Mountain plant communities: Uncertain sentinels?

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Abstract
Mountain plant communities are thought to be sensitive to climate change and, thus, able to reveal its effects sooner than others. The status as sentinels of two plant communities are reviewed. Alpine treeline ecotones and alpine vegetation have been observed to respond to climate change in recent decades. The treeline has moved upslope and alpine communities have had some species increase and others decrease. The response for both, however, has been inconsistent if taken as a whole. Problematic factors for this response are outlined for both: abiotic and biotic interactions partially decouple the plant communities from climate. Differences across spatial and temporal scales complicate interpretation. Partial decoupling leads to non-linear responses and difficulties for prediction and for planning mitigation.

Keywords
Disequilibrium, indicator, climate change, alpine vegetation, alpine treeline, monitoring

I Purpose and concept

The potential ecological impacts of current anthropogenic climate change were noted (e.g. Emanuel et al., 1985) and heralded as an indicator of ongoing climate change – that is, as sentinels (Hansen et al., 1988) over three decades ago. The sentinel concept derives from the need to identify simple indicators of climatic or other drivers and their impacts early in the process so that changes might be understood, anticipated, and mitigated. However, identifying good indicators is difficult, and strong indicators may be specialized in the driver they indicate (Simberloff, 1998). Here, we broaden the sentinel concept to include a plant community perspective. Specifically, we review how one type of landscape – high-elevation mountains – has been investigated for sentinels, and focus on the two plant communities, alpine treeline ecotones and alpine vegetation.

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Mountains have been identified as ones where climate change may have earlier and more detectable impacts on ecosystems (Becker and Bugmann, 2001), and effects are already visible (Settele et al., 2015: 317). Reasons include that ecological conditions change strongly over relatively short distances; the highest parts of mountain ranges are minimally affected by human activities; mountains are inherently biodiverse; they have acted as refugia during past climate changes, retain plant assemblages isolated from their continental distribution, and may provide refugia in the future; and elevation-dependent warming (Pepin et al., 2015) would accelerate climate change impacts. With this impetus, biogeographers have set out to determine, first, whether plants in mountain regions could be used as sentinels of climate change and, later, as indicators of the impacts and dynamics that could be driven by climate change (e.g. Grabherr et al., 2000; Kupfer and Cairns, 1996; Malanson et al., 2011a; Smith et al., 2009).

The alpine treeline ecotone (hereafter, simply for convenience, we will use 'treeline' modified as appropriate for other instances such as latitudinal treelines) and alpine vegetation represent two kinds of change: 1) change in location and spatial structure of a physiognomic type, and 2) change in community species composition (recognizing the feedback). For treeline, spatial changes are driven by new seedling establishment in the leading edge with local extinction at what becomes the retreating edge for the alpine. Changes in spatial structure include density and height, respectively by lateral growth or new establishment and from dwarf trees or krummholz to full-tree (i.e. 2 m) form. Beyond treeline, spatial changes are not so clear because of the heterogeneity of habitat at the fine scale (lacking a linear ecotone), but in addition to locational changes, tundra will exhibit high rates of population turnover and extinctions (cf. Hampe and Jump, 2011).

To examine mountain plant community sentinels we focus on the American West to exclude areas where other drivers, particularly long histories of land use, would interfere with the link between climate and plants. These are relatively protected mountain areas that are also buffered from major direct human disturbance by the surrounding landscapes where less intensive disturbance occurs (with grazing and fire less extensive and persistent than in other regions; e.g. Cairns et al., 2007). Thus, changes to high-elevation plant occurrence and distribution can be attributed to climate change with more confidence, and we can better anticipate future change where it may be of most conservation concern – in relatively pristine systems. These places are where discussions on mitigation, such as assisted migration, are most fraught but also can have the greatest effect. We do, however, refer to other regions when comparisons or contrasts are apt. We further restrict our focus to the last century, or, approximately, since the end of the Little Ice Age (given as 1570–1900 by Matthews and Briffa, 2005). We are informed by changes earlier in the Holocene, but for a discussion of sentinels the period of recent warming is most relevant.

II Treeline

1 Expectations

Treeline is a well-recognized biogeographic pattern (Holtmeier, 2009; Körner, 2012). Treeline position over much of the globe coincides with primarily temperature-determined minimum length of growing season (Paulsen and Körner, 2014), and by inference treelines should be responsive to climate warming (e.g. Ettinger et al., 2011; Gehrig-Fasel et al., 2008; Holtmeier and Broll, 2005; Kupfer and Cairns, 1996). However, despite average temperatures increasing globally, treeline advance in the past century is not ubiquitous (Harsch et al., 2009). Most inconsistency can be attributed to differences in scale and study objectives or approaches.

Studies at broader spatial and temporal scales capture general relations and responses to changes in temperature, while those at finer scales find more heterogeneity in environmental relations and responses, with water being relatively more important (Malanson et al., 2011a). Also expected are the expansion and coalescing of tree islands or patches and increased density within them (e.g. Bourgeron et al. (2015), who rightly argued that the pattern should be educed in three dimensions, which affect feedbacks into climatic and other drivers of vegetation change).

