 2011. Spatial variability of biotic and abiotic tree establishment constraints across a treeline ecotone in the Alaska Range. *Ecology* **92:** 496–506.
23. Lenoir, J. *et al.* 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* **320:** 1768–1771.
24. Moritz, C. *et al.* 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* **322:** 261–264.
25. Harsch, M.A. *et al.* 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecol. Lett.* **12:** 1040–1049.
26. Chen, I. *et al.* 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* **333:** 1024–1026.

27. Lau, J.A. & J.T. Lennon. 2012. Rapid responses of soil microorganisms improve plant fitness in novel environments. *Proc. Natl. Acad. Sci. U. S. A.* **109:** 14058–14062.
28. Svenning, J. & F. Skov. 2007. Ice age legacies in the geographical distribution of tree species richness in Europe. *Global Ecol. Biogeogr.* **16:** 234–245.
29. Zhu, K. *et al.* 2012. Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biol.* **18:** 1042–1052.
30. Clark, J.S. *et al.* 2003. Estimating population spread: what can we forecast and how well? *Ecology* **84:** 1979–1988.
31. Tylianakis, J.M. *et al.* 2008. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* **11:** 1351–1363.
32. Paine, R.T. 1966. Food web complexity and species diversity. *Am. Nat.* **100:** 65–75.
33. Tilman, D. & D. Wedin. 1991. Dynamics of nitrogen competition between successional grasses. *Ecology* **72:** 1038–1049.
34. Bever, J.D. 1994. Feedback between plants and their soil communities in an old field community. *Ecology* **75:** 1965–1977.
35. Callaway, R.M. *et al.* 2002. Positive interactions among alpine plants increase with stress. *Nature* **417:** 844–848.
36. Gilman, S.E. *et al.* 2010. A framework for community interactions under climate change. *Trends Ecol. Evol.* **25:** 325–331.
37. Pateman, R.M. *et al.* 2012. Temperature–dependent alterations in host use drive rapid range expansion in a butterfly. *Science* **336:** 1028–1030.
38. Cudmore, T.J. *et al.* 2010. Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naive host tree populations. *J. Appl. Ecol.* **47:** 1036–1043.
39. Loarie, S.R. *et al.* 2009. The velocity of climate change. *Nature* **462:** 1052–U111.
40. Dobrowski, S.Z. *et al.* 2013. The climate velocity of the contiguous United States during the 20th century. *Global Change Biol.* **19:** 241–251.
41. Adler, P.B. & J. HilleRisLambers. 2008. The influence of climate and species composition on the population dynamics of ten prairie forbs. *Ecology* **89:** 3049–3060.
42. Ims, R.A. *et al.* 2008. Collapsing population cycles. *Trends Ecol. Evol.* **23:** 79–86.
43. Adler, P.B. *et al.* 2012. Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? *J. Ecol.* **100:** 478–487.
44. Suttle, K.B. *et al.* 2007. Species interactions reverse grassland responses to changing climate. *Science* **315:** 640–642.
45. Carreiro, M. & C. Tripler. 2005. Forest remnants along urban–rural gradients: Examining their potential for global change research. *Ecosystems* **8:** 568–582.
46. Ackerly, D.D. *et al.* 2010. The geography of climate change: implications for conservation biogeography. *Divers. Distrib.* **16:** 476–487.
47. Scherrer, D. & C. Koerner. 2010. Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biol.* **16:** 2602–2613.
48. Ford, K.R. *et al.* 2013. Spatial heterogeneity in ecologically important climate variables at coarse and fine spatial scales in a high-snow mountain landscape. *Plos One* **8:** e65008.
49. Case, M.J. & D.L. Peterson. 2005. Fine-scale variability in growth–climate relationships of Douglas–fir, North Cascade Range, Washington. *Canadian J. Forest Res.* **35:** 2743–2755.
50. Peterson, D.W. & D.L. Peterson. 2001. Mountain hemlock growth responds to climatic variability at annual and decadal time scales. *Ecology* **82:** 3330–3345.
51. Peterson, D.W. *et al.* 2002. Growth responses of subalpine fir to climatic variability in the Pacific Northwest. *Canadian J. Forest Res.* **32:** 1503–1517.
