

Wind exposure and light exposure, more than elevation-related temperature, limit tree line seedling abundance on three continents

Eliot J. B. McIntire^{1,2}, Frida I. Piper^{3,4} and Alex Fajardo^{3*}

¹Canadian Forest Service, 506 Burnside Road W, Victoria, BC V8Z 1M5, Canada; ²Canada Research Chair – Conservation Biology, Département des sciences du bois et de la forêt, Université Laval, Québec, QC G1K 7P4, Canada; ³Centro de Investigación en Ecosistemas de la Patagonia (CIEP) Conicyt–Regional R10C1003, Universidad Austral de Chile, camino Baguales s/n, Coyhaique, Chile; and ⁴Instituto de Ecología y Biodiversidad – IEB, Santiago, Chile

Summary

1. The transition from seedlings into trees at alpine tree lines is a temperature-limited process that ultimately sets the tree line elevation at a global scale. As such, tree lines may be key bioassays of global warming effects on species distributions. For global warming to promote upward tree line migration, as predicted, seedlings must be available. We examined, for the first time at a global scale, elevational patterns and drivers of seedling availability at tree lines.

2. Working at 10 sites across five mountain regions (dry Andes, humid Andes, Patagonian Andes, Swiss Alps and US Rocky Mountains) with different tree line forms (abrupt and diffuse) and dominated by different tree species (broadleaves and conifers), we answered the following question: How is seedling abundance affected by elevation (as a coarse grain surrogate of temperature), light exposure (openness immediately above plots) or wind exposure (an index for openness in the horizontal direction), or combinations thereof and what is the relative importance of each factor?

3. We tested five biological hypotheses to determine the relative strength of these tree line drivers on variable-size sampling plots of seedling abundance (S) ($n = 1056$). Specifically, we tested likely combinations of temperature limitation (T), light as a resource (light, L) and as a radiation stress (via high light at low temperature, R), wind exposure as a tree line stressor (W) and tree line form (a coarse scale test: abrupt vs. diffuse, D).

4. We found strong, moderate and weak negative effects of our estimates of wind exposure, radiation stress and elevation-related temperature on seedling abundance, respectively. We also found a positive effect, at tree line, for site-level tree line diffuseness. Two distinct facilitation mechanisms likely improved seedling abundance at tree line elevation: wind blockage by neighbourhood trees (the sheltering effect) and partial shading by overhead trees.

5. Synthesis. Seedling abundance at alpine tree lines is limited by multiple simultaneous factors with the temperature decrease with elevation playing a relatively minor role. We therefore note that if the temperature threshold limiting the conversion from seedlings to adult trees is relaxed because of global warming, upward tree line migration will depend on the availability of shelter sites for seedlings.

Key-words: alpine tree lines, facilitation, generalized linear mixed models, hierarchical modelling, plant–climate interactions, Rocky Mountains, Southern Andes, stress gradient hypothesis, Swiss Alps

Introduction

The upper limit of the elevational distribution of erect trees > 3 m in height (i.e. tree line, *sensu* Körner 2012) is a natural

ecotone that at the global level has been shown to be physiologically controlled by low temperature and hence considered one of the most responsive to global warming (Körner 1998, 2012; Jobbágy & Jackson 2000; Grace, Berninger & Nagy 2002; Körner & Paulsen 2004). Low temperature is considered a critical factor in the seedling-to-tree transition, which

*Correspondence author: E-mail: alex.fajardo@ciep.cl

in turn determines tree line formation and elevation (Körner 1998). Although global warming is expected to promote an upward tree line migration (Beniston 2003; Truong, Palmé & Felber 2007), this ultimately depends on seedlings availability. The objective of this study was to simultaneously assess multiple drivers controlling seedling abundance at the alpine tree line.

At a global scale, it has been proposed that the temperature decrease with elevation is not a major constraint for seedling establishment (Körner 1998). This is because short stature vegetation – like tree seedlings – by being near the ground, can experience conditions somewhat decoupled from atmospheric, free-air temperatures (Scherrer & Körner 2010; Fajardo & Piper 2014). Such decoupling from free-air temperatures may imply that seedling responses to global warming cannot be simply predicted from atmospheric temperature records (i.e. weather stations), as most vegetation models assume. However, although the decoupling may attenuate air temperature at a given elevation, the temperature decrease along elevational gradients does still occur at the ground level (Mark *et al.* 2001, 2008; Cavieres *et al.* 2007; Bansal & Germino 2010; Fajardo & Piper 2014), suggesting that low free-air temperature should nevertheless be a potential constraint for seedlings at a coarser, landscape scale. Evidence for a minor role of temperature decreased with elevation on seedling establishment has been mixed, with some studies showing no clear association between elevation and seedling survival (e.g. Ferrar, Cochrane & Slatyer 1988), and others showing a clear negative association (e.g. Cuevas 2000). In addition, seedling availability depends on the reproductive success of local adult trees, which can be strongly controlled by the temperature decrease with elevation trend (Sveinbjörnsson, Kauhanen & Nordell 1996; Cuevas 2000). Thus, reduced seedling abundance with elevation is not an infrequent pattern (Cuevas 2000; Resler 2006; Cierjacks *et al.* 2008), suggesting that temperature has some control on seedling availability. There is also evidence of increased recruitment at tree line in response to higher temperatures (Daniels & Veblen 2004; Wang, Zhang & Ma 2006). Global warming would then allow these short seedlings to be released and grow into the free-air temperature environment that was too cold for growth, ultimately causing an infilling if there are erect tree islands (Innes 1991; Gehrig-Fasel, Guisan & Zimmermann 2007) or tree line advance if the released seedlings were above the current tree line. The validity of such expectations depends on the tendency for free-air temperature to be the main limitation currently determining seedling abundance at tree line.

Shelter is critical for seedling establishment at tree line (Batllori *et al.* 2009; Holtmeier & Broll 2010; Körner 2012; Renard, McIntire & Fajardo 2016). Under the harsh conditions of alpine tree lines, seedling establishment benefits from any shelter (e.g. krummholz, rocks, vegetation) that provides suitable microsite or safe sites for seedling development (Hättenschwiler & Smith 1999; Germino, Smith & Resor 2002; Maher, Germino & Hasselquist 2005; Batllori *et al.* 2009), ultimately determining the spatial distribution of