2 Observations

For context here, paleoecological work on the altitudinal change of treelines in the West has indicated plant response to climate change over centuries to millennia. In the Late Pleistocene, forests were as much as 300–700 m downslope from their modern position (Fall, 1997), while they may have been higher during wetter periods of the Holocene (Jiménez-Moreno and Anderson, 2013; Pisaric et al., 2003). Modern climate and treeline appear to have been established at most sites in the West by $\sim$ 3000 yr BP (Mensing et al., 2012). Similar findings elsewhere corroborate the general idea of an upward advance in the Holocene (e.g. Kullman, 1995).

We characterize and summarize observations of change in recent centuries by focusing on treeline position, growth form, and the process of establishment.

2.1 Treeline position. In a global meta-analysis, Harsch et al. (2009) reported that treelines with a diffuse form and those that experienced stronger winter warming were more likely to advance. Abrupt and krummholz treelines, in contrast, may be more strongly limited by damage due to wind, snow, or winter desiccation. Advance at these sites may require an increase in winter temperature sufficient to ameliorate

the impact of these other constraints. While spatial form is important (Harsch and Bader, 2011), change may vary by location as well. In the Rocky Mountain region, some sites have advanced while others are stable (Bolton et al., 2018; Butler et al., 1994). In most areas, the change depends on local conditions such as aspect and exposure (Elliott and Cowell, 2015; Elliott and Kipfmueller, 2011; Harsch et al., 2009; Sakulich, 2015).

2.2 Growth form. Where tree growth has been suppressed to more lateral growth form such as krummholz, some climatic amelioration can allow more vertical growth and potentially develop into an upright tree form. The initial transition, the development of vertical leaders that would presage a vertical trunk, can begin during periods of higher temperatures and/or more precipitation (Millar et al., 2004; Weisberg and Baker, 1995). Wind should also play a major role, given that krummholz often appears to be a response to wind (e.g. Cairns, 2001; Hadley and Smith, 1983; Holtmeier and Broll, 2010; Marr, 1977), but consistent long-term observations of winds at treeline elevations are rare.

2.3 Tree recruitment/seedling establishment. Malanson et al. (2009) suggested that seedling establishment and initial survival was the most climate-coupled and critical phase in the recruitment of new trees and changing the position of treeline. Seedling establishment in the Rocky Mountains seems to be episodic and more likely in warmer and/or wetter periods (Germino et al., 2002; cf. Lloyd and Graumlich, 1997, for Holocene context). Establishment occurs most often in periods with more snow (Elliott and Petruccelli, 2018; Hessl and Baker, 1997), which may be linked to the Pacific Decadal Oscillation (Alftine et al., 2003). Experimental work and meta-analyses have supported the link between seedling establishment and

snow cover (Bader et al., 2018; Lett and Dorrepaal, 2018).

In contrast, Körner (2016) contended that potential recruits have already established and exist in 'sufficient' numbers to drive an advance. Small seedlings can persist for long periods in this form, from which they can quickly start to grow and constitute a visible advance following either warmer temperatures or less wind. This view identifies this growth to a size greater than the surrounding shelter, rather than seedling establishment per se, as the critical ontological step. Körner (2016) may be influenced by observations in Europe as we have been by experience in North America. Treelines in Europe are generally thought to be well below a climatically determined equilibrium elevation because of past land uses such as grazing (Holtmeier, 2009). One can imagine that seedlings might more readily establish in the elevation zone between current treeline and the climatic equilibrium elevation in Europe, while a similar zone may be small or nonexistent at North American treelines.

3 Complications

Factors that make treelines problematic sentinels are abiotic differences among places, in climates and climate change, and in geomorphology and substrate; biotic interactions with other organisms and inter- and intra-specific variability; differences in both abiotic and biotic variation with spatial scale; and time lags in the spatial responses to climate change. All of these factors cause treeline dynamics to be only loosely coupled, if not decoupled, from climate change at decadal to century scale.

3.1 Abiotic complications. Efforts to explain the elevation of alpine treeline using temperature variables are fraught because temperature must be interpolated in most cases and elevation is necessary to calculate the interpolation – thus, the 'independent' variable is not. To step around

this problem, several approaches have been tried. Jobbágy and Jackson (2000) adjusted temperatures to those at sea level for the location by using a standard lapse rate. Grafius et al. (2012) used the residual elevation from that predicted by a temperature variable as dependent in subsequent analyses. Others have used the presence of trees or other vegetation as dependent variables in logistic regressions. For example, Brown (1994) used logistic regression with four types: closed forest, open forest, tundra, and bare area; and Bader and Ruijten (2008) focused on forest/non-forest within the treeline ecotone. These uncertain relations are further confounded.