52. Ettinger, A.K. *et al.* 2011. Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology* **92:** 1323–1331.
53. Brown, J.H. *et al.* 1996. The geographic range: size, shape, boundaries, and internal structure. *Annu. Rev. Ecol. Syst.* **27:** 597–623.
54. Loehle, C. 1998. Height growth rate tradeoffs determine northern and southern range limits for trees. *J. Biogeogr.* **25:** 735–742.
55. Ettinger, A.K. & J. HilleRisLambers. 2013. Climate isn't everything: competitive interactions and variation by life stage will also affect range shifts in a warming world. *Am. J. Bot.* **100:** 1–12.
56. Larson, A.J. & J.F. Franklin. 2010. The tree mortality regime in temperate old-growth coniferous forests: the role of physical damage. *Canadian J. Forest Res.* **40:** 2091–2013.
57. van Mantgem, P.J. *et al.* 2009. Widespread increase of tree mortality rates in the western United States. *Science* **323:** 521–524.
58. Littell, J.S. *et al.* 2010. Forest ecosystems, disturbance, and climatic change in Washington State, USA. *Clim. Change* **102:** 129–158.
59. Korner, C. & J. Paulsen. 2004. A world-wide study of high altitude treeline temperatures. *J. Biogeogr.* **31:** 713–732.
60. Smith, W. *et al.* 2003. Another perspective on altitudinal limits of alpine timberlines RID E-6789–2011. *Tree Physiol.* **23:** 1101–1112.
61. Rochefort, R. & D. Peterson. 1996. Temporal and spatial distribution of trees in subalpine meadows of Mount Rainier National Park, Washington, USA. *Arct. Alp. Res.* **28:** 52–59.
62. Henne, P.D. *et al.* 2011. Did soil development limit spruce (Picea abies) expansion in the Central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape model. *J. Biogeogr.* **38:** 933–949.
63. Johnson, D. *et al.* 2004. Abiotic factors limiting photosynthesis in Abies lasiocarpa and Picea engelmannii seedlings below and above the alpine timberline. *Tree Physiol.* **24:** 377–386.
64. Maher, E.L. & M.J. Germino. 2006. Microsite differentiation among conifer species during seedling establishment at alpine treeline. *Ecoscience* **13:** 334–341.
65. Billings, W.D. & L.C. Bliss. 1959. An alpine snowbank environment and its effects on vegetation, plant development, and productivity. *Ecology* **40:** 388–397.
66. Hodkinson, I. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biol. Rev.* **80:** 489–513.
67. Eckert, C.G. *et al.* 2010. Plant mating systems in a changing world. *Trends Eco. Evol.* **25:** 35–43.

68. Sagarin, R.D. *et al.* 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends Eco. Evol.* **21:** 524–530.
69. Fagan, W. & J. Bishop. 2000. Trophic interactions during primary succession: herbivores slow a plant reinvasion at Mount St. Helens. *Am. Nat.* **155:** 238–251.
70. Zhou, Y. & M. Kot. 2011. Discrete–time growth–dispersal models with shifting species ranges. *Theor. Ecol.* **4:** 13–25.
71. Best, A.S. *et al.* 2007. Which species will succesfully track climate change? The influence of intraspecific competition and density dependent dispersal on range shifting dynamics. *Oikos* **116:** 1531–1539.
72. Caswell, H. *et al.* 2003. Demography and dispersal: life table response experiments for invasion speed. *Ecology* **84:** 1968–1978.
73. Travis, J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc. R. Soc. B–Biol. Sci.* **270:** 467–473.
74. Clark, J.S. *et al.* 2010. High–dimensional coexistence based on individual variation: a synthesis of evidence. *Ecol. Monogr.* **80:** 569–608.
75. Urban, M.C. *et al.* 2012. On a collision course: competition and dispersal differences create no–analogue communities and cause extinctions during climate change. *Proc. R. Soc. B–Biol. Sci.* **279:** 2072–2080.
76. Sheldon, K.S. *et al.* 2011. Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure. *Ecol. Lett.* **14:** 1191–1200.
77. Elmendorf, S.C. *et al.* 2012. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nat. Clim. Change* **2:** 453–457.
78. Pauli, H. *et al.* 2012. Recent plant diversity changes on Europe's mountain summits. *Science* **336:** 353–355.
79. Daly, C. *et al.* 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *Int. J. Climatol.* **28**: 2031–2064.