seedlings (Camarero *et al.* 2005; Wiegand *et al.* 2006; Batllori *et al.* 2009). Safe sites provided by taller neighbours can protect seedlings from multiple stressors including two key ones: strong solar radiation and wind (Körner 2012). Radiation is not a stressor *per se* – light is a resource – but at high intensity can lead to high ground temperature, high vapour pressure deficit or top soil desiccation, all factors potentially harmful for seedlings and alpine vegetation (Bader, van Geloof & Rietkerk 2007). Thus, shade provided by taller trees may facilitate seedling establishment at tree line by, for instance, improving the soil water availability (Maher, Germino & Hasselquist 2005). In a similar way, excessive wind at tree line should be detrimental to seedlings either causing biomass removal or tissue desiccation (see Smith *et al.* 2003; Resler 2006; Holtmeier & Broll 2010). Wind also influences the microclimates by affecting the aerodynamic boundary layer and thus has indirect effects on convective heat loss, evaporative cooling and the distribution of snow (Körner 2003). Nearby structures and neighbour plants can provide protection for seedlings during the growing season, through the accumulation of a snowpack during winter period that lessens the drought effects of frost, inhibiting night-time reradiation (Kullman 2007) or, in general, by reducing wind's mechanical damage (Bowman *et al.* 1993; Batllori *et al.* 2009; Renard, McIntire & Fajardo 2016). While the importance of shelter for seedling establishment at tree line is undeniable, we still lack a general quantification of its importance in determining seedling abundance. We also have a poor understanding on the critical factors that shelter controls, that is which are the key stressful factors of seedling abundance that are attenuated by shelter.

Neighbours and overhead protection will also create competition for other resources, possibly limiting seedling survival and growth considerably (Hobbie & Chapin 1998; Körner 2012) and eventually reducing seedling abundance. Consistently, Maher, Germino & Hasselquist (2005) found that canopy cover promotes higher survival of *Pinus albicaulis* at tree line, but with watering, canopy cover had a negative effect on survival. In contrast, below tree line, most tree line species and particularly the most light demanding ones should show good establishment in gaps where high radiation and wind are not threats (Veblen 1979; Fajardo & de Graaf 2004). We can expect then that at and near tree line elevation the non-resource factors – low temperature, high radiation and wind scouring – may limit seedling abundance more than resource availability (light) and so shelter (e.g. the presence of overhead shade-providing neighbours and nearby wind-blocking neighbours) would become more important. This is not only because non-resource factors become more constraining with elevation, but also because light availability becomes less limiting (i.e. crowns are sparser, Körner 2012). The increasing importance of safe sites for seedling abundance as elevation increases to tree line is in accordance with the stress gradient hypothesis (SGH) (Bertness & Callaway 1994). The SGH predicts that with increasing physical harshness of the environment (e.g. abiotic stresses), positive plant interactions (i.e. facilitation) among neighbours become more important

than competitive interactions, that is some species can mitigate limiting stressors to create more favourable habitat for other species (Bertness & Callaway 1994; McIntire & Fajardo 2014). What is often unclear is which of the many limiting factors are being ameliorated under field conditions.

The main objective of this study was to examine the relative effects of elevation-related temperature, light exposure and wind exposure on seedling abundance at and near tree line. To do this, we estimated coarse-grained temperature using elevation, light exposure using very local canopy cover (< 5 m radius) and wind exposure using the openness of neighbouring plots ('fetch'). We quantified the relative importance of these factors on seedling abundance across ten sites in five different mountain regions (dry Andes, humid Andes, Patagonian Andes, Swiss Alps and Montana Rocky Mountains) with different dominant species (*Nothofagus pumilio* [Andes], *Larix decidua* and *Pinus cembra* [Alps], and *P. albicaulis* [Rockies]). Specifically, we asked, is seedling abundance affected by low free-air temperature, high radiation, low light, wind exposure or combinations thereof and, what is the relative importance of each? To answer these questions with maximal inference in this observational study, we used a suite of alternative biological hypotheses (Chamberlin 1965; Burnham & Anderson 2002; McIntire & Fajardo 2009) in conjunction with precise predictions from each and used statistical tools that have the necessary resolution to test these predictions.

Materials and methods

STUDY SITES AND TREE LINE SPECIES

We sampled alpine tree line ecotones from 10 sites (two sites in each of five mountain regions) on three continents (Table S1 in Supporting Information). The first region (*Termas de Chillán* and *Garganta del Diablo* sites, 36°S, 'dry Andes') is in a Mediterranean-type area in central Chile, which has a predominant drought period during summer (Fajardo, Piper & Cavieres 2011). The second region is in the Antillanca area within the Puyehue National Park (*Antillanca 1* and *Antillanca 2* sites, 40°S, 'humid Andes'), a very humid area where precipitation can reach *c.* 4000 mm per year (Daniels & Veblen 2004; Fajardo, Piper & Hoch 2013). The third region (*El Fraile* and *El Portezuelo* sites, 46°S, 'Patagonia') is in the Aysén Region, Chilean Patagonia; the annual precipitation here is 890 mm (Coyhaique National Reserve weather station). In all these locations, *Nothofagus pumilio* is the main tree line species, occasionally accompanied by *N. antarctica* and *N. betuloides*. The fourth region is the Rocky Mountains, USA (*Pioneer*, 45°N, and the *Gravelly*, 44°N, 'Montana Rockies'), with the two sites located 120 km from each other. *Pinus albicaulis* is the dominant tree species at the tree line with some association with *Abies lasiocarpa* and *P. flexilis* at lower elevations (Fajardo & McIntire 2012). The fifth region is in the Swiss Central Alps (*Stillberg 1* and *Stillberg 2*, Dischma Valley, Davos, 46°N, 'Alps'). Here, tree line is naturally formed by *Larix decidua* and *Pinus cembra* (Fajardo, Piper & Hoch 2013). Our sampling covered six abrupt (all Andean) and four diffuse (all Northern Hemisphere) tree line locations of contrasting climates. We recognize that any main effect we detect of abrupt vs. diffuse tree line will be confounded with species and hemisphere. Nevertheless, we found

numerous differences within each group, suggesting that they are by no means similar tree lines.

We tried to select tree line sites that have not been noticeably affected by human activity, disturbed by landslides or avalanches, but represent the natural climatic tree limit of the respective region. Finding such places in the Andes and the Rockies is less difficult than in Eurasia (e.g. Switzerland), where traditional human land use near tree line has been common (Gehrig-Fasel, Guisan & Zimmermann 2007). We define here tree line as the uppermost limit of individuals having an upright growth form of at least 3 m (Körner 2012), which also includes, in some cases, *krummholz* (i.e. stunted individuals) that become erect after a period of horizontal growth. We followed the criteria of Wiegand *et al.* (2006) to define abrupt tree lines as a sharp boundary where large trees in closed stands change over to treeless alpine vegetation in a matter of few metres and diffuse tree lines as a gradual change from large trees to shrubs and *krummholz*.