The expectations of an upslope advance of treeline with global warming are qualified by water relations. Millar et al. (2012) have reported dieback within the treeline caused by drought. In manipulative experiments, Gill et al. (2015) reported increased seedling survival with watering, and Kueppers et al. (2017) found that warming inhibited seedling establishment in the absence of increased water supply. The latter study was complemented by specific measures of the moisture stress tolerance of seedlings, which inhibit population response to warming (Lazarus et al., 2018). In transplant experiments at a tropical treeline, Rehm and Feeley (2016) found that shade, rather than increasing temperatures, increased seedling survival. From a seed-addition experiment, Davis and Gedalof (2018) concluded that winter snow and high summer soil temperatures limited potential treeline advance in the Canadian Rockies. The general importance of water for establishment of the same species found at treeline was documented by Andrus et al. (2018) for the subalpine zone in more arid mountains.

The direct effects of differences in the radiative environment have been observed for seedlings at treeline. Johnson et al. (2004) found that the combination of daytime insolation and nighttime temperature due to sky exposure accounted for carbon gain. Although these are

climate effects, they confound the expectations for changes in temperature and precipitation alone and are further implicated in biotic interactions, as discussed in 3.3, below.

Treeline research in the 21st century has seen an increase in interest in the roles of geology, topography, and geomorphology at alpine treeline (e.g. Butler et al., 2007, 2009a; Holtmeier and Broll, 2012; Leonelli et al., 2009; Zong et al., 2014). Studies, and the importance of these variables, vary in spatial scale but can be broadly categorized as 'landscape scale' and 'fine scale' (which incorporates the 'microsite' and 'patch' scales of Bourgeron et al. (2015)).

At the landscape scale, Butler et al. (2007) described how geomorphology, topography, and geology could accelerate, decelerate, or stop an upslope advance of treeline in response to climate change. They illustrated controls of current treeline by geologic structure, lithology, glacial topography, and slope processes such as mass movement. As an extreme example at landscape scale, Case and Duncan (2014) attributed the lower elevations of treeline in earthquake-affected areas to earthquake-induced mass movements that prevented tree establishment.

At meso-scales, exposure to the broader environment affects process and pattern. For example, Greenwood et al. (2015) illustrated that topographic sheltering (elevation differences at 10-m distance) was strongly related to seedling establishment patterns, and Dearborn and Danby (2018) reported differences in growth with aspect. Aspect or exposure also affects the limiting process of winter desiccation (e.g. Cairns, 2001; Hadley and Smith, 1983).

At a fine scale, geomorphology and topography affect treeline through topographic shelters that protect seedlings from damage and desiccation by wind (Elliott, 2012a, 2012b). Boulders and/or turf-banked terraces/solifluction lobes creating variations in elevation close to 10 cm provide shelter for seedlings (Butler et al., 2004; Resler, 2006; Resler et al., 2005). In contrast,

some of the related processes, such as frost heaving and churning, could either inhibit or enhance seedling establishment through direct disruption or exposing soil, respectively (Butler et al., 2009a).

Edaphic factors also obscure treeline response to climate change. Davis et al. (2018) found differences in seedling viability of *Picea engelmannii* among treeline soil types in an experimental setting. Trees and seedlings may be less sensitive to some soil conditions than to other factors; however, Malanson et al. (2002), for example, found that soil depth did not affect patterns of treeline development. Soil effects are difficult to discern because the trees (or dwarf trees or krummholz) alter the soils while responding to other drivers (e.g. Holtmeier and Broll, 1992; Lloyd, 1998).

While fire may not be common at alpine treelines, it does affect stand structure (Cansler et al., 2018; Stueve et al., 2009) and the edaphic conditions for seedling establishment (Stine and Butler, 2015) in ways that will affect responses to climate change. Fire may become more frequent at treelines with warmer temperatures and more dead fuel (Grafius and Malanson, 2015).

3.2 Biotic complications. Significant interactions among organisms at western North American treelines include competition, predation, dispersal, pests and pathogens, mutualism, and facilitation.

The most significant competitive process is the maintenance of lower soil temperatures under existing trees, dwarf trees, or krummholz. Körner (1998) identified this effect as central to his theory that treeline dynamics (and, more generally, Körner, 2015) are limited by the mobilization and transfer of carbon reserves, not by carbon gain through photosynthesis (cf. Cairns and Malanson, 1998). Increasing density among individuals of varying size has been shown to reduce recruitment and growth at treelines in Tibet (Liang et al., 2016; Wang et al., 2016). Also, denser or taller alpine tundra

reduces tree seedling success (noted by Malanson and Butler (1994); observed by Maher and Germino (2006); and experimentally verified by Loranger et al. (2017)), but the effects vary with size and density of tundra plants, and the timing of seedling emergence and the physiological mechanism is uncertain.

Interspecific variability also confounds responses of treelines to climate change. Differences among species have been reported for growth responses to neighbors (Dullinger et al., 2005), and seedling establishment in response to temperature and moisture (Loranger et al., 2016) have been reported. Dispersal capacity could change the spatial response of treelines (Malanson, 1997; Malanson and Rodriguez, 2018). Smithers et al. (2018) found that recent upslope movement of treeline in the Great Basin varied among species in addition to among lithologies; *Pinus flexilis* was able to move upslope past higher *Pinus longaeva* because of its broader dispersal kernel and broader environmental tolerances of its seedlings.

