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Global drivers of tree seedling establishment at alpine treelines in a changing climate

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Abstract

1. Alpine and Arctic treeline expansion depends on establishment of tree seedlings beyond the current treeline, which is expected to occur with climate warming. However, treelines often fail to respond to higher temperatures, and it is therefore likely that other environmental factors are important for seedling establishment.
2. We aimed to analyse our current understanding of how temperature and a range of other environmental drivers affect tree seedling establishment at the alpine and Arctic treelines worldwide, and to assess the relative importance of temperature compared with other factors and how they interact.
3. We collected 366 observations from 76 experimental and observational papers for a qualitative analysis of the role of a wide range of environmental factors on tree seed germination, tree seedling growth, survival and natural occurrence. For a subset of these studies, where the experimental design allowed, we conducted formal meta-analyses to reveal if there were global drivers for different seedling life traits.
4. The analyses showed that a wide range of abiotic and biotic factors affected tree seedling establishment besides from temperature, including water, snow, nutrients, light, and surrounding vegetation. The meta-analyses showed that different seedling life stages do not respond similarly to environmental factors. For example, temperature had positive effects on growth, while tree seedling survival and germination showed mixed responses to warming. Further, warming was as often as not the strongest factor controlling tree seedling establishment, when compared to with one of five other environmental factors. Moreover, warming effects often depended on other factors such as moisture or the presence of surrounding vegetation.
5. Our results suggests that population dynamics of trees at the alpine and Arctic treeline are responsive to environmental changes and show that there is a clear need for multi-

factorial studies if we want to fully understand and predict the interplay between warming and other environmental factors and their effect on tree seedling establishment across current treelines.

Introduction

The latitudinal and altitudinal treelines delineate the boundary between the low-statured Arctic and alpine tundra and the boreal and montane forests. Changes in position of these treelines, for example in response to global change, may strongly feed back to our climate, through reductions in albedo and carbon storage (Chapin *et al.* 2005; Hartley *et al.* 2012; Parker *et al.* 2015). Globally, a growing season mean soil temperature of 6.7 (±0.8 SE) °C coincides with the treeline position (Körner & Paulsen 2004; Körner 2007a) and global warming is therefore generally assumed to cause treeline shifts. However, treelines often fail to respond to higher temperatures (Lavoie & Payette 1996; Dalen & Hofgaard 2005; Harsch *et al.* 2009; Aune *et al.* 2011; Vuorinen *et al.* 2017). Other environmental factors, such as moisture (Moyes *et al.* 2015), snow cover (Hagedorn *et al.* 2014), nutrient availability (Sullivan *et al.* 2015), surrounding vegetation or disturbances (Cairns & Moen 2004), are therefore likely involved in regulating treeline responses. Tree seedling establishment beyond the treeline is a key step for treeline expansion (Germino *et al.* 2002; Smith *et al.* 2003; Holtmeier & Broll 2005; Moen *et al.* 2008). Understanding how temperature and other environmental factors regulate tree seedling establishment beyond the treeline is thus crucial for predicting responses of the treeline to climate change, but so far, an overview of the relative importance and interactions of such factors is lacking.

A lack of positive responses of treelines to increases in temperature may indicate that other factors than temperature are more limiting for tree establishment beyond the treeline. Due to their small size and therefore limited reserves or protective structures, establishing tree seedlings can potentially be limited by a wide range of other environmental factors. Relative to adult plants and seeds, tree seedlings are highly sensitive to desiccation (Leck *et al.* 2008) and soil moisture is thus likely one important factor for tree seedlings, even at the cold alpine or Arctic treeline. Further, as temperature limits mineralization in cold ecosystems (Schmidt *et al.* 2002), nutrients, especially nitrogen (N), limit growth in many alpine and Arctic ecosystems (Bowman *et al.* 1993; Van Wijk *et al.* 2003) and treelines can be N-limited (Sullivan *et al.* 2015). Snow can be an important driver of treeline advances (Hallinger *et al.* 2010; Kirdyanov *et al.* 2012; Hagedorn *et al.* 2014) through its thermal insulation and effects on soil nutrient status (Schimel *et al.* 2004), and wind exposure; this can have especially large effects at the seedling stage. At alpine treelines, high elevation and absence of a tree canopy causes light intensities to be high, especially at low latitudes. This may stress seedlings above the treeline through cold-induced photo inhibition (Facelli 2008). Locally, but also at a larger scale, disturbance by herbivores can be the main control of the treeline (Cairns & Moen 2004), potentially through its control of seedling establishment (Speed *et al.* 2010). As temperature increases, these other environmental factors may become more or less limiting for tree establishment (Barber *et al.* 2000). For example, warming may induce drought stress if soil moisture is not high enough to meet the seedlings' increased demand for water under higher temperatures (Moyes *et al.* 2015). Warming may also change interactions between plants and enhance competition from surrounding vegetation (Anthelme *et al.* 2014). Multiple environmental factors may thus simultaneously affect seedling establishment at the treeline, be more or less important than temperature, and interact depending on the local context.

Successful establishment of tree seedlings is dependent on the presence of viable seeds at the treeline and on their germination. Subsequently, seedlings have to survive and grow into mature trees. Each step can be a bottleneck and be affected differently by environmental factors. In fact, germination might be promoted by factors that decrease subsequent seedling growth (Schupp 1995; Cranston & Hermanutz 2013), and survival might be enhanced by investment in structural tissues or defence compounds, which at the same time might be at the cost of fast growth (Grime 1977). A large body of literature exists that investigates or compares how these different tree seedling stages and life strategies are affected by one or a few environmental factors at the alpine and Arctic treeline. However, there is to date only a limited overview of how a range of multiple environmental factors can impact on the different phases of seedling establishment, and therefore we currently do not fully understand their relative importance or how they interact.

In this paper, we aim to synthesise our current knowledge about how tree seedling establishment at alpine and Arctic treelines globally are impacted by multiple environmental factors. Below, we therefore analyse and discuss findings from published literature, to answer: (i) how are different seedling life traits related to establishment (germination, survival, growth and occurrence) affected by a range of abiotic and biotic factors at the alpine and Arctic treeline? (ii) What is the relative importance of temperature compared to other environmental factors with regard to seedling establishment at the treeline, and (how) do these factors interact? Finally, we will indicate gaps in our current knowledge.

Methods

Literature and data search and selection

To answer our two research questions, we performed a search on the Web of Science (Thomson Reuters) on 5 March 2018 using the following search string: Topic=((treeline* OR tree-line OR "treeline" OR "upper limit") AND (tundra OR alpine) AND tree* AND (seedling* OR sapling* OR germinat*) AND (germinat* OR growth OR biomass OR surviv* OR emerg* OR establish* OR recruit*)) AND Language=(English) AND Document Types=(Article). The search resulted in 214 papers, which covered the period from 1988 – 2018. To retrieve as many relevant data as possible, we further searched through the reference lists of all papers and added any additional papers that we were aware of or that were forwarded to us by colleagues.

We only included original data studies conducted in the field at or above or north of the alpine or Arctic treeline, respectively. To keep the data as comparable as possible, only data from treeless treeline sites were included. Data were included if they investigated the effect of environmental conditions on seedling establishment (seedling occurrence, growth or survival or seed germination) of tree species native to the treeline where the study was conducted. Seedlings were defined as being smaller that one meter. Seedling growth was defined as biomass increase, length growth or photosynthesis. If papers included several of these growth responses, biomass increase was preferred over length growth, which was preferred over photosynthesis. Data comparing effects of internal factors, such as age or species provenance, on tree seedling success were excluded. This resulted in 76 papers (= 'studies'). If several environmental factors, tree species or years were investigated, studies were split up into different 'observations', which were further analysed for the effects of individual environmental factors, and, in case multiple environmental factors were included, for their relative importance and potential interactions (see below).

The retrieved studies varied in their design and approach. For most germination, survival and growth studies, seeds or seedlings were placed/transplanted in either naturally varying environments or under experimental manipulation of environmental factors. However, in some studies, naturally occurring seedlings were located and their survival and growth were monitored as a response to natural environmental variation or to imposed treatments. These different types of studies vary in their power to provide understanding of different environmental drivers *versus* how well they represent reality. For example, studies linking natural occurrence of tree seedlings to environmental characteristics provide valuable insights in where seedlings actually establish but lack power in describing why they are there and not elsewhere. However, in combination these different types of approaches may complement each other and provide a powerful mechanistic understanding of the drivers of alpine and Arctic treeline responses to global change.

Analyses of the individual effect of abiotic and biotic factors

For the analysis of the individual effect of a range of abiotic and biotic factors (question 1), many studies did not qualify for a quantitative analysis such as a formal meta-analysis, because of lack of distinct treatment and control. This was for example the case for all studies investigating natural occurrence of seedlings. We therefore chose to perform both a formal meta-analysis of environmental effects on seedlings, providing more formal testing but covering only a (for some factors quite limited) sub-set of observations that fulfilled additional criteria (see below), and a qualitative analysis, which included all observations for each factor. Only 14 genera (274 total observations from 37 studies) were covered by the meta-analysis, whereas the full qualitative analysis dataset covered 23 genera (366 total observations from 76 studies).

Quantitative meta-analysis

The meta-analysis mainly included observations where seeds or seedlings had been exposed to a manipulation of environmental factors. However, in a few cases we also included observations that used environmental gradients (such as elevation) as proxy for temperature, but only if the authors clearly stated that they kept other factors, such as exposure, soil conditions and vegetation, constant.

For observations suited for inclusion in the meta-analysis, a database was constructed. The same study ID was given to multiple observations from the same study.