FIELD SAMPLING

Sampling was conducted in the mid of summer for all tree lines: February for the southern Andes locations (2007, 2008) and August for the Rocky Mountains (2007) and the Swiss Alps (2008). We established spatially clustered plots ('2-dimensional belt transects'), allowing an assessment of a neighbourhood on the scale of tens of metres that included a wide range of elevations at each site (Table S1). Our criterion to limit the elevational range at each site was to cover the complete alpine tree line ecotone for seedling occurrence; this means we started looking for recruitment in the bare rock, scree and talus above the tree line, that is the 'species line' *sensu* Körner (2012), and we went down to the elevation where the mature forest occurred, that is where canopy is closed and the presence of canopy gaps and treefall legacies are pervasive. Thus, elevation ranges varied across locations (from 200 m in Antillanca to 400 m in Stillberg, Table S1). In all cases, the uppermost seedlings, the 'seedling line', that we found were all < 40 m elevation above the uppermost erect trees. In our figures, we rescale elevations such that this seedling line elevation is zero and all others as 'elevation from seedling line'. At each site, we set a grid of 95–135 sampling plots, where 5–25 sampling points were located in each of 4–20 perpendicular-to-the-slope transects, covering the complete altitudinal gradient. Sampling points were separated by at least 25 m in all directions (i.e. up/down or across slope). In these transects, to minimize the impact of zeros in plots where counts are made – a potentially severe problem for our regression models – we used variable-size plots. We increased the size of any plot that resulted with 0 or 1 seedlings per 1 m² after sampling a 1-m² plot. We increased to 2 m² then 50 m² if there were still 0 or 1 seedlings per plot. Thus, for plots with densities between 0 and 2, we were able to resolve to 1/50th of a seedling per m². We subsequently rescaled all counts to numbers per 50 m² to run our models. In each plot, we counted seedling number. Tree seedling was defined as any seedling < 20 cm of height and < 0.5 cm of basal diameter. Using this relatively wide range of seedling sizes (i.e. ~1 to 20 cm), we integrate across mast years and therefore do not consider annual variation in seed production to be a driver of our results. Furthermore, we did not have any *a priori* reason or evidence to presume differences in masting along the elevational ranges assessed. We determined elevation and coordinates of each sampling plot with a multiple averaged global positioning system (GPS) sample. To characterize canopy openness, we took digital hemispherical photographs of the above canopy from a height of ~50 cm located at the centre of each plot. We used a 7-mm Nikon f 7.4 fisheye lens (the lens has an orthographic projection of 180° angle of view), mounted on a Nikon

Coolpix 5000 digital camera (Nikon Corporation, Tokyo, Japan). Photographs were taken under cloudy sky conditions or late in the day to avoid the direct exposure to sun. Photographs were also underexposed by two stops, to increase contrast between the sky and foliage (Zhang, Chen & Miller 2005). Canopy openness was computed for each plot using the GAP LIGHT ANALYZER (GLA ver. 2) software (Frazer, Canham & Lertzman 2000).

ECOLOGICAL HYPOTHESES

Although many factors may influence seedling abundance at tree line, based on the existing literature and our own observations, we identified five dominant factors that are biologically meaningful: temperature, high radiation, low light, wind exposure and tree line form (abrupt and diffuse). To enhance mechanistic inference in the observational study presented here, we followed the 3-part recommendations of McIntire & Fajardo (2009): we used the literature to establish multiple alternative hypotheses, we deduced predictions, and we used statistical tools (nonlinear effects, specific interactions) that could adequately test these hypotheses. Because of these steps, we improve our inference from simply correlative relationships as it is unlikely that spurious relationships are driving such concordance between precise predictions and results. Thus, we present a detailed description of the alternative biological hypotheses and the predictions of the aforementioned factors on seedling abundance (S , the response variable). The five hypotheses are as follows: seedling abundance is negatively affected by (i) low elevation-related temperature (T) (e.g. because low seed production, germination, seedling survival), (ii) reduced light (L) (e.g. due to reduction of photosynthesis) at all elevations, (iii) high radiation (R) at tree line (e.g. via top soil desiccation), (iv) wind exposure via direct effects such as abrasion or scour or indirect

effects such as convective heat loss, evaporative cooling and the distribution of snow (Körner 2003), but *only at or near tree line* (W , and 5) tree line form (D), which will likely be related to stress microsites, for example sites more exposed to low temperature, high wind exposure and radiation. Using elevation to estimate temperature effects, we integrated temperature effects into a single coarse-grained estimate (i.e. across seasons, no extreme events). We are explicit about the dual role of light, both as potential radiation stressor (R) and as resource through light availability (L) (Table 1). Clearly these five hypotheses may not be acting in isolation. We translated these hypotheses into 17 most possible statistical models, which included many interactions (Tables 1 and S2). Where the ecological hypotheses suggested a monotonic relationship, we used linear effects; where the ecological hypotheses suggested a relationship at an optimum value, we used quadratic effects; interactions between effects could be with the linear or quadratic terms, depending on the hypothesis (Table S2).

The relationship between ecological hypotheses and statistical models is not one to one; many statistical models can represent a single ecological hypothesis (Table 1). We show predictions if each of the hypotheses is supported in Table 1 and provide details here. To test the first hypothesis, if low free-air temperatures (T) limit seedling abundance, we predict that the relationship between S and elevation (e) *must* be negative and it *may* have a curvilinear relationship if there is a rapid decline of S at tree line (tested in all models except 0, 3, 4 and 8). This becomes a little more complicated when elevation is part of an interaction term. For example, the main effect of elevation does not have to be negative to support a hypothesized negative effect of elevation *if* there is a negative interaction with wind exposure or openness. For the second and third hypotheses about radiation (high radiation stress R , and light availability L), we test a linear and quadratic canopy openness term in virtually all models because we have

Table 1. Description of alternative models and predicted sign of all coefficients relating elevation (e , used to test free-air temperature, T), plot-level canopy openness (c , to test linear light, L , or high radiation at tree line, R), fetch (f , used to test wind exposure, W) and tree line form (D , abrupt vs. diffuse) to seedling abundance (S)

Biological hypothesis	Model ID	Main effects					Interactions					
		d	e	e^2	c	c^2	f	$e*f$	e^2*f	$e*c$	e^2*c^2	$e*d$
T	1		–									
T	2		±	–								
L	3				+							
R	4					–						
TL	5		–		+							
TL	6		–		+	–						
TL	7		±	–	+	–						
W	8						–					
TLW	9		–		+	–	–					
TLW	10		±	–	+	–	–					
$TLW+W$	11		±	±	+	–	±	±	–			
$TLWD+W$	12	±	±	±	+	–	±	±	–			
$TLW+R$	13		±	±	+	±	–			±	–	
$TLWD+R$	14	±	±	±	+	±	–			±	–	
$TLWD+RW$	15	±	±	±	+	±	±	±	–	±	–	
$TLW+RW$	16		±	±	+	±	±	±	–	±	–	
$TLW+RWD$	17	±	±	±	+	±	±	±	–	±	–	±

A '+' indicates a predicted positive relationship; '–' is a predicted negative relationship; '±' no *a priori* prediction of sign of effect. Ecological hypotheses following the asterisk sign (*) indicate an interaction term with elevation. Predictions are substantially more precise than simply the sign of the relationship as shown in this table; for example, to observe high radiation effects on seedling abundance at tree line, the e^2*c^2 interaction *must* be negative *in such a way* that only *at or near* tree line does the negative quadratic effect between openness and regeneration become visible.

strong evidence that all tree species we are evaluating are light demanding. But to test for high radiation *only* at tree line (R), we predict an interaction effect between squared canopy openness (c^2) and squared elevation (e^2) on S . This translates to a situation where we predict that the optimal light environment at tree line will have lower than 100% canopy openness; below tree line, the optimal light environment should be 100% open (R ; tested in models 13–16). Thus, support for the high radiation hypothesis is not simply a significant main effect of light on S but a precise prediction of a set of interactions.