Experimental analyses of the consequences of intraspecific variability on treeline response to climate change have indicated the importance of the genetic provenance of individuals dispersing into treelines; seeds derived from distant sources are less successful (Kueppers et al., 2017). Known intraspecific variability in specific traits, such as the susceptibility of *Pinus albicaulis* to white pine blister rust, caused by *Cronartium ribicola*, could also differentiate treeline responses to climate change (Smith-McKenna et al., 2014).

Interactions across trophic levels are also intricate. Cairns et al. (2007), concentrating on herbivory, and Holtmeier (2012), more generally, explained the role of animals in affecting treeline dynamics and location. Holtmeier (2012) documented positive effects, such as those related to geomorphology (above) and seed dispersal by birds (e.g. Neuschulz et al., 2018; Tomback, 1982), as well as negative ones

such as trampling and burrowing. Additional work has highlighted the herbivory of small and large mammals in affecting seedling fate at treeline in eastern Canada and Sweden (Munier et al., 2010; Van Bogaert et al., 2011), respectively. The impact of herbivory has been sparsely documented in the West; while how animals as geomorphic agents could affect seedling establishment at treeline has been thoroughly examined (Butler, 2012; Kambo and Danby, 2018a; Whitesides and Butler, 2016). However, it is likely that the many mammals (e.g. gophers, ground squirrels, goats, sheep, elk) also graze on seedlings.

A dynamic area of research spurred by interest in sentinels is facilitation (Maestre et al., 2009). Facilitative effects can consist of relief from physical stress or increases in resource supply, both of which can be direct or indirect. At treelines, trees, krummholz, and tundra plants modify the microclimate (and most notably provide shelter from wind for seedlings; Kambo and Danby, 2018b; McIntire et al., 2016; Maher and Germino, 2006; Pyatt et al., 2016; Smith et al., 2003), exposure to cold night skies (Germino and Smith, 1999), soils (Cairns, 1999; Liptzin et al., 2013; Seastedt and Adams, 2001), and snow cover (e.g. Geddes et al. 2005; Hiemstra et al. 2002). At treelines in the West, facilitation is likely an important factor in the development of one of the most significant forms of spatial structure by which the ecotone changes: hedges (sensu Holtmeier, 1982; linear features parallel to the dominant wind direction), which progressively amplify their own effects (Alftine et al., 2003; Resler and Fonstad, 2009). Facilitation could possibly more tightly couple vegetation response to climate change, or, because it requires an intervening step, create time lags (Elliott, 2011). Moreover, variation in the location and intensity of facilitation complicates, or even 'may distort or counter' responses to climate change (Batllori et al., 2009).

Less well understood is the impact of pests and pathogens. Mountain pine beetles are creating widespread mortality in populations below treeline because they seldom infest individuals of small diameter (Bentz et al., 2010), but these larger trees may be the primary source of seeds for treeline recruitment. White pine blister rust does affect small individuals of *Pinus albicaulis* at treeline, and, given this species foundational role, it could disrupt the entire dynamic of tree island creation and response to climate change (Resler and Tomback, 2008; Tomback et al., 2016).

3.3 Spatial scale complications. Controlling factors vary with spatial scale (Elliott and Kipfmueller, 2011; Malanson et al., 2007, 2011a). While the control of treelines by temperature at the global scale is complemented by generally predictable trends in temperature with elevation and latitude, local-scale variations – for example, in seasonal temperature changes, such as the extent to which sites have experienced summer or winter warming or variation by aspect – are factors in observed changes (Elliott, 2011; Harsch et al., 2009). The secondary control of treelines by water relations, mostly at the local scale, is complemented by the heterogeneity of patterns of precipitation and soil moisture in mountains because of less predictable interaction of topography with synoptic climatology. At these scales, the particular drivers vary across regions and ranges (Grafius et al., 2012; Weiss et al., 2015), in part because of differences in species (Malanson et al., 2007), in addition to differences in the geography of ranges (Malanson and Butler, 2002; Wang et al., 2017). Most other entanglements are also at the local scale (e.g. Butler et al., 2009b), or even at 'microsite' scale (sensu Bourgeron et al., 2015; e.g. Pansing et al., 2017) – that is, the scale at which sentinels might be useful.

3.4 Temporal-scale complications. Although treelines may be coupled with temperature at

millennial time scales (Bruening et al., 2018), at decadal to century scale, the most significant problem for treelines as sentinels is time lag. Treelines will not respond fast to climate change because the critical step, multiple seedling establishment events across the landscape just above current treeline, would be the sum of many low-probability events, of which producing seed is the first limiting step (e.g. Kambo and Danby, 2018c). Holtmeier and Broll (2007) concluded that treelines will respond to rising temperatures mainly with a gradual infilling of the gaps between existing trees and patches, and, to a lesser extent, with the establishment of trees above the present tree limit. Thus, an observable altitudinal shift of the treeline would lag behind climate change by decades or even centuries. Given that the climate has been changing continually, ongoing responses could be affecting current coupling, transient dynamics may be novel (Hastings et al., 2018), and, thus, time lags are multiplied.