However, observations from multiple sites included in the same study were considered as independent studies and were given separate study IDs. This yielded 42 for germination, 136 observations for growth, 96 for survival and none for occurrence. The observations for each seedling life trait were then categorised with respect to the following environmental factors: temperature, water (including soil moisture and precipitation), snow cover, nutrient availability, light and surrounding vegetation. While this resulted in a considerable number of observations for several of the factor × life trait combinations, there were also many combinations with low or very low numbers of observations (Fig. 2a). To enable comparison across a range of abiotic and biotic factors, we present results from formal meta-analyses appropriate for small sample sizes (<20, see below) for each combination with two or more observations, together with the corresponding sample size. However, generalisations of results based on very low replicate numbers should be done carefully and in combination with the qualitative analysis.

For each observation, we extracted mean, standard deviation (sd) and number of replicates (n) from controls and treatments. Data were mainly extracted from tables, figures and main text. In some cases when this was not possible, authors were contacted to provide raw data or calculated means and sd. For each environmental factor, we calculated the mean size of its effect on seedling survival, germination or growth separately as Hedges' g:

$$g = \frac{\bar{Y}_1 - \bar{Y}_2}{\sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 - n_2 - 2}}} J$$

Where $J = 1 - \frac{3}{4(n_1 + n_2 - 2) - 1}$

And the variance (v) of Hedges' g is found as:

$$v_g = \frac{n_1 + n_2}{n_1 n_2} + \frac{g^2}{2(n_1 + n_2)}$$

Where Y is the mean, n is sample size and s is the standard deviation from groups 1 and 2 (treatment and control). Hedges' g is appropriate for estimating effect sizes when the sample size is low (<20) (Koricheva *et al.* 2013). We analysed if the mean effect size for each environmental factor and response variable was significantly different from zero using random effects models, to account for between-study variability. This was relevant in our case as studies differed in their approach, design and location. We used restricted maximum likelihood estimators as is recommended for minimizing unbiased estimates (Viechtbauer 2005). Study ID number was used as random factor to take into account potential interdependence of observations from the same study. All analyses were performed in R statistical software (R Core Team 2016) using the Metaphor package (Viechtbauer 2010) for meta-analysis.

Qualitative analysis

The total dataset, used for qualitative analysis, included 45 observations for seed germination, 123 for seedling growth, 148 for survival, and 50 for occurrence. The observations for each seedling life trait were categorised with respect to the following environmental factors: temperature, water (including soil moisture and precipitation), snow cover, nutrient availability, light, surrounding vegetation and other factors (Herbivory, disturbance, fire, wind and frost)., We then summarised if observations of environmental factor effects on tree life traits (occurrence, germination, survival or growth) at alpine or Arctic treelines in the field were positive, negative, neutral or complex.

Complex results were those where the main effect of a factor was shown to be non-linear or where the study design included more complexity than what a simple assessment of the direction of a result could describe. The direction of the effect for each observation was based on the sign and significance level from the statistical analyses reported in the original study.

Relative importance and interactions of temperature and other factors

The relative importance of environmental factors for seedling establishment can be evaluated across observations by comparing effect sizes. However, across studies, the environmental context may vary, which potentially can affect the outcome of the response. For our second question, we therefore focused on studies that manipulated temperature together with at least one other environmental factor, and that included explicit testing of statistical interactions. Because several of the studies manipulated more than one factor in addition to temperature, we retrieved 11 observations for germination, 27 for growth and 38 for survival from 13 studies altogether. However, since these relatively few observations were related to six different environmental factors (Table 1), we did not to perform a formal meta-analysis of these results. Instead, we qualitatively summarized across studies for each seedling life trait if the relative effects of two factors (within each study) differed and if they significantly interacted (within studies). The significances and effect sizes (for each observation) compared were based on the results (tables, figures) and the statistical analyses reported in the original studies.

Environmental drivers of seedling establishment beyond the treeline

The majority (>90 %) of all 366 observations were from the Northern Hemisphere, with a large over-representation of observations from North America and Europe (86%, Fig 1). Around 80 % of all observations were from medium to high latitudes (>40°, Fig 1a). Seedling survival and growth were most studied (148 and 123 observations, respectively), followed by natural occurrence (50 observations) and seed germination (45 observations, Fig 1b). Across all observations, the effects of temperature (92 observations) and surrounding vegetation (94 observations) on seedling establishment have been investigated most intensively, followed by the effects of light (61 observations), water (38 observations), snow (30 observations) and nutrients (16 observations) The effects of herbivory, disturbance, fire, wind and freezing each have been studied less than 10 times. These patterns were largely similar across the sub-set of observations included in the meta-analysis (data not shown). Below we discuss the emerging understanding and knowledge gaps of how each of these environmental factors affects the different seedling life traits related to establishment.

Temperature

As temperature determines the rate of many physical, chemical, and biological processes in nature, it is also a key driver of processes in organisms that cannot actively regulate their temperature, including germination, physiology and growth of plants. Tree seedling occurrence thus often declines with decreasing temperature along increasing elevational gradients (Cierjacks *et al.* 2008; Mamet & Kershaw 2012; McIntire Eliot J. B. *et al.* 2016; Shen *et al.* 2018).

Indeed, higher growing season temperature seemed to have mostly positive effects on germination, (8 out of 14 observations in the qualitative analysis; Figs. 2a and 2b). However, this was not significant in the meta-analysis (p=0.14, n=12(3):

observations(studies), Fig 2a), not because of a small average effect size, but because of the large variation among these. Tree seedling growth also seemed to respond positively to higher growing-season temperatures (13 out of 25 observations in the qualitative analysis; Fig 2b), which was supported by the meta-analysis (p=0.005, n=45(14), Fig 2a). In contrast, seedling survival response to higher temperature seemed mostly neutral (18 out of 29 observations; Fig 2b), which was confirmed in the meta-analysis (p=0.65, n=27(6), Fig 2a).

The large variation of the germination responses suggests that the strength of this response to temperature may be particularly variable between species or depend on the local environmental conditions or on the experienced degree of warming. For example, in Arctic tundra, as little as 1°C experimental warming led to strong increases in germination in all five tested tree species (Hobbie & Chapin 1998). Such generally high temperature sensitivity suggests that small differences in the experienced degree of warming can have strongly different effects on germination.

In the 25 observations that considered both survival and growth of the same individuals, temperature had similar effect in 15 observations (Hobbie & Chapin 1998; Johnson & Yeakley 2013; Zurbriggen *et al.* 2013; Renard *et al.* 2016; Bader *et al.* 2017), a more positive effect on growth than survival in 7 cases (Hobbie & Chapin 1998; Grau *et al.* 2012, 2013), while the opposite was true only in three cases (Zurbriggen *et al.* 2013) . That growth responds more positively to warming than survival could be a result of a fundamental trade-off, as an increased investment in growth may prevent investment in strategies to resist, for example, cold winter temperatures or herbivory (Grime 1977; Kitajima & Myers 2008). Altogether, across Arctic and alpine treelines worldwide, higher temperatures thus positively affect particularly tree seedling growth and sometimes germination, while seedling survival is not affected.

Water

Water is crucial and can be limiting for plants, as it is lost during uptake of carbon dioxide. Water is a cue for germination, and newly germinated seedlings are, due to their small size, lack of periderm and limited access to water via their shallow roots, very sensitive to desiccation (Moles & Westoby 2004; Leck *et al.* 2008). Soil water availability is highly variable across space and time and determined by the balance between precipitation, evapotranspiration, inflow and run-off as well as the water holding capacity of the soil. Further, if present, bedrock or, at higher altitude or latitude, permafrost can prevent drainage and cause excess of soil moisture. As such, the importance of water for tree seedling establishment beyond the treeline can thus be expected to vary spatially.

Across the different seedling life traits, the effect of (increases in) water (precipitation or soil moisture) on tree seedlings seemed relatively homogenous, with mostly neutral to positive effects (44 out of 47 observations in the qualitative analysis, Fig 2b). Growth was even enhanced by water in 8 out of 11 observations. However, the meta-analysis showed no significant effects of water on any of the three analysed life traits, but a large variation in effect size of water for survival. All life trait meta-analyses, however, relied on relatively few observations (Fig 2a; 5-13 observations from 1-3 studies).

The large variation in seedling survival response to water suggests that, at least for this seedling life trait, the effect of water can thus be very variable. While water can be essential for seedling survival if soil moisture is low, adding more water to an already healthy seedling population might not change the overall survival. Indeed, positive survival responses in the meta-analysis were mainly from two North American sites with an annual precipitation around 900 mm (Maher *et al.* 2005; Gill *et al.* 2015), whereas survival was less responsive in a site in the European Alps with annual precipitation of 1200 mm (see Appendix S1 in Supporting Information, Loranger *et al.* 2016). It is thus likely that effects of water on particularly seedling survival are strongly dependent on local hydrology, but more or targeted multi-factor studies are needed to verify this.

Snow cover

Snow insulates the soil and organisms underneath. Snow therefore protects low-statured plants and plant roots from extreme climate conditions and variations, such as frost damage from low temperatures in winter, freeze-thaw cycles during autumn and spring, and damage and dehydration caused by icy winds, dry winter air and frozen soils (Hardy *et al.* 2001; Wipf & Rixen 2010; Shen *et al.* 2014). Further, protection by snow improves soil nutrient status (Schimel *et al.* 2004). Natural occurrence of tree seedlings can therefore be associated with a sufficiently thick snow cover (Hättenschwiler & Smith 1999; Batllori *et al.* 2009). On the other hand, a long-lying snow pack usually causes shortening of the already short growing season at the treeline, and a too thick snow cover can therefore also be associated with lower occurrence of tree seedlings (Hättenschwiler & Smith 1999; Moir *et al.* 1999) (Fig. 2b).