For the fourth hypothesis, if wind (W) is a driver of regeneration, wind exposure or *fetch* (f) will have a negative effect on regeneration (models 8–10, 13 and 14). From the ecological literature and our own experience studying tree lines, we believe there is support for a positive relationship between fetch size and wind exposure, and between exposure in general and seedling regeneration. We argue that fetch strongly determines microsite characteristics and in turn seedling abundance; for example, see Lortie & Cushman (2007) for a dune system and Latif & Blackburn (2010) for a forest system. To test the hypothesis that wind exposure (W) matters only at tree line, we predicted an interaction between fetch and elevation squared (f interacting with e^2 ; tested in models 11, 12 and 15–17). We defined fetch of a focal plot as the average canopy openness in neighbouring plots, adjusted for relative elevation, relative tree height, cross-slope position and distance, but *not* including the focal plot. Since we did not know what correct effective calculation of fetch should be (i.e. what is the wind neighbourhood experienced by regenerating trees), we chose to run a large selection of possible fetch parameters, select those definitions that provide the greatest variation among plots (i.e. to create a quantitatively useful measure), then use AIC among the most variable estimates of fetch and look at the consistency between fetch estimators. Using the distance limited, d_{\max} , nearest neighbours to every focal plot, we define fetch using the following equations:

$$\omega = 1 - \frac{2 \operatorname{atan}(|\Delta e_{lev} * e^w|)}{\pi}, \quad \text{eqn 1}$$

$$d' = \frac{e^{m(d-\theta)}}{1 + e^{m(d-\theta)}}, \quad \text{eqn 2}$$

$$E = \operatorname{scale}(\Delta e_{lev} + h), \quad \text{eqn 3}$$

$$f = \overline{\operatorname{rescale}(\omega d'(E + \operatorname{scale}(o)))}, \quad \text{eqn 4}$$

where w is the weighting parameter for a ‘cross-slope’ measure of fetch (i.e. should fetch be defined only as plots that are at the same elevation, or all plots in a circle around the focal plot), Δe_{lev} is the difference in elevation between focal plot and neighbouring plots, atan is the inverse tangent function, m is the slope of the *logit* function, θ is the half maximum value of the *logit* function, d is distance in m between focal plot and neighbouring plots, E is emergence (how high the ground of the focal plot is above the neighbouring tree tops), h is tree height of the tallest trees in the neighbouring plots, o is canopy openness in the neighbouring plots, *scale* means subtract the mean, divide by the standard deviation, *rescale* means transforming the resulting estimate of fetch onto the scale from 0 to 1 by subtracting the minimum value and dividing by the maximum value, and long bar is the mean. In eqn 1, ω , the horizontal bias, converts the elevation difference between the focal plot and its neighbours into a

weight index from 0 to 1. In eqn 2, d' , the *logit* distance to neighbours, converts the linear distance into a *logit* distance (i.e. asymptote at 1 when close and asymptote at 0 when far). In eqn 3, E , the index of emergence (how high the ground of the focal plot is above the neighbouring tree tops), estimates the difference in elevation between the focal plot and neighbouring plots *plus* the height of the tallest trees in the neighbouring plots. Thus, in eqn 4, f or fetch is an index from 0 to 1 that estimates the openness of the neighbourhood, not including the focal plot, weighted by the elevation above or below the focal plot, the height of the trees in the neighbouring plots, distance from neighbouring plot and the openness of those neighbouring plots. Since we do not know the values of w , d_{\max} or m , that give the best estimate of fetch, we attempted 5000 combinations of values for w (–8 to 1), d_{\max} (30–80 m), m (0.1–8) and a minimum number of neighbours (1–6) and chose the estimate that maximized variance. Because all estimates of fetch we calculated use the same functional form which describes the openness of the horizontal neighbourhood (following eqns 1–4), we feel that the whole range of values we assessed for the parameters will create *reasonable* estimates of fetch. We nevertheless feel that some will be better at distinguishing effects, that is those that are most variable. This means that our estimate of fetch is the ‘most informative measure possible, given the particular model form’.

Finally, to test the hypothesis that tree line form (D) affects regeneration, for example as a way to create stress microsites, we included a site-level indicator (diffuse or abrupt) as a categorical factor. We do not have strong predictions as to which way tree line form (d : diffuse or abrupt) should affect regeneration, although Harsch & Bader (2011) suggested that abrupt tree lines – like *Nothofagus* – will respond slowly or not respond at all to global warming. We tested this categorical factor in 4 models (D in Tables 1 and S2; tested in models 12, 14, 15, 17), with only one where it interacts with elevation to explicitly test ‘tree line form at tree line’ ($e*d$) in model 17. The SGH would suggest that more safe sites would be better, implying that diffuse tree lines should have more regeneration, that is more tree islands that can act as facilitation spots (Renard, McIntire & Fajardo 2016). Because this is a major issue in the literature, with variable predictions, we tested it here with no directionality to the prediction (Table 1).

STATISTICAL ANALYSIS

Because we were analysing count data (i.e. number of seedlings in a plot), we used generalized linear mixed effect regressions with a negative binomial family, a log link function and a random effect on site. To analyse our data, we used the *glmmADMB* package (Skaug *et al.* 2012) in *R* (R Development Core Team 2012). We also evaluated a zero inflated model with Poisson family, but these models were, in all cases, vastly inferior to the negative binomial family models based on AIC (results not shown). In denoting combinations of effects in models, we used ‘+’ to denote an additive effect, where no interactions were considered, and ‘*’ to denote inclusion of interactions (Tables 1 and S3). For statistical reasons, models with higher order effects (either quadratic main effects or interaction effects) required that we included all lower order effects. All statistical models are outlined in Table S2 with their linkages to the five individual ecological hypotheses and their combinations that we were testing (Table 1). Thus, the ‘complete’ statistical model that tests all five hypotheses is model 17 because it includes interaction effects of elevation and tree line form, plus the light and wind at tree line interaction effects. Unlike the elevation by fetch interactions, we included a *squared* elevation by *squared* canopy openness term because we expected that the

relationship between these needed to be very flexible to be capable of estimating radiation problems at tree line.