Even geomorphic limits to treeline response could be thought of as a long time lag requiring slope and soil adjustments to climate, and some will respond to the development of treeline vegetation (Schmid et al., 2009; Zeng et al., 2007). Disturbance legacies may further influence treeline position and its ability to respond to climate changes. Past disturbances can shape treeline structure and influence initial recruitment patterns, but subsequent patterns of recruitment and spread may be more strongly controlled by climate (Bolli et al., 2007; Holtmeier and Broll, 2005; Vittoz et al., 2008). Hence, rather than affecting the probability of recent advance, disturbance may influence when advance initiates and thereby causes disequilibrium.

III Alpine vegetation

1 Expectations

The alpine biome, even more than treeline, is a well-recognized biogeographic division

(Körner, 2003; Nagy and Grabherr, 2009). It includes a range of often prostrate shrubs, moss, and lichen, in addition to the usually dominant grasses, sedges, and forbs. The habitat is defined primarily as the range of climate where too little energy or heat exists to support trees, but enough to prevent permanent snow and ice. Climate change could threaten some alpine tundra because, with warmer temperatures and longer growing seasons advancing, treelines could figuratively push alpine tundra off the top of mountains (Peters and Darling, 1985). While trees could advance upward into alpine tundra, a similar movement of tundra is more limited by topography (or lack thereof), and, therefore, its spatial and biogeographic change is limited. Within the advance of shrublines has been documented (Myers-Smith and Hik, 2018).

The current area of alpine vegetation could decrease and change substantially within decades (Diaz and Eischeid, 2007; Halloy and Mark, 2003; Kullman, 2010). The sentinel model posits an upward shift in alpine treeline, and even allowing for the colonization of now bare areas the total area should decrease because mountain peaks are conical. Along with upward movement, areas such as saddles or cols that join higher alpine areas could become tree-covered, further isolating the remaining vegetation. However, while habitats might shift upslope, they are not zonally divided by elevation. Instead, meso- and microtopography create differences in energy, water, and soil resources that are interpreted as dimensions of niche space within which different types of vegetation exist (e.g. Scherrer and Körner, 2011). Climate impacts are best thought of in terms of responses in species composition to changes in niche, in addition to changes in area. Still, higher, sparsely vegetated areas are changing (e.g. Zeng et al., 2018), and, in general, the process of 'thermophilization' – the increase in warmer-climate-adapted plants in any

setting – is ongoing in the alpine (e.g. Gottfried et al., 2012)

2 Observations

Such thinking led to the creation of alpine vegetation monitoring efforts. The most developed of these is the Global Observation Research Initiative in Alpine Environments network (GLORIA) (Grabherr et al., 2000). GLORIA is a network of >120 sites at which summit vegetation is monitored, with the idea that responses will be most easily detected at summits because these are some of the harshest environments for plants to survive and even subtle warming might have distinct impacts in plant composition, phenology, and growth. Visited every five years, GLORIA sites in Europe have shown shifts in vegetation composition toward more warm-adapted species in initial analyses (Gottfried et al., 2012). Other mountain summit vegetation responses in Europe have been examined by re-visiting sites established as far back as 1835 and reported an accelerated increase in plant species richness as climate changes have occurred (Wipf et al., 2013). The link to warming has been further strengthened by Steinbauer et al. (2018), who reported a continental-wide acceleration in the rate of increase in plant species richness after reviewing data from 302 European mountain summits that spanned 145 years. More focus indicates that species of the highest elevations may be declining as others increase in abundance (Rumpf et al., 2018).

GLORIA includes some sites in the West, but more restricted monitoring has yielded useful results. Lesica (2014; Lesica and Crone, 2017; Lesica and McCune, 2004; Lesica and Steele, 1996) established plots for monitoring alpine vegetation change in Glacier National Park in 1988. Lesica and Steele (1996) concluded that consideration of the character of individual species would be important, repeat plots are preferable to random plots, and ephemeral habitats and species that are hypersensitive to the driver

of interest will not be useful indicators. Lesica and McCune (2004) reported a shift toward drier vegetation types, and Lesica (2014) found declines in the cover of species with narrow, high-elevation distributions. However, absence of change predominated. For a broader study that included some of the same sites and, again, focused on species at the southern end of their ranges, Lesica and Crone (2017) reported differences in trends based in phylogeny (monocots more stable because their root systems are more adaptable to dry periods).

Research on change in alpine has taken advantage of preexisting data not originally designed for long-term monitoring. For example, for Scotland, Britton et al. (2009) reported that the overall community structure had converged over five decades, indicating a simplification of the floristic complexity. For plots on Niwot Ridge, CO, Spasojevic et al. (2013) found that community change could be substantial but transient and varied in degree with the initial community recorded. Changes that could be responding to broader-scale drivers such as climate change were differentiated by fine-scale variability in temporal and spatial scale – that is, some of the complications discussed in 3.3 and 3.4, below. The use of satellite imagery also provides a temporal perspective, and Bolton et al. (2018) reported that most change in the vicinity of treelines in the Yukon was in the herbaceous vegetation.