The relatively low number of observations of snow cover effects on growth and survival reported neutral (10 out of 15 and 12 observations, respectively, Fig. 2b) or otherwise positive effects. This resulted in a positive snow effect on survival in the meta-analysis, (p=0.013, n=8(2), Fig. 2a), but not on growth (p=0.66, n=9(1), Fig 2a). No studies considered the effects of snow on tree seed germination, despite the fact that snow can affect dormancy of seeds in alpine and subarctic plants via its effects on winter soil temperatures (Milbau *et al.* 2009; García-Fernández *et al.* 2015).

Although the meta-analysis relies on studies from only two locations, the Alps and subarctic Sweden, changes in snow patterns have been associated with treeline movements elsewhere (Hagedorn *et al.* 2014; Renard *et al.* 2016). However, snow may play a different role at different latitudes. For example, at tropical alpine treelines, cold weather occurs as stochastic events and not as one long winter. Snow cover is therefore not persistent at the alpine treeline here (Smith & Young 1987) and may play a smaller or different role for tree seedling establishment. At mid to high latitude treelines, with a defined cold season, snow is essential for plant protection during winter. Even further towards the poles and at higher elevations the growing season is increasingly short, and thick and thus persisting snow cover can also have negative effects on plant production (Wipf & Rixen 2010). In addition, long-lasting snow cover can also lead to increased susceptibility to pathogenic fungi (Olofsson *et al.* 2011; Barbeito *et al.* 2013). Because of the general importance of snow in cold climates and predictions of changes in snow patterns in climate models (IPCC 2013), studies targeting snow thickness and duration are thus necessary to understand the full role of snow and predicted changes therein for seedling establishment at the alpine and Arctic treeline.

Nutrient availability

In cold regions, low temperatures generally limit soil nutrient availability, especially nitrogen (N) (Schmidt *et al.* 2002). At the Arctic treeline, seedling occurrence was thus explained by availability of soil nutrient (Sullivan & Sveinbjoernsson 2010) (Fig. 2b). While nutrients can be expected to positively affect seedling establishment at the treeline, the respective effects of nutrient availability and temperature can be difficult to tease apart.

For tree seedling growth or survival, higher nutrient availability either had positive (6 or 3 out of 8 or 7 observations, respectively) or neutral effects (Fig. 2b). However, our meta-analysis showed no effect of nutrients on growth ($p=0.89$, $n=2(2)$, Fig. 2b), potentially owing to the very low number of observations. No suitable observations were available for a meta-analysis of survival. No studies were found that investigated the effects of nutrients on tree seed germination at the treeline, although N can be a trigger for germination of seeds in general (Baskin & Baskin 1998).

While the absence of significant positive effects of nutrients on seedling growth may be due to the very low number of retrieved observations, the role of nutrients at the alpine and Arctic treeline may also not be straightforward. Higher nutrient availability can have positive effects on tree seedling survival, by increasing their winter survival in cold ecosystems (Weih & Karlsson 1999). At the same time, increased growth at higher nutrient concentrations might cause lower stress resistance and thereby decreased survival (Körner 1984). While types of nutrients were generally not differentiated or independently manipulated in the retrieved studies, nitrogen is generally considered the main nutrient limiting plant growth in alpine and Arctic ecosystems (Atkin 1996). However, phosphorous may co-limit plant production especially at higher elevation (Gordon *et al.* 2001; Weg *et al.* 2009). The type of nutrient considered may thus be important for its effect on tree seedling establishment at higher elevation treelines. Further, the few studies investigating nutrient effects on tree seedling establishment were confined to middle and high northern latitudes (>40°), although plants often are nutrient limited at lower latitude alpine ecosystems as well (Anthelme *et al.* 2012). Finally, no studies so far have explicitly addressed limitations for seedling establishment from potential absence of suitable mycorrhizae above the current treeline, while such symbioses can promote seedling establishment (Van Der Heijden & Horton 2009) and is crucial for nutrient uptake in cold and nutrient-limited ecosystems (Hobbie & Hobbie 2006). Studying the effect of different nutrients or nutrient-acquisition mechanisms on tree seedling establishment at a wider range of alpine and Arctic treelines is therefore necessary to understand the relative importance this factor.

Light

Light is essential for plant growth. However, at low temperatures, seedling sensitivity to intense radiation increases and can even cause light inhibition (Keeley & van Mantgem 2008). Where skies are clear, radiation increases with elevation and due to the lack of protection from trees, plants in alpine and Arctic tundra are more exposed than when trees are present (Körner 2007b). Both day length and light intensity or quality can trigger germination for some plant species (Koller *et al.* 1962). However, four studies of natural occurrence of tree seedlings all showed negative or no association with light (Fig 2b) (Akhalkatsi *et al.* 2006; Hughes *et al.* 2009; Johnson & Yeakley 2016; McIntire Eliot J. B. *et al.* 2016).

In the qualitative analysis, light had dominantly neutral to negative effects on all seedling life traits (Fig 2b). In the meta-analysis, light overall had a negative effect on seedling survival (p=0.001, n=19(5), Fig 2a), but no effect on germination (p=0.26, n=10(2)) and growth (p=0.93, n=15(3)).

The generally negative to neutral effects of high light intensities indicate that tree seedlings, especially their survival, can suffer from the higher radiation found beyond the treeline, where there is no shading tree canopy. However, all but one study related to light were performed at latitudes below 50°. Here, higher light intensities (but shorter growing-season day-lengths) are more prevalent than at higher latitudes. In addition, differences in irradiance between day and night are more distinct during the growing season at lower latitudes than at higher latitudes, which may cause more frequent night frost and thus induce photo inhibition (Germino & Smith 2000). In contrast to these generally neutral to negative results at lower latitudes, the only study performed at higher latitude found positive effects of light intensity on tree seedling establishment (Cranston & Hermanutz 2013). While tree seedlings at lower-latitude treelines thus seem hampered or unaffected by the high light availability, light availability or the associated radiative heating might be a limiting factor for tree seedlings at higher-latitude treelines, but more studies are needed to verify this.

Surrounding vegetation

Plant interactions have traditionally been considered to be mainly negative, in the form of competition. However, plant interactions at alpine treelines can be expected to also include facilitation, as plants, including seedlings, increasingly rely on protection from neighbours when climatic conditions get harsher (Callaway *et al.* 2002). Indeed, examples of both competition and facilitation at the treeline are found. Natural tree seedling occurrence was more often associated with patches without vegetation than with patches with surrounding vegetation in 7 out of 23 observations (Moir *et al.* 1999; Ninot *et al.* 2008; Batllori *et al.* 2009; Greenwood *et al.* 2015; Stine & Butler 2015), indicating competition. In contrast, in 9 observations tree seedling occurrence was more associated with vegetation (Camarero & Guitiérrez 1999; Germino *et al.* 2002; Akhalkatsi *et al.* 2006; Hughes *et al.* 2009; Mamet & Kershaw 2012; Perkins 2015; Gelderman *et al.* 2016), indicating facilitation. (Fig 2b). Vegetation type likely plays an important role for the outcome of interactions. For example, graminoids and herbs were consistently associated with negative effects on seedling occurrence, possibly because of their usually high density at the ground surface. Further, in 4 of the 23 observations, seedling occurrence was more associated with certain vegetation types than others (resulting in complex overall vegetation response, Fig 2b, (Anschlag *et al.* 2008; Sullivan & Sveinbjoernsson 2010; Dufour-Tremblay *et al.* 2012; Wang *et al.* 2012). Only in 3 of the studies, did surrounding vegetation not predict the number of naturally occurring tree seedlings (Cierjacks *et al.* 2008).

For germination, the effect of neighbours was less studied than for the other life traits. Here, the qualitative analysis showed rather mixed effect of neighbours, with 1, 5, and 2 observations showing negative, neutral and positive responses, respectively. However the meta-analysis revealed a positive trend (p=0.09, n=13(5), Fig 2a). For growth, the qualitative analysis showed that neighbours had a negative effect in more than half of 26 observations (Fig 2b). The negative mean effect size in the meta-analysis was, however, not significantly different from zero (p=0.29, n=38(15), Fig 2a). The effect of neighbouring vegetation on survival was mixed in the qualitative analysis, with 7, 16 and 12 observations showing negative, neutral and positive responses, respectively (Fig 2b), which was supported by no significant effects in the meta-analysis (p=0.15, n=21(13), Fig 2a).

Across the relatively large number of observations of impacts of surrounding vegetation on tree seedling growth and survival, the results were thus variable, with clear positive and negative effects in individual studies, resulting in no overall 'global' impact but potentially complex relations with other environmental conditions. Also, it is possible that some of this variation for seedling growth stems from the use of different response parameters between individual observations. For example, seedlings might grow taller in the presence of a neighbour to compete for light but without gaining more biomass. However, the relatively high number of studies reporting negative effects of vegetation on tree seedling growth suggests that competition at the treeline is not uncommon in many sites. Facilitation tends to affect germination in general and promotes survival in a substantial part of treeline sites. The variation in the impact of surrounding vegetation on seedlings between observations and between seedling life traits is my partly be caused by the various natures of these impacts. Positive effects of surrounding vegetation likely operate through enhancing accumulation of snow or via protection from light and wind (Akhalkatsi *et al.* 2006; Grau *et al.* 2012). However, protection by other vegetation from the aboveground harsh environment at the treeline does not necessarily mean that there is no simultaneous competition for light, or belowground for nutrients or water. For example, the facilitative effect of plants can change towards competition when protective elements against wind are installed (Renard *et al.* 2016). Similarly, cover by tall grasses protected conifer seedlings from radiation, but when the closest herbaceous plants where removed, only the negative effects from belowground competition remained and survival decreased (Germino *et al.* 2002). Further, the different stages of development from seed to seedling have different resource requirements and limitations and may thus show different sensitivities to competing or facilitating roles of neighbours.