The likelihood model we tested was as follows:

$$S \sim \text{NegBin}(s, a) \quad \text{eqn 5}$$

$$\log(s) = \beta\mathbf{X} + \alpha_k, \quad \text{eqn 6}$$

where S is the number of seedlings found in the 50-m² plot equivalent, β are the coefficients to estimate for the \mathbf{X} covariates, and α_k is the random intercept effect representing the $k = 10$ sites, ' \sim ' indicates 'is distributed as', $\text{NegBin}(\cdot)$ indicates the negative binomial distribution with two parameters where s is the expected value and a is the size parameter to estimate. The covariates and different models and combinations we used (Tables 1 and S2) were as follows: e , the plot elevation; c , the plot canopy openness; f , the fetch index; and d , a categorical factor representing the tree line form (abrupt vs. diffuse). All continuous variables were centred (subtract the global mean value of the variable). We included quadratic terms and interactions to determine whether there were nonlinear relationships between S and e or c , respectively, including a possible optimum elevation or light level for S . f is much larger (15–80 m radius) than a canopy light opening (c) and thus represents larger scale, horizontal effects such as wind exposure. With higher f , a seedling's exposure to horizontal processes increases. c and f tended to be somewhat collinear (between 0.6 and 0.9 depending on the estimate of fetch used). To ensure that this collinearity was not unduly affecting our statistical models, we ran our models repeatedly using different estimators of fetch. Since the collinear nature of each estimator of fetch would be different, if we see consistent support for a distinct effect of fetch and canopy openness across different estimators of fetch, we would consider that this provided good evidence that collinearity was not affecting our results.

COMPARING HYPOTHESES

We used Akaike's information criterion (AIC) as a model selection approach. Since our hypotheses included higher order effects, comparing ecological hypotheses is not as easy as simply comparing model coefficient of main effects, even though they are standardized. Interactions among variables make this somewhat more challenging. To visualize these interactions and to assess variable importance, we assessed the impact of small (~10% of the range in the data for each variable) changes in each of the three primary variables (canopy openness, fetch and elevation) on predicted S , using the best supported model. We note that these three variables do not have long-tailed distributions (elevation is linear, and fetch and canopy openness are bounded between 0 and 1), so 10% of the whole range is a useful quantity. For this, we chose 10% changes in canopy openness, 10% changes in fetch and 20 m changes in elevation. To compare slight changes in the elevation effect, we compared S with 20 m downslope changes (across all values of f and c). Since all sites covered at least 200 m of elevation change, this had the approximate effect of a 10% change in our data set. We note that 20 m elevation change is somewhat arbitrary: we present the results in such a way that we can choose any other elevation range for comparison. We report the median of these predictions to compare the relative importance of each factor (canopy openness, fetch, elevation) at each elevation.

MODEL PREDICTIONS BY SITE

For visualizing model predictions by site, we show how the different sites vary in their seedling abundances across the elevation gradient.

This shows the variation across sites in the free-air temperature effect, given unchanging fetch and light conditions. Of the factors that we measured here, only free-air temperature is being directly affected by the current context of a changing climate and thus may give insight into the different site responses to any warming that may occur.

Results

COMPARING HYPOTHESES

AIC analysis showed that model 17 was consistently the best fit to the data (i.e. lowest AIC), regardless of which estimate of fetch was used (Table 2; Table S3 for coefficients and P -values). Models 14 and 15 had somewhat weaker support, and the remaining models all had trace levels of support. The strongest models (14, 15 and 17) were all quite similar and varied only in higher order effects (Table 1). Model 15 differs from model 17 by having no tree line form by elevation interaction. Model 14 differs from model 15 by having no higher order fetch by elevation effects. Using model 17 to make model predictions, a 10% change in fetch (f) had the greatest effect on S at the upper elevations (e.g. 0 m from highest seedling), almost 10× stronger effect than a 20 m change in elevation (Fig. 1). Thus, for roughly similar quantities of change, radiation and temperature are not the most important effects on S at the highest elevations. Conversely, S

Table 2. AIC ranking of alternative hypothesized models and statistics† relating elevation (used to test free-air temperature), canopy openness (used to test light and high radiation), large canopy opening or fetch (used to test wind exposure) and tree line form (abrupt vs. diffuse) on seedling abundance at several alpine tree lines (southern Andes of Chile, Central Rocky Mountains in the United States and the Swiss Alps)

Model	Ranking _{avg}	K	$\Delta\text{AIC}_{\text{avg}}$	w_{avg}
17	2.45	12	0.261	0.57
14	4.67	9	3.582	0.10
15	4.88	11	4.096	0.08
7	5.35	5	5.826	0.06
10	6.25	6	6.302	0.04
12	6.40	9	4.905	0.05
13	6.78	8	6.282	0.03
4	7.78	3	7.159	0.03
16	8.20	10	7.012	0.02
11	9.38	8	7.717	0.02
6	9.95	4	8.684	0.02
9	10.95	5	8.875	0.02
3	11.35	2	10.449	0.01
5	12.55	3	11.897	0.01
8	14.55	2	17.495	0.00
2	15.43	3	26.843	0.00
1	16.55	2	31.786	0.00
0	17.55	1	191.424	0.00

Ranking_{avg} is the average of rankings attained by each model across the 40 most variable estimates of fetch; K is the number of parameters to be estimated; $\Delta\text{AIC}_{\text{avg}}$ is the mean delta AIC of that model, w_{avg} is the AIC scaled weight (the sum of all weights is 1 within a given estimate of the fetch index). Because these are averages across many estimates of fetch, there is no $\Delta\text{AIC}_{\text{avg}}$ equal to zero. Model 0 is included for AIC comparison: it is the 'intercept-only' model.

predictions downslope showed that f progressively decreases in importance, while canopy openness (c) increases in importance, consistent with mature forest gap dynamics (Fig. 1). We note several interesting predictions: (i) a 10% change in f at the highest elevations has a stronger effect than 160 m downslope temperature warming (sum of elevation bars of 20 m downward change in Fig. 1), and this effect of fetch on seedling survival is stronger for diffuse than abrupt tree lines; and (ii) a 10% change in c well below tree line has a substantial positive effect on S (i.e. gap dynamics), and this effect is stronger for abrupt tree lines.

FREE-AIR TEMPERATURE TEST

In the best supported model, the main effect of elevation and squared elevation was not significantly related to S (Table S3, Fig. 2). However, it was important when it interacted with both c and f and tree line form indicating that there is an important effect of elevation, but indirectly through other drivers.