Numerous studies have examined changes in growth and/or phenology. Walker et al. (1995) observed increased growth and changes in phenology years with more snow, and Walker et al. (1999) added carbon flux in response to natural and experimentally increased snow cover (with consequent warmer sub-snow temperatures). They noted the importance of the increase in water supply. Both observational (Wagner and Reichegger, 1997) and experimental (Galen and Stanton, 1995) studies of climate effects on flowering and seed development have yielded significant results. Intensive study in our focal

region has highlighted damage from earlier flowering due to subsequent frost and has established the timing of snowmelt as an important driver that is affected by climate change (e.g. Inouye, 2008). In the alpine, earlier snowmelt may shorten growing seasons and reduce plant productivity (Ernakovich et al., 2014).

3 Complications

Factors that make tundra problematic sentinels fall into the same categories as those for treeline: abiotic drivers, biotic interactions, and spatial- and temporal-scale issues.

3.1 Abiotic complications. The variation in alpine communities may be only weakly correlated with abiotic variables (Bueno de Mesquita et al., 2016; Malanson et al., 2017; Suding et al., 2015). Although alpine vegetation occupies a small range of environmental conditions among all Earth's biomes, it is found across a broad range of moisture conditions within the limits of low heat, and differentiation of plant communities may be related to water availability (e.g. Le Roux et al., 2013a; Winkler et al., 2016) in addition to temperature gradients (Elmendorf et al., 2012). The moisture conditions are as much or more controlled by topography at multiple scales (ranging from orographic precipitation/rain-shadow effects to microtopographic rills), and so the geographic spatial expression of species on environmental gradients is multidimensional and beta diversity is high within alpine landscapes (Le Roux et al., 2013c; Litaor et al., 2008; Opedal et al., 2015). Thus, alpine habitats come in a variety of types and vary over short distances and, because it is found in a wide variety of microclimates, a general loss is not a necessary outcome of warming (e.g. Cannone et al., 2008; Randin et al., 2009) or may be habitat specific (Kudo et al., 2010).

Soil differences can also alter tundra response to climate change. Soils may differentiate among

alpine communities (Buri et al., 2017), but plant–soil interactions vary among tundra communities. This relationship is complex because of the biotic mediation of processes by organisms ranging from bacteria to vertebrates. At fine scales, the inertia of the system to climate change will vary with edaphic conditions conditioned by microtopography (Suding et al., 2015). Beyond inherent soil properties, nitrogen deposition can change plant communities and will vary among sites, with some relatively close to major anthropogenic sources being most affected (e.g. Bowman and Steltzer, 1998).

Climate change is a direct complication in that potentially novel climates could set the stage for novel ecosystems (Ferrarini et al., 2017; Mahony et al., 2017; Young, 2014). Vuorinen et al. (2017) have shown that in addition to the difficulties enumerated above, novel climates will create novel entanglements of these factors in alpine vegetation.

3.2 Biotic complications. A high degree of interspecific variability is inherent in the heterogeneity of abiotic environments occupied, and intraspecific variation is also common (e.g. Hamann et al., 2017; Massatti and Knowles, 2014). Different functional types are expected to vary in their responses to climate change, as observed by Lesica and Crone (2017), as are different ecotypes. Changing phenology in relation to climate change exhibits confounding factors (De Keyzer et al., 2017). Some phenological responses are habitat-specific or species-specific – or even vary within species. The degree of interannual variability observed when plots are monitored regularly could be a significant problem. For phenology, the sensitivity of plants to climatic factors changes during the reproductive cycle and by ecotype (Carbognani et al., 2018). These constraints can either limit the usefulness of alpine plant communities as sentinels or guide the selection of the most useful elements.

Biological interactions in alpine tundra are recognized (e.g. Kikvidze et al., 2011; Le Roux et al., 2013b). Facilitation has been well-documented in the alpine, with the role of cushion plants repeatedly emphasized. (e.g. Cavieres et al., 2014). The nature of benefactor individuals and the responses of the beneficiaries has been empirically verified (e.g. Michalet et al., 2016), although the intervening processes and the implications for long-term dynamics less so. In the West, grazing effects can be strong but are localized (Zeigenfuss et al., 2011), and the related effects of trampling are known mostly for human trails (e.g. Willard and Marr, 1970).

A number of experiments on Niwot Ridge have shown an association between small mammals and types of tundra communities (Forbis et al., 2004; Sherrod et al., 2005; Thorn, 1982). Perhaps most notable was the rapidity of the overall change in the ecosystem. Soil microorganisms further elaborate edaphic abiotic drivers. Bueno de Mesquita et al. (2016) found that community structure varied with microbe community structure, and Tobias et al. (2017) found that alpine seeds were replete with associated fungi, which could affect germination – but of *Zea mays* as a model species; this problem merits investigation with an array of native species.