Despite the high number of studies on seedling – neighbour interactions across all latitudes, there were no clear latitudinal patterns, likely because the direction of plant interactions are strongly dependent on other factors, such as precipitation or wind, which vary at a local scale. Conducting multifactorial experiments in order to unravel the dependencies on environmental context is thus important to fully understand the outcome of seedling – neighbour interactions.

Other factors

Besides the environmental factors discussed above, several other factors could be important for seedling establishment at the alpine and Arctic treeline, e.g. herbivory, fire, (ground) disturbance, wind or frost. However, none of these factors has been investigated with enough replication or consistency to allow a formal meta-analysis or even qualitative comparison (see Appendix S2). Below, we therefore review some current insights to identify potential additional research gaps.

Despite an acknowledged important role for treeline dynamics (Cairns & Moen 2004) only few studies investigate effects of herbivores at the tree seedling stage and find that herbivores presence has mixed effects on seedlings occurrence (Cierjacks *et al.* 2007, 2008; Speed *et al.* 2010). Negative effects are likely due to browsing damage (Hofgaard *et al.* 2010; Munier *et al.* 2010; Speed *et al.* 2011), whereas positive effect could be due disturbance through digging or trampling leading to increased germination through increased exposure for the seeds to moist substrate (Munier *et al.* 2010). Another disturbance factor at some alpine and Arctic treelines is fire, which makes nutrients available and open establishment sites to establishing plants (Stine & Butler 2015). However, loss of protective plant neighbours (Green 2009) or inoculum for mycorrhiza (Hewitt *et al.* 2017) due to fires could have negative effect for seedlings. Seedling exposure to e.g. wind (Batllori *et al.* 2009; Greenwood *et al.* 2015; McIntire *et al.* 2016; Tomback *et al.* 2016; Bürzle *et al.* 2018) and freezing (Germino & Smith 2000; Shen *et al.* 2014) seems to play an important role but only few studies specifically consider such effects. Fire frequency and intensity may increase with climate warming (Hu Feng Sheng *et al.* 2010) and herbivory is determined by varying livestock management. Getting a better understanding of how tree seedlings are affect by these major disturbance factors thus seems crucial.

Relative importance and interactions of environmental factors

As discussed above, establishing tree seedlings can potentially be affected by a wide range of environmental factors, due to their small size and therefore limited reserves or protective structures. Because of the generally harsh conditions at the alpine treeline, it is likely that multiple environmental factors act simultaneously and their relative importance may vary in space or time. Moreover, they may alter each other's impacts. Understanding the relative effects on seed germination, and seedling growth and survival of different environmental factors compared with temperature, as well as their interactions, is thus needed to understand the controls on tree seedling establishment at the alpine or Arctic treelines in a changing climate.

Germination

Across the 11 observations (3 studies) that investigated the effects of temperature and at least one of two other environmental factors on tree seed germination, temperature caused a stronger response that the other factor in two cases, while the opposite was true for 6 cases (Table 1). The effects and relative importance of temperature and soil moisture varied strongly between seven tree species (Loranger *et al.* 2016; Kueppers *et al.* 2017) (Table 1). However, three significant interactions between soil moisture and warming indicated that the two factors might enhance each other's impacts. Further, in 3 out of 4 observations, ground disturbance alone or in combination with herbivore exclusion had a 2-10 times higher positive effect on germination of *Picea Mariana* seeds than did the 2.2°C warming treatment (Table 1, Munier *et al.* 2010). Similar results were found for 17 sub-alpine and alpine non-tree species, where disturbance rather than temperature limited seed germination (Milbau *et al.* 2013). The effect of warming on germination was increased by disturbance, likely due to improved contact to moist substrate (Munier *et al.* 2010), which is in line with the generally positive effects of moisture on germination found in the singe-factor studies. The general paucity of multi-factor studies on tree seed germination at the treeline and the occurrence of several significant interactions suggest that further studies are needed in order to understand how and where climate warming will impact the treeline via seed germination.

Growth

Across the 27 observations (8 studies) that compared the effect of temperature on tree seedling growth to at least one of 5 other environmental factors, the majority (19 observations) found responses of similar size of temperature and the other factor. Temperature caused a stronger response than the other factor in three cases, while the opposite was true for four cases (Table 1). Especially when warming and neighbouring vegetation was compared, the response of the seedlings to neighbours varied with both stronger and weaker relative responses compared to warming (Table 1). The relative importance of factors may partly depend on the size of the manipulation. For example, in the study of Okano & Bret-Harte (2015) where warming caused a larger effect on growth than vegetation removal, temperature was increased by almost 7°C. This is 3-7 times more than the temperature increase in other studies (see Appendix S3) and most likely more than can be expected from climate change.

Warming interacted in 8 observations (out of 23 studies) with another factor's effect on tree seedling growth (Table 1). Seedling growth of 4 coniferous tree species responded more positively to warming in combination with watering, suggesting that they became water limited under warmed conditions (Moyes *et al.* 2015; Lazarus *et al.* 2018). So although water did not affect growth in the single-factors meta-analysis, its importance for moderating warming responses should be pointed out. Further, two studies found that when local vegetation was removed, seedling growth response to temperature was increased (Grau *et al.* 2013; Okano & Bret-Harte 2015). At the same time this lead to a decrease in the facilitative effect of vegetation (Grau *et al.* 2013) or an actual turn towards competition (Okano & Bret-Harte 2015). This suggest that with climate warming, alpine vegetation could exert an increased competitive barrier for tree seedling success, as also observed in alpine communities for non-tree species (Anthelme *et al.* 2014). Okano & Bret-Harte (2015) suggested that increased competition following warming may be caused by an increased N-demand. In line with this, seedling growth responded less to warming in the presence of shrubs potentially due to competition (Grau *et al.* 2013). Further, tree seedlings were more responsive to higher nutrient availability under elevated temperatures at the alpine treeline (Grau *et al.* 2012) and under controlled conditions (Hoch 2013; Lett *et al.* 2017a), suggesting that the demand for nutrients at the alpine treeline increases with warming.

Based on these relatively few studies, it seemed that surrounding vegetation might be more important for seedling growth than warming, while resources (i.e. water and nutrients) may not. Further, both surrounding vegetation and soil moisture may strongly alter the effect of warming. The results demonstrate that while temperature often (co-) limits tree seedling growth at the alpine or Arctic treeline, its specific role can depend on the context.

Survival

Thirty-eight observations (9 studies) compared the effects of temperature to one of five other environmental factors. Despite the many studies most (27 observations) showed similar sized responses between the two factors. In 5 observations, temperature had a stronger, negative effect on seedling survival, while in 6 observations, the other factor had a stronger effect (Table 1). In all but one of 8 observations, soil moisture had a similar or more positive effect on seedling survival than warming. Snow addition had similar neutral or positive effects on survival in 12 observations (Bader *et al.* 2017; Lett *et al.* 2017b).

The effect of warming on seedling survival was only changed by that of another factor in three out of the 32 observations where this was tested (Table 1). As such, seedlings growing at colder elevations benefitted more from increased snow cover than those in a warmer environment in two observations (Lett *et al.* 2017b) and moisture addition changed the effect of warming from negative to positive (Loranger *et al.* 2016). In summary, as warming had a relatively small negative or no effect on survival, other factors played a relatively larger role. The interactions between snow or moisture with warming highlights that the outcome of changes in precipitation and temperature (IPCC 2013) could affect seed germination at the treeline.

Conclusions and implications for future research

The studies published so far show that although temperature is often limiting tree seedling establishment at alpine and Arctic treelines, many other factors affect tree seedlings as well. It is also apparent that different seedling life traits do not respond similarly to environmental factors. A good place to germinate is not necessarily a good place to grow or survive (Schupp 1995). The meta-analysis showed that tree seedling growth was clearly increased by temperature while germination tended to be increased by the presence of plant neighbours and survival was enhanced by increased snow cover and decreased by light. However scarcity of studies for some environmental factors and some response parameters prevent us from concluding if these are the only important drivers for tree seedling establishment at the alpine treeline. Whether tree species of different life strategies consequently show different responses to temperature and other environmental factors was not evaluated here but this likely plays an important role (Maestre *et al.* 2009). Experimental studies including species representing different strategies simultaneously could help answer this question.

Comparing the effect of warming with other environmental factors showed that warming was as often as not the strongest factor influencing seedling establishment. However, in most cases the response was of a similar size. Also, it was not uncommon that the effect of warming interacted with the other factor. For example soil moisture and neighbouring vegetation often moderated the warming effect. As global change often involves more than just temperature changes alone this highlight the need for multifactorial experiments for truly understanding tree seedling establishment beyond the alpine and Arctic treeline.

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Author contributions

SL and ED designed the study. SL collected and analysed the data. SL wrote the manuscript with contributions from ED.

Data accessibility

Data are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.6cm5d7f (Lett & Dorrepaal 2018).