RADIATION/LIGHT TESTS

Supporting the dual prediction that increasing light (L) increases S , until radiation stress (R) at the highest elevations, the best model showed the exact combination of parameter values necessary to match the prediction (Table S3, Fig 2). Specifically, we found that at mid- to lower elevations c had a positive effect on S but at the highest elevations the effect of c on S became negative at high radiation (too much radiation, less S). At lower elevations (e.g. -160 m from seedling line), radiation effects on S were positive and high (see upward curving pale lines at the right hand side of Fig. 2). In contrast, at the highest elevation, maximum S occurred below maximum openness (dark line with downward

curvature, with a maximum near 85%, Fig. 2). These results match exactly our precise radiation stress predictions. Diffuse tree lines showed the same pattern, but fewer seedlings predicted overall (Fig. 2).

WIND EXPOSURE TEST

Our set of predictions from our wind exposure hypothesis derived from the SGH – namely wind protection will confer a strong positive effect, but only at the highest elevations – were exactly supported. Specifically, in support of the wind exposure hypothesis (W), we found that f had a negative effect on S with increasing elevation (Fig. 3). At lower elevations, however, we found that the effect of f on S disappeared completely (i.e. the effect of f became negligible at -160 m), as predicted by the SGH (Fig. 3). We also found that f was correlated with elevation in all sites (Fig. S2).

MODEL PREDICTIONS BY SITE

As expected, we found variation among sites (see Table S4 for random effects). For example, S in the Alps and the Montana Rockies showed very little increase with decreasing elevation, suggesting that they are minimally temperature-limited (Fig. 4). In contrast, we found that seedlings at all Andean sites showed greater increases with decreasing elevation, though the two Montana Rockies sites showed substantial variation.

Discussion

In order of importance, we found support for the following hypotheses explaining tree seedling abundances at and near

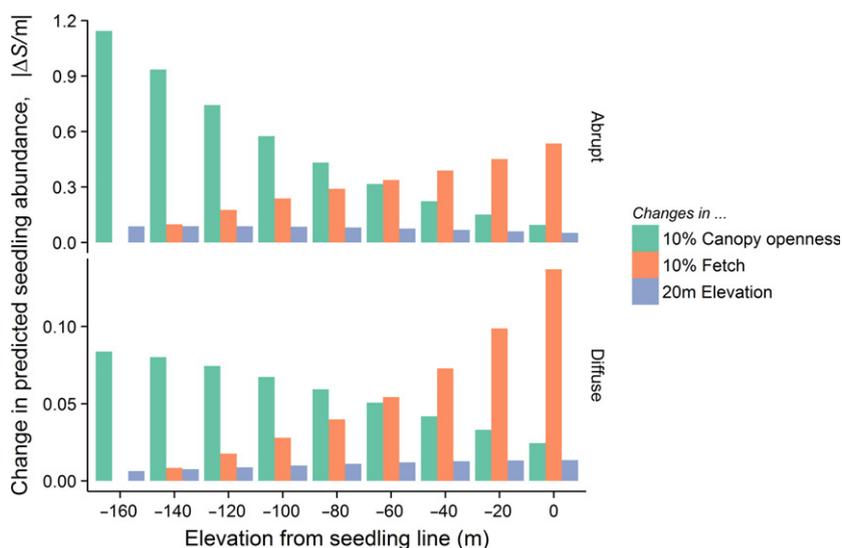


Fig. 1. Comparison of the relative strength of small changes in three drivers on seedling abundance at several alpine tree lines (southern Andes of Chile, Central Rocky Mountains in the United States and the Swiss Alps) grouped into abrupt and diffuse tree line forms. Bars show the mean absolute effect of the following changes on seedling abundances at each elevation shown on the x-axis: 10% increase in canopy openness, 10% increase in fetch and 20 m downward elevation. In each case, we assess each change across all possible integer values of the other variable (i.e. to assess 10% change in fetch, we set light sequentially to 30%, 31%, 32%) and assessed the effect of each 10% increase (e.g. 30–40%, 31–41%, 32–42%). From this predicted matrix, we show the mean of the absolute values. Seedling line is defined as the uppermost elevation where we found seedlings.

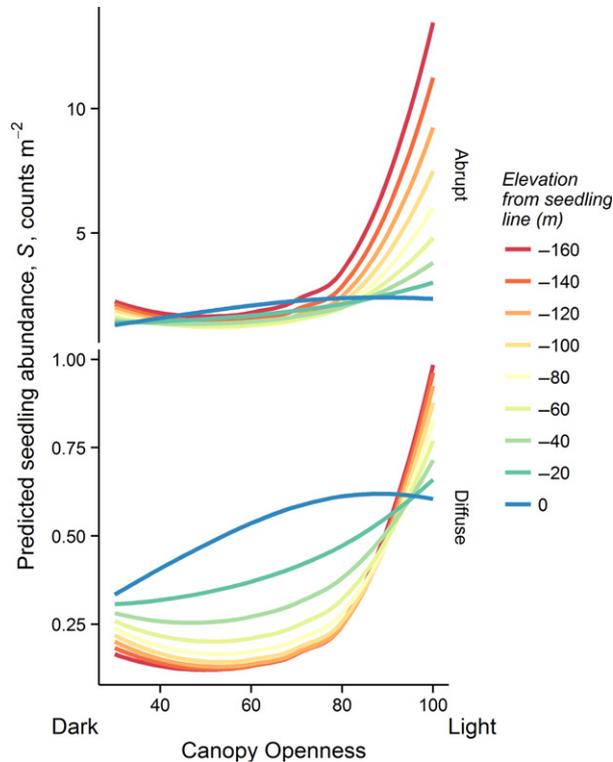


Fig. 2. Predictions from model 17 for seedling abundance (S) across levels of canopy openness (c , testing light as resource, L , and radiation as stressor, R , at tree line) at different elevations in the highest 200 m of several alpine tree lines (southern Andes of Chile, Montana Rocky Mountains in the United States and the Swiss Alps) grouped into abrupt and diffuse tree line forms. There is a shift from a linear positive relationship between c and S at lower elevations to a quadratic positive relationship at tree line elevation, where too much light is detrimental for S . Seedling line is defined as the uppermost elevation where we found seedlings.