3.3 Spatial-scale complications. Examining sites within ranges reveals heterogeneity (Engler et al., 2011). For instance, energy and water resources vary at fine scale in alpine environments (e.g. Saunders and Bailey, 1994; Suvanto et al., 2014), as does disturbance (e.g. Randin et al., 2009). For example, Malanson et al. (2011b) also reported that the degree of dissimilarity in alpine vegetation across >1000 km of the Rocky Mountains could be found within a 4101 km^2 area, the extent of Glacier National Park, Montana. Suding et al. (2015) found that assessment of community stability was scale dependent. Even the details of microtopography at decimeter horizontal and vertical resolution

affect composition and diversity (Loneragan and del Moral, 1984; Rose and Malanson, 2012). For centimeter-scale neighbors, Bowman and Swatling-Holcomb (2018) reported facilitation for some species but found that stochasticity outweighed biotic interactions for most. Thus, much of the environmental variation that determines the differentiation of alpine plant communities is local (and, thus, similar to treeline) (Malanson et al., 2018).

3.4 Temporal-scale complications. At Last Glacial Maximum, the extent of alpine vegetation may have been much greater than it is now (Harris, 2007). Applying 'extinction debt' to climate change (Dullinger et al., 2012; Malanson, 2008), we expect disequilibria in responses of the extant number of species as area decreases and isolation increases. Given continual changes in climate, an equilibrium for diversity and compositions may not have existed for millennia, and short-term variability can muddle long-term response.

The consequences of disequilibrium for alpine vegetation are that the relations between species distributions and the environment will not be optimal – that is, the realized niche of a species could be anywhere and everywhere within its fundamental niche, and current observations of the presence and abundance of species in relation to the environment, and to climate in particular, will not have predictive power.

IV Summary and conclusions
1 Mountains and their disequilibria

Treelines and alpine vegetation may be poor sentinels of the impacts of recent and ongoing climate change. The most useful sentinels seem to be at the extremes of environmental gradients where even more extreme conditions are expected. Secondarily, a focus on ecotones within alpine tundra might be useful where they can be identified. Thus, the ecotone-summit approach of the GLORIA project was well conceived and serves as an example for other monitoring; although significant findings for diversity are most common (e.g. Pauli et al., 2012), community and trait changes are at least as important.

The central problem for the sentinel concept is that the biogeographical response of mountain plant communities is only loosely coupled in time to climate drivers. Time lags exist for multiple reasons:

- Plants have lifespans, and climate drivers that will change eventual reproduction and growth do not necessarily cause immediate mortality (but dieback does occur; Millar et al., 2012).
- Plants are affected by other drivers, such as edaphic conditions, that change at longer time scales and themselves have time lags in their response to their climate drivers.
- Changing geographic distributions for plants requires dispersal, which is often stochastic (e.g. Engler et al., 2009) and, thus, not instantaneous.
- Interactions among organisms include competition by extant plants for dispersing seeds, climate-driven pests and pathogens lowering seed source strength, and lags in pollinators (although not so common in this environment).

The theme of disequilibrium has been developed for mountain systems. Alexander et al. (2018) nicely summarized the consequences of time lags in dispersal, establishment, and extinction processes for a mountain elevation gradient. For treeline, Butler et al. (2007, 2009b) developed the theme of loose coupling and time lags caused by biotic and abiotic constraints, and others explored how positive feedbacks decouple rates (e.g. Alftine and Malanson, 2004; Bekker, 2005; Zeng and Malanson, 2006). For
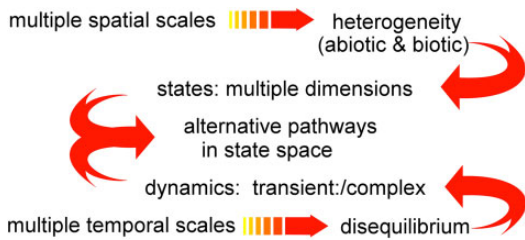
Figure 1. Multiple spatial and temporal scales, both of which affect alpine treelines and vegetation, can lead to alternative pathways in state space.

the alpine, Malanson et al. (2015, 2017), noting work on disequilibrium by Kammer et al. (2007) and Harris (2007), concluded that the weak relationship of tundra floristic composition in the West could be the result of time lags in response to climatic changes throughout the Holocene.

Disequilibrium can be addressed with a set of theories on nonlinearity and complexity that require specification of temporal scale to improve prediction (Burkett et al., 2005). At this point, our understanding of the principles and consequences of disequilibrium is ahead of our ability to apply this knowledge. We can identify five problems associated with predicting change in these ecosystems:

- Lack of ongoing vegetation change can be compensated by later change (time lags are not infinite).
- Later change could be in the form of thresholds or tipping points – that is, much more rapid than the change in the drivers now observed.
- The transient period may have no-analog conditions (not previously existing), and these may change suddenly or include significant short-term variability.
- Complexity can lead to multiple pathways in state space (Figure 1), making prediction impossible, but can also include constraints on the range of pathways.