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Data sources

List of studies used for qualitative analysis and meta-analysis. Data extracted from these studies are deposited in the Dryad Digital Repository (reference will be add upon acceptance)

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Supporting Information

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

Appendix S1 Individual forest plots for each seedling life trait and response parameter combination

Appendix S2 Distribution of effects of "other factors"

Appendix S3 Overview of relative effects and interactions between warming and other factors

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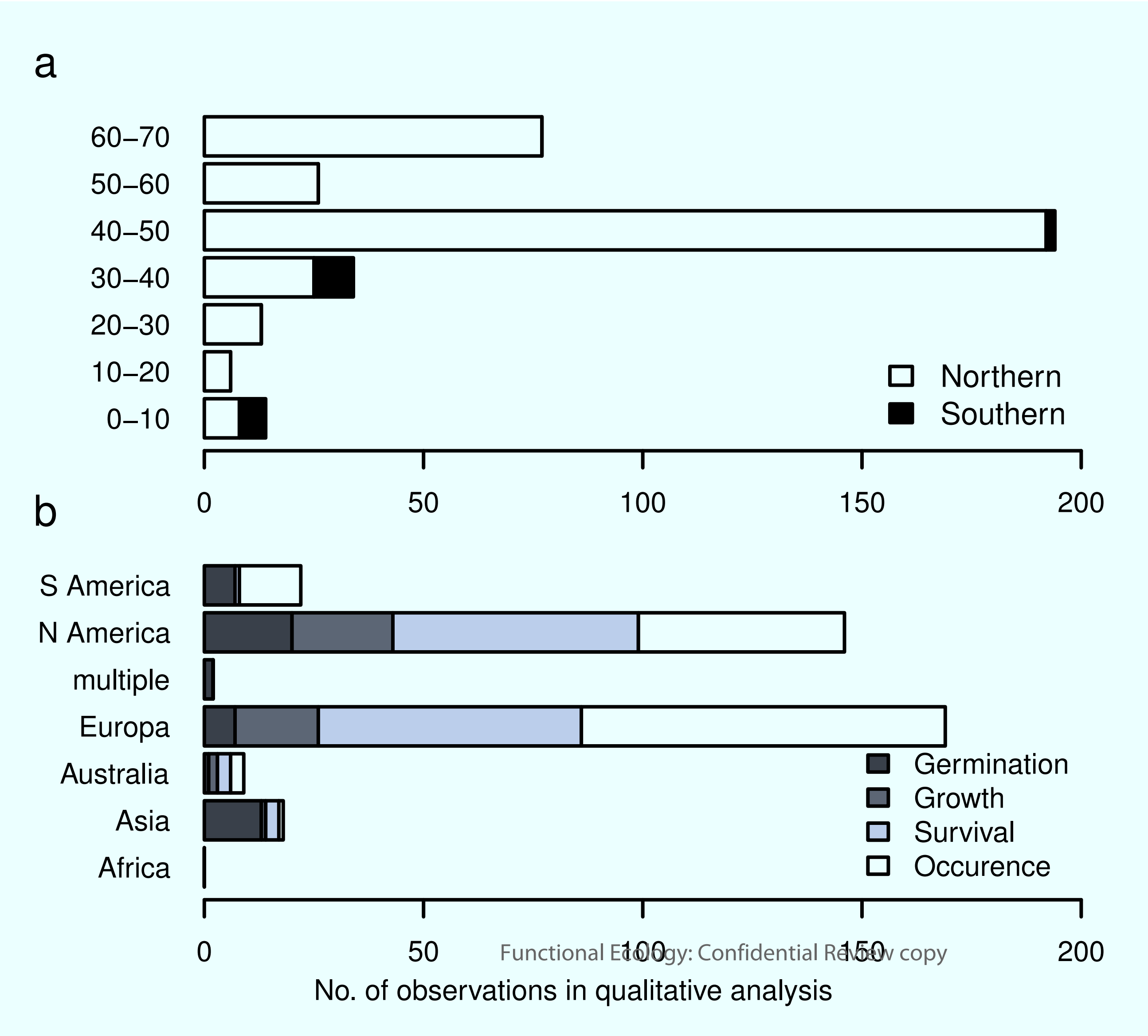
Table 1 Overview of number of observations from experimental studies were the effect of warming and other environmental factor was tested simultaneously. Relative strength of response indicate sum of observations where seedling responded less (<), equally (=) or more (>) to warming (W) than the other factor (OF). Number of significant interactions (INT) between W and the OF out of the number of observations where this was tested for are given and if the outcome of the interaction was positive (+), negative (–) or complex, i.e involving a third factor. NAs indicate where no test for interactions were performed. See Appendix S3 in Supporting Information for full table with direction of responses.

		Relative strength of response			
Seedling life trait	Factor compared with warming	W<OF	W=OF	W>OF	INT / # tested (outcome of INT)
Germination	Soil moisture	3	2	2	2/2 (+ and –)
	Dist. /herbivore excl.	3	1	0	3/3 (+ and –)
Growth	Soil moisture	0	4	0	4/4 (–
	Snow addition	0	10	0	0/10
	Fertilisation	1	1	0	1/2 (+)
	Vegetation (removal)	2	3	2	3/7 (+ and complex)
	Dist./herbivore excl.	1	1	1	NA
Survival	Soil moisture	3	4	1	1/7 (+)
	Snow addition	2	10	0	2/12 (–)
	Fertilisation	0	2	0	0/2
	Vegetation (removal)	0	9	4	0/13
	Dist. /herbivore excl.	1	1	0	NA

Fig 1 Distribution of observations from the alpine or Arctic treeline across latitude and hemisphere (northern: white, southern: black) averaged across studies on germination or seedling survival, growth or occurrence (a). Distribution of observations of tree seed germination or tree seedling survival, growth or occurrence across continents (b).

Fig 2 Effect size (mean Hedges' g ± 95% confidence interval; significance and sample size) across observations of the impact of environmental factors on germination or seedling survival or growth of tree seedlings at the alpine or Arctic treeline (a). Observe that a negative effect size indicates a positive effect of the treatment. Distribution of observations investigating effects of environmental factors on germination or seedling survival, growth or occurrence of tree seedlings at the alpine or Arctic treeline, and obtaining negative, neutral, positive or complex impacts of the investigated factor (b).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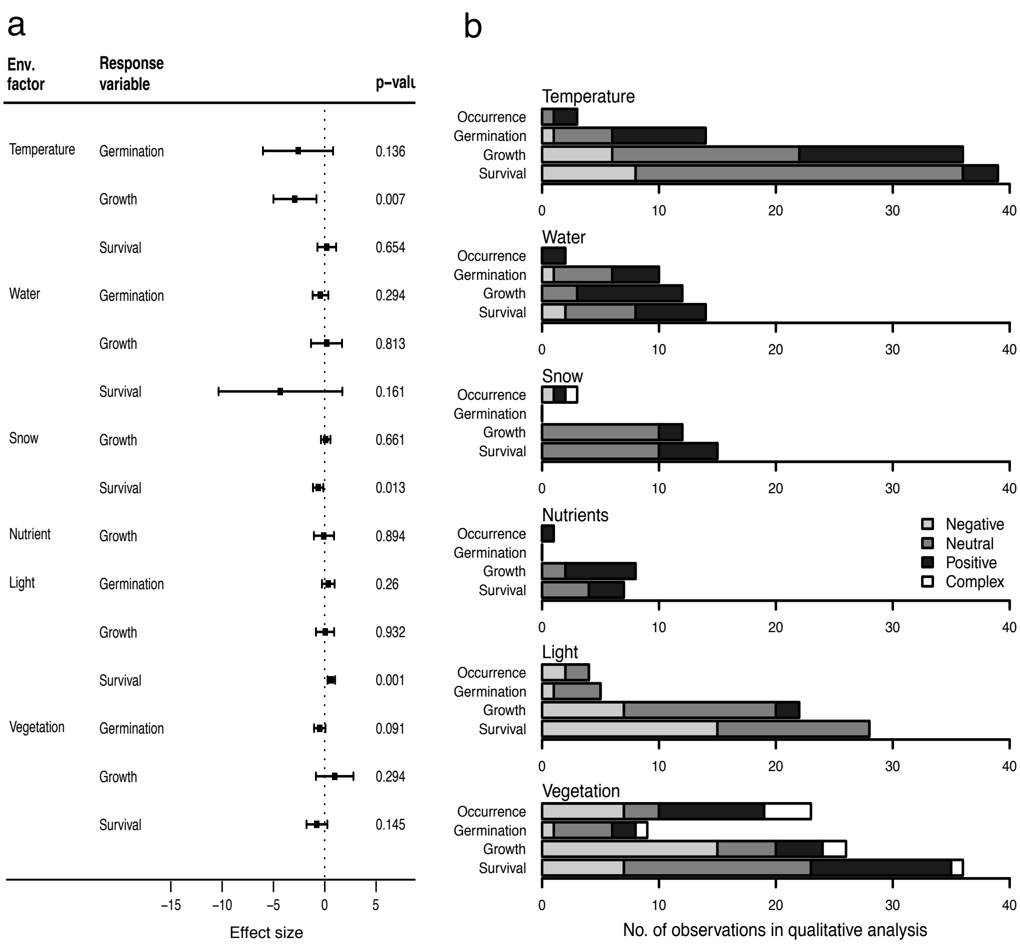
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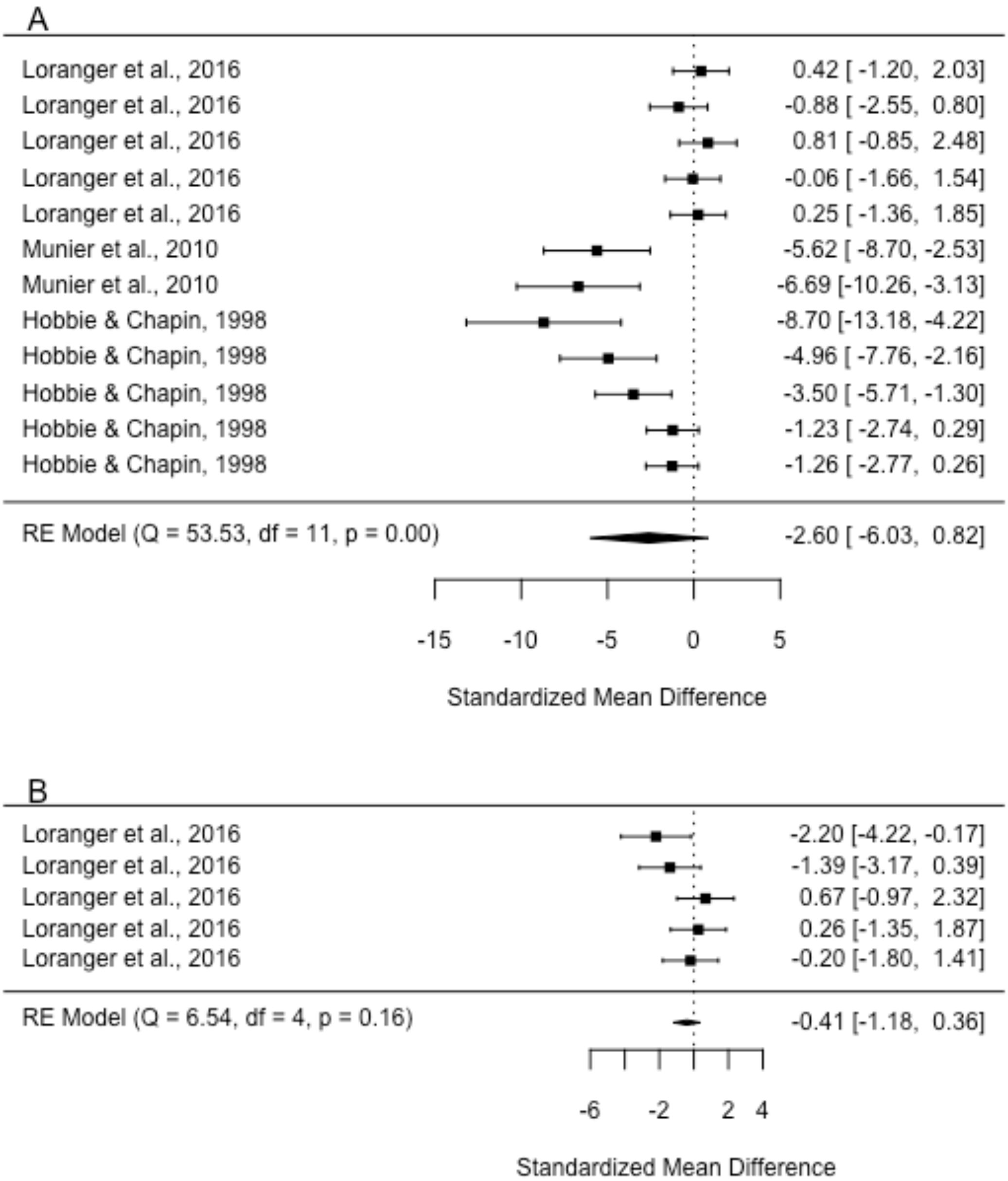
Functional Ecology