tree line: wind exposure as a stressor, light as a resource, low free-air temperature as a stressor, high radiation as a stressor. We also found support for tree line form (diffuse vs. abrupt) as a determinant of seedling abundance, but we could not rank the importance of this as it was not a quantitative covariate. Although low free-air temperature, radiation and wind exposure have each been identified as potential bottlenecks for seedling abundance at tree line (e.g. Germino & Smith 1999; Maher, Germino & Hasselquist 2005; Batllori *et al.* 2009; Holtmeier & Broll 2010), our study adds an assessment of the relative importance of each of these components for seedling abundance at diverse tree lines (i.e. three continents), which is important for general prediction particularly under global warming. As expected, we did not find a single, main driver, but rather a combination that best explains seedling abundance. Although elevation constrains regeneration processes at tree line, such as flowering, seed production, germination and seedling survival (Sveinbjörnsson, Kauhanen & Nordell 1996; Cuevas 2000), and elevation has been found to strongly limit seedling abundance (Cuevas 2000; Resler 2006; Cierjacks *et al.* 2008), our approach revealed just a minor role for elevation on seedling abundance. This suggests that free-air temperature is not the major constraint for seedling

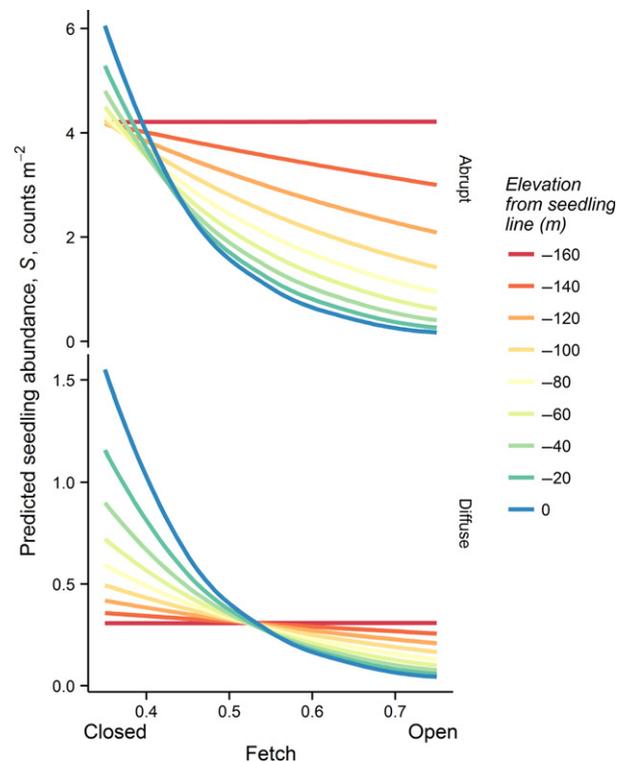


Fig. 3. Predictions from model 17 for seedling abundance (S) across levels of fetch index (f , testing wind as a stressor hypothesis, W) at different elevations in the highest 200 m of several alpine tree lines (southern Andes of Chile, Central Rocky Mountains in the United States and the Swiss Alps) grouped into abrupt and diffuse tree line forms. There is a clear shifting from a non-significant relationship between f and S at lower elevations to a quadratic one at tree line, where high fetch is very detrimental for S . Seedling line is defined as the uppermost elevation where we found seedlings.

establishment at our tree lines. The fact that the temperature experienced by seedlings can be significantly decoupled from atmospheric, free-air temperature (Scherrer & Körner 2010) could account for this result. Nevertheless, in our analysis by sites, the Andean sites did show a positive response of seedling abundance with warmer free-air conditions. These are also the sites with the least shelter at and above tree line. Our results suggest that if Andean sites did have shelter sites, they would therefore be the most likely to respond to warming conditions. Such potential response could involve upward tree line migration if global warming reduces the temperature limitations that impede seedlings to become trees at the current tree line elevation (Körner 1998). Overall, our results imply that seedling distribution may be poorly inferred from climatic models based on air temperature records of weather stations either because of a weak relationship with free-air temperature (Körner 1998) or a lack of shelter sites where such a relationship is stronger.

We found a double effect of radiation: as a necessary resource (light) for seedlings across elevations, as shown with a positive parameter value, and as a stressor at the highest elevations, as shown with the quadratic decline with high light at high elevations. This shift suggests an increasing need

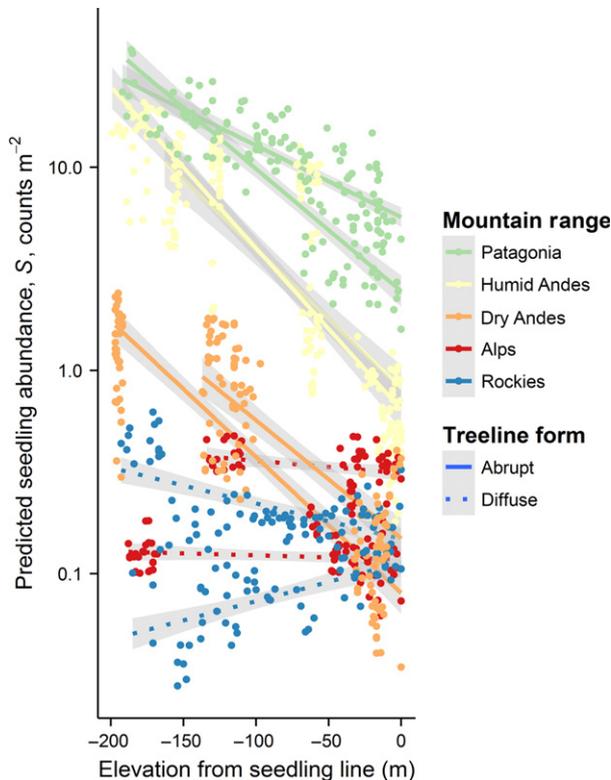


Fig. 4. Predicted seedling abundances in different alpine tree line ecotone regions as a function of elevation from tree line. Fetch and canopy openness were set to their mean values. Each region is represented by two lines, one for every sampling site. Seedling line is defined as the uppermost elevation where we found seedlings.

by seedlings for some slight protection from excessive radiation at high elevation (at 80% of canopy openness, Fig. 2), which is consistent with results from previous studies identifying excessive solar radiation as the causal factor hindering seedling survival at the tree line (Germino & Smith 1999; Bader, van Geloof & Rietkerk 2007). In our study, slightly shaded sites provided by adult, taller conspecifics (because our tree lines are essentially monospecific and do not have a dense shrub layer) appear to have a modest facilitation effect on the establishment of seedlings under their canopy even when this shading has some detrimental effect on seedling establishment via light limitation at all other elevations (Fig. 2) (see also Maher, Germino & Hasselquist 2005; Renard, McIntire & Fajardo 2016). In contrast, fully open-light conditions were beneficial for seedlings at lower elevations (Fig. 2). Additionally, the increase in seedling abundance with shading is rather skewed towards the right (Fig. 2), meaning the negative effects of high radiation are overall minor and occur at the highest levels of canopy openness only. This pattern is in agreement with the shade-intolerant character of most tree line species.