- Plant communities in disequilibrium might be indistinguishable from those in equilibrium but without niche determinants – that is, as expected in the neutral theory of biodiversity and biogeography.

2 Research frontiers

We see six grand challenges for future research on these mountain plant communities. The primary challenge, because it is most relevant to sentinel status, is to establish background turnover rates. Turnover rates can be expected to be low, given that mountains, although not islands, have some degree of isolation and the possibility of rescue effect; In terms of sentinels background turnover, still must be subtracted from observed ongoing change. Steinbauer et al. (2018) at least demonstrated that rates of change have increased, and one might use their early rates as a background for other observations – but probably only in Europe.

Second, the complexity of interactions at tundra and treelines have largely been ignored in projecting change at broad spatial scales. These interactions depend on the densities of the individuals and their spatial patterns, all of which would be changing with climate, novel species combinations, and different intensities. Upscaling results from local studies is a challenge.

Third, increasing human pressures on treeline and alpine ecosystems must be further assessed, possibly following international examples in North America (cf. Bonanomi et al., 2018). Land use changes can have more extensive impacts such as invasive species (Resler et al., forthcoming), which have their own climatic drivers (Dainese et al., 2014). Disentangling drivers with similar effects challenges both researchers and policy makers.

Fourth, how do processes change with spatial scale (cf. McGill, 2010)? This is a challenge which is further confounded by specific geography. Insight and generality on spatial scale might be gained in research where elevational

treeline merges into latitudinal treeline and tundra transitions from oroarctic to arctic (cf. Virtanen et al., 2016) as spatial compression of the climate gradient is gradually extended.

Fifth, a number of specific complications need further investigation; among these are experimental manipulation of water, temperature, soil microbes, and CO_2, and geomorphic processes. Experiments such as those of Moyes et al. (2015), Kueppers et al. (2017), Souza et al. (2017), and Lazarus et al. (2018) can start to untangle abiotic and biotic interactions but probably should be coupled with process- and/or theoretical models. Approaches to geomorphic control of treeline dynamics have focused on static conditions and need to address processes that could be climate-driven (e.g. Annandale and Kirkpatrick, 2017).

Sixth, as discussed previously, disequilibrium challenges explanation and prediction. The complications for treeline and tundra have elements in common and can be summarized as follows:

- Increasing spatial scale → abiotic and biotic heterogeneity → multidimensional states
- Time lags/loose coupling → transient/complex dynamics → multiple pathways

While the multidimensionality of the environment is a core concept in ecology and biogeography, pathways in the state spaces defined this way are less familiar. Recognizing this link can lead to useful research questions and designs for biogeographical monitoring.

3 Alternative futures and actions

What possible actions might be warranted, given our current understanding of treeline and tundra as sentinels for a changing climate? First, as previously stated, we must continue to learn more about the complexities that drive alpine treeline and tundra vegetation dynamics and influence their value as sentinels of change in mountain landscapes. Mountains are important to humanity for their unique research values and also because of their underappreciated services to people. If an objective is to manage alpine vegetation to preserve the existing biodiversity, options are limited. We see five levels of potential direct action:

1. The most easily achieved, but passive, action is to accept changes without intervention. In this case, public land managers should to inform stakeholders and the public about expected outcomes and address the changing function, and perceived value, of public lands. Legal and regulatory mandates may need to be changed as a response to altered plant occurrence and distribution. For instance, required action to address rare and threatened species recovery might be waived if climate changes make it very unlikely to succeed.
2. A direct action could be to reduce other stressors to alpine plant communities since climate cannot be locally controlled. Minimizing other stressors, such as the infrequent high-elevation wildfires, helps to remove a compounding effect of climate change. Controlling the spread of invasive plants into native alpine plant communities would be another direct action that could be taken.
3. Another direct action, implemented at landscape scales, would be to move the boundaries of protected areas to encompass the new areas where climate changes are allowing species of interest to persist. Similarly, ensuring that migration corridors are intact can allow natural dispersal mechanisms to function. Migration corridors include elevational gradients, which are poorly represented in protected mountain areas globally (Chala et al., 2017; Elsen et al., 2018).

Both of these options could require major land use changes.

4. The next level of direct action would be to conduct assisted migration whereby plants are actively moved to new areas, where they are expected to thrive under a changed climate. There are many obstacles to legally, and in some views ethically, transplanting threatened species to new areas because of potential threats to existing vegetation in the new location. The efficacy of transplanting many of the potential threatened alpine species in question is also not known.

5. The direct intervention of last resort would be to archive, propagate, and otherwise manage these plants only in controlled environments to preserve limited populations in perpetuity. Genetically modifying plants to better tolerate a changing climate could also be attempted but would likely be resisted on either practical or ethical grounds.

All of these direct actions, and other action options not listed, will benefit from a greater understanding of plant–climate relationships in alpine tundra and treeline. In turn, this will help us better determine the status of alpine plants as sentinels in a changing world.

Declaration of conflicting interests

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