Appendix S1 Individual forest plots for each seedling life trait and response parameter combination



Global drivers of tree seedling establishment at alpine treelines in a changing climate

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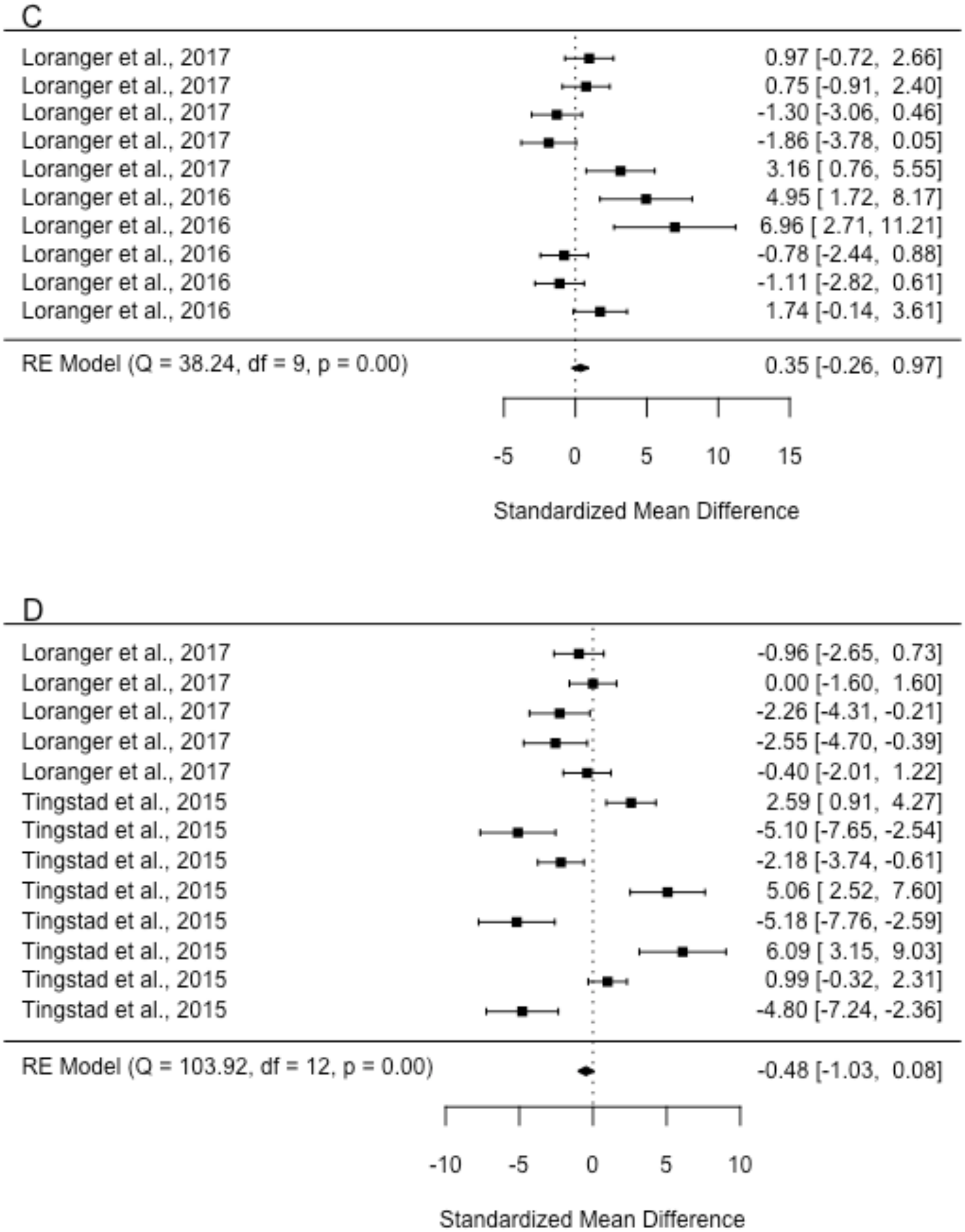
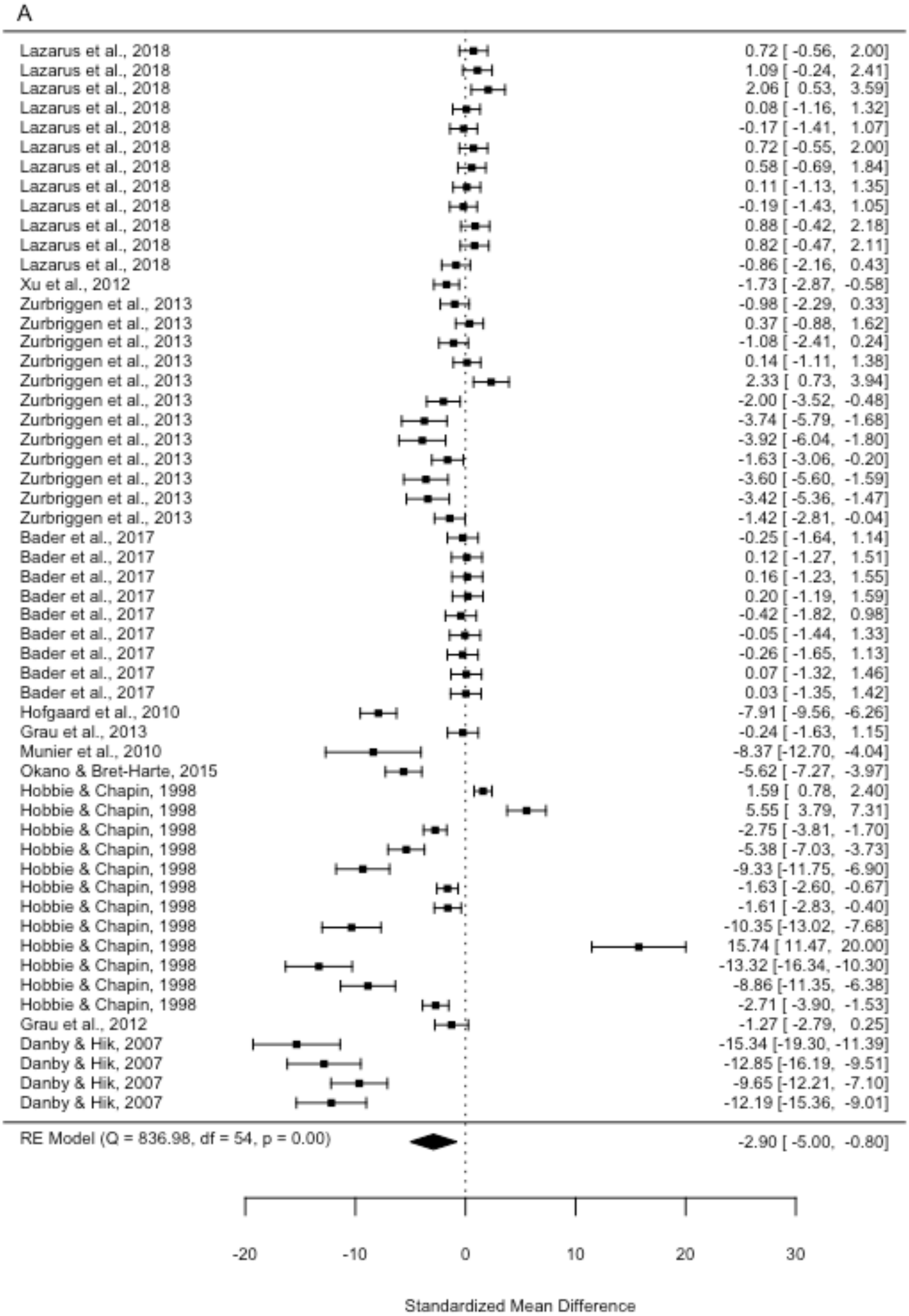
Functional Ecology



Forest plots for individual meta-analyses of environmental factor (A: temperature, B: water, C: Light and D: vegetation) effects on seed germination of tree seeds at the alpine or Arctic treeline. In brackets of each plot is the output of the test for heterogeneity (Q-test). Studies are ordered according to approximate latitude (10 degree intervals) with studies from lowest latitudes placed highest in the plot.

Functional Ecology



Global drivers of tree seedling establishment at alpine treelines in a changing climate

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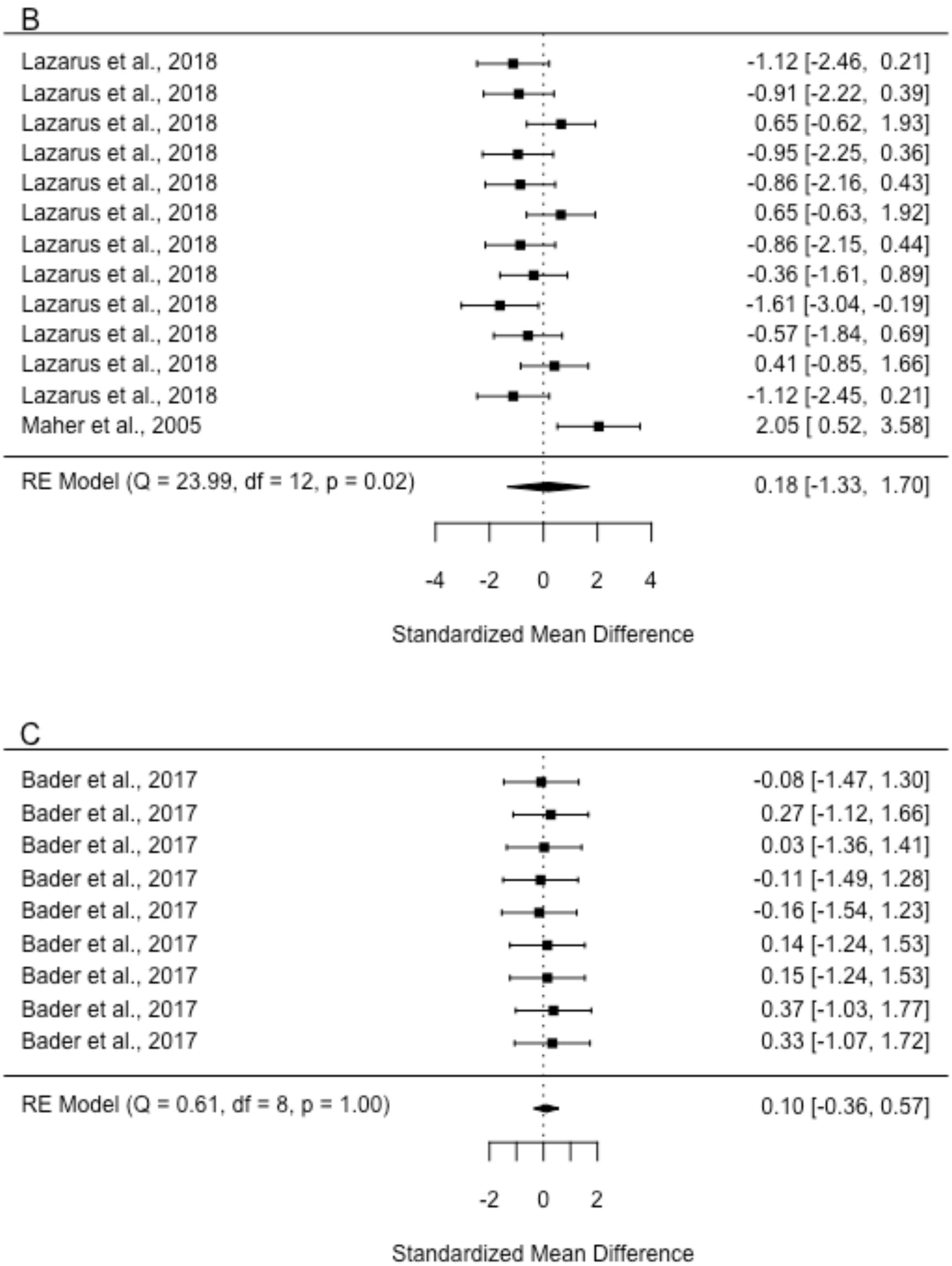

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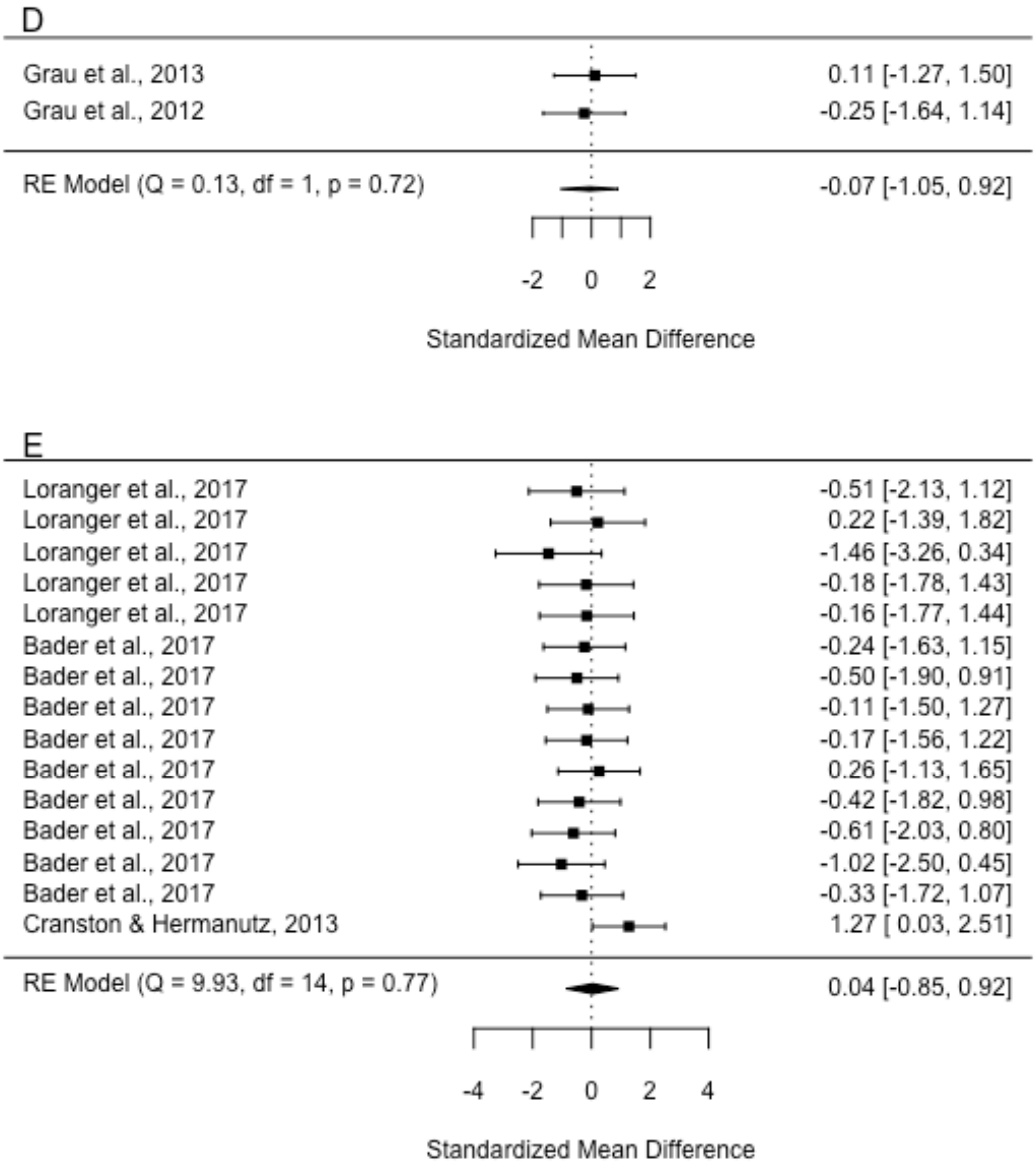

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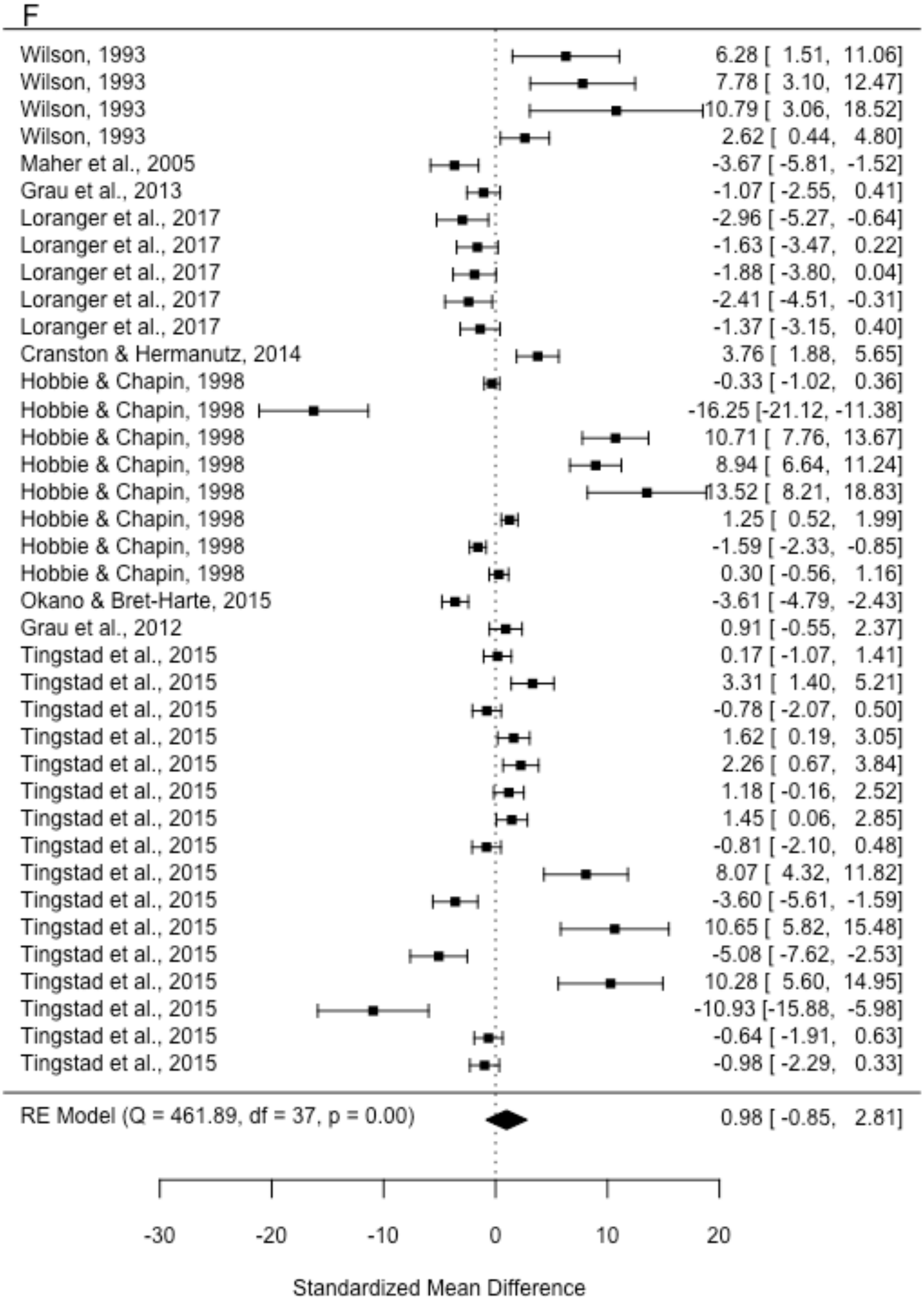

Forest plots for individual meta-analyses of environmental factor (A: temperature, B: water, C: Snow, D: Nutrient, E: Light and F: Vegetation) effects on tree seedling growth at the alpine or Arctic treeline. In brackets of each plot is the output of the test for heterogeneity (Q-test). Studies are ordered according to approximate latitude (10 degree intervals) with studies from lowest latitudes placed highest in the plot.

Global drivers of tree seedling establishment at alpine treelines in a changing climate

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Global drivers of tree seedling establishment at alpine treelines in a changing climate

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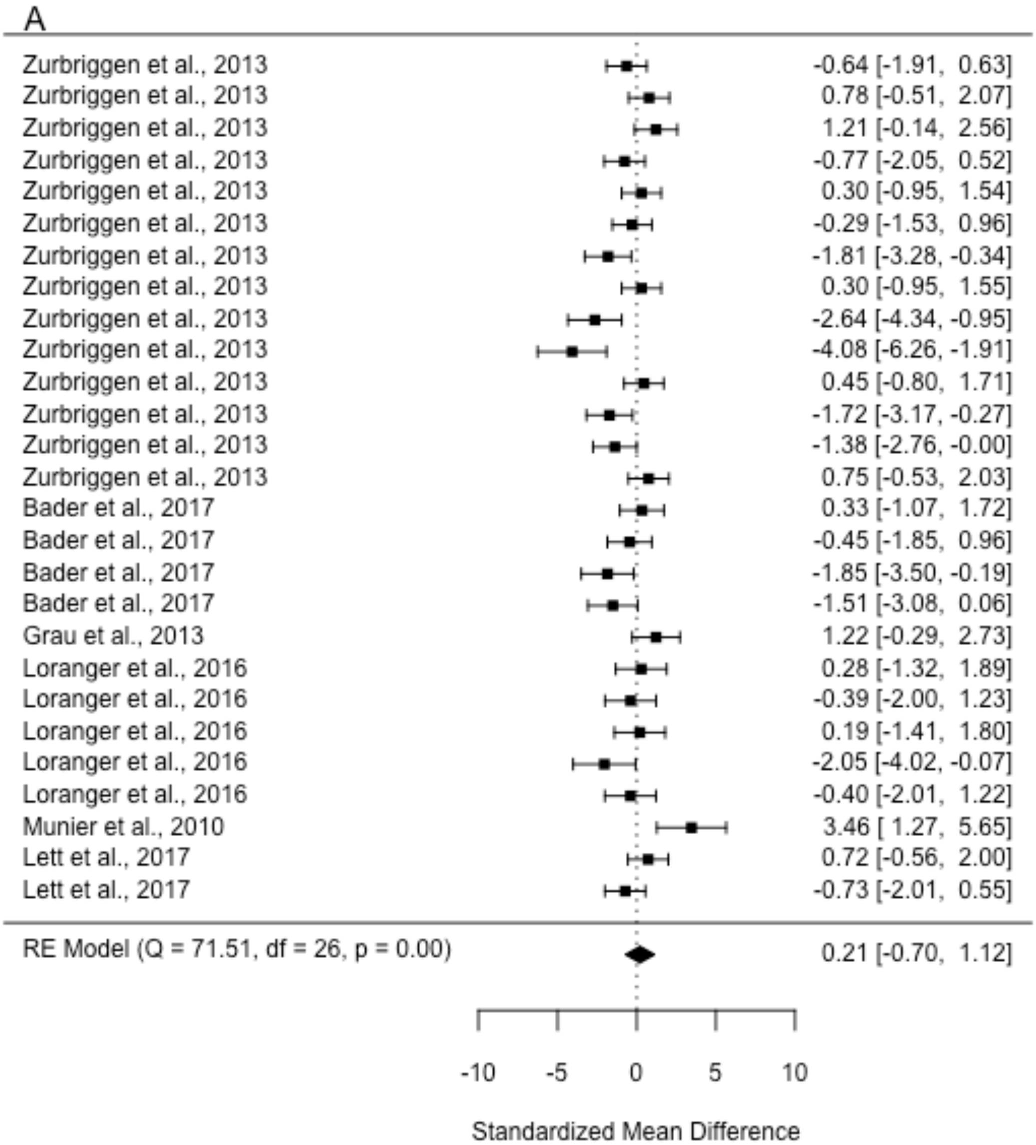
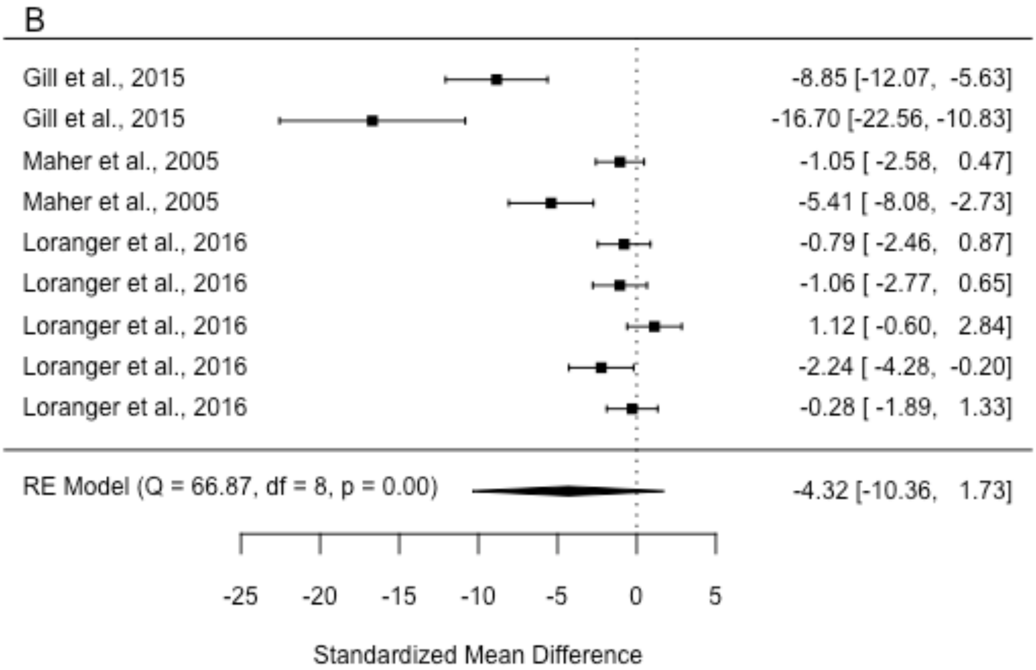