Our wind exposure index (fetch) was, by far, the main determinant of seedling abundance at tree line. Our results indicate that high wind exposure has a strong detrimental effect on seedling abundance at tree line (Fig. 1). While the

importance of shelters or safe sites as a protection of wind scour for seedlings has been largely demonstrated for different tree lines (Bowman *et al.* 1993; Batllori *et al.* 2009; Renard, McIntire & Fajardo 2016), our study reveals that shelter from wind is a major factor determining seedling availability. When wind exposure is small at upper tree line elevations, it is possible that there will be patchy accumulations of snow or the presence of large-scale safe sites, represented by tree barriers, favourable windward slopes or big outcrops that would improve seedling establishment (Smith *et al.* 2003; Resler 2006; Holtmeier & Broll 2007) (Fig. 3). Wind exposure, however, had no impact at low elevations (virtually flat pale line; Fig. 3). This result is consistent with the fact that wind, and other microclimatic factors associated with large-scale openings (e.g. temperature oscillations), is likely not detrimental for seedling abundance at low elevations where abiotic conditions are less harsh – gap size was not related to wind speed in low-land forests of North West England (Latif & Blackburn 2010). Above all, however, our study indicates that the well-reported advantage of shelters at tree line might be the mechanism behind the negative effects of wind exposure, as suggested by previous studies (Hättenschwiler & Smith 1999; Holtmeier *et al.* 2003; Smith *et al.* 2003; Resler 2006). Fetch is a coarse, landscape-scale mechanism that integrates many finer (e.g. physiological, site-level) mechanisms. Specifically, in addition to fetch indicating direct effects of wind, such as abrasion, it is also integrating the numerous indirect effects of a wide open locale, such as modified soil water content, relative humidity and microscale snow pack (Körner 2003; Resler 2006; Holtmeier & Broll 2010). In a coastal dune system, where wind exposure may be comparable to tree line elevation, Lortie & Cushman (2007) found a strong relationship between shelter distance and wind exposure (measured here as fetch) which led to changes in the community composition. Thus, our finding that wind exposure – and its complement of direct or indirect effects – is the strongest driver of seedling abundance is consistent with numerous studies about seedlings at exposed locations and the need for shelter.

Our results suggest that abrupt tree lines have greater seedling abundance. This appears to conflict with our other result that plots with low wind exposure at the highest elevations had much higher seedling abundances. However, we caution this comparison because we cannot separate species, hemisphere and tree line form in our analysis as they are confounded. To separate these effects, we would need to find *Nothofagus pumilio* tree lines that have a diffuse form or Northern Hemisphere conifer tree lines that are abrupt. Alternatively, future studies that use reciprocal transplants of conifers in Southern Hemisphere abrupt tree lines and vice versa may resolve this. Identifying the effect of tree line form unambiguously remains unresolved.

SUPPORT FOR THE STRESS GRADIENT HYPOTHESIS

We found that the highest seedling abundance at tree line occurs with low wind exposure and under some shade, but these patterns disappear at lower elevations. With this result,

we show support for two distinct mechanisms of facilitation (protection from wind exposure and protection from too much light exposure) under the SGH at the intraspecific level as well as determining their relative strength under *in situ* conditions. There are many one-site studies that have found or suggested support for facilitation at the tree line ecotone (e.g. Brett & Klinka 1998; Callaway 1998; Germino, Smith & Resor 2002; Bekker 2005; Maher, Germino & Hasselquist 2005; Wiegand *et al.* 2006; Batllori *et al.* 2009; Renard, McIntire & Fajardo 2016). Each of these studies mostly tested one potential mechanism at a time (but see Maher, Germino & Hasselquist 2005), finding facilitation occurring typically through immediate neighbours' shelter. From these studies, Brett & Klinka (1998), Callaway (1998), and Renard, McIntire & Fajardo (2016) have found explicit support for the SGH. For example, Callaway (1998) found that at high elevation *Abies lasiocarpa* seedlings were highly aggregated around mature *Pinus albicaulis*, while at lower elevations the positive spatial association pattern disappeared. While the pattern of tree line seedlings being sheltered by adult trees is widespread and known, our study has demonstrated the prevailing importance of facilitation at geographically different tree lines and has identified the factors that facilitation ameliorates.

Conclusions

Current trends of global warming are altering the range of species and performance, and population-level effects may be more readily detected or predicted in boundary areas of species distributions (Innes 1991; Hayhoe *et al.* 2004). At alpine tree lines, temperature during the growing season has been identified as the primary driver on tree line formation and maintenance due to its effect on mature trees (Körner 1998; Körner & Paulsen 2004). As a result, tree lines should be slow to migrate upwards because it takes decades for trees to germinate, grow and mature. However, if a particular tree line currently has seedlings growing in between krummholz trees or shrubs (i.e. the 'species line' *sensu* Körner 2012 extends above the tree line, which is > 3 m tall erect trees), persisting above the tree line due to low wind exposure and slight cover from full sun, our results indicate that these tree lines will respond more quickly to globally warming temperatures than previously expected. We show here that the response would be a rapid infilling if there are mature tree islands, and it would be an advance if the establishing seedlings are currently at higher elevation than the highest elevation erect trees (i.e. if the seedling line is above tree line). This rapid response would be because it is a growth release process rather than a full regeneration from seed process. Accordingly, we found that seedling abundance is limited by multiple simultaneous factors with free-air temperature playing a relatively minor role and protection from wind exposure playing a much stronger role. This main result also suggests two predictions. First, because wind exposure and light exposure were found to be more limiting than free-air temperature at tree line, an upward colonization is not inevitable with warming (Holtmeier & Broll 2007; Harsch *et al.* 2009; Fajardo &

McIntire 2012). Secondly, because of the strong effect of wind exposure on seedling abundance at our highest elevations (at or above the tree line), our results provide a mechanistic explanation of why diffuse tree lines, that is tree lines that have low average wind exposure at tree line, should respond more rapidly to warming (Harsch & Bader 2011).

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Data accessibility

Data available from the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.j0v43> (McIntire, Piper & Fajardo 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of all alpine treeline ecotone sites under study and their dominant tree species.

Table S2. Description and short word representation of *a priori* models concerning the effects of elevation (*e*, a surrogate for temperature, T), plot-level canopy openness (*c*, a surrogate for light, L, or shade,

R), large canopy opening or fetch (*f*, a surrogate for wind, *W*) and treeline form (*D*, abrupt vs. diffuse) on seedling abundance at several alpine treelines (Southern Andes of Chile, Central Rocky Mountains in the US, and the Swiss Alps).

Table S3. Estimated slope parameters (standard error) for the best model.

Table S4. Estimated random effects for the best model.

Figure S1. Summary of 5000 parameter combinations attempted and the top 40 (based on highest variance) combinations used to calculate fetch.

Figure S2. Fetch estimate by site, mountain range, and treeline form (*d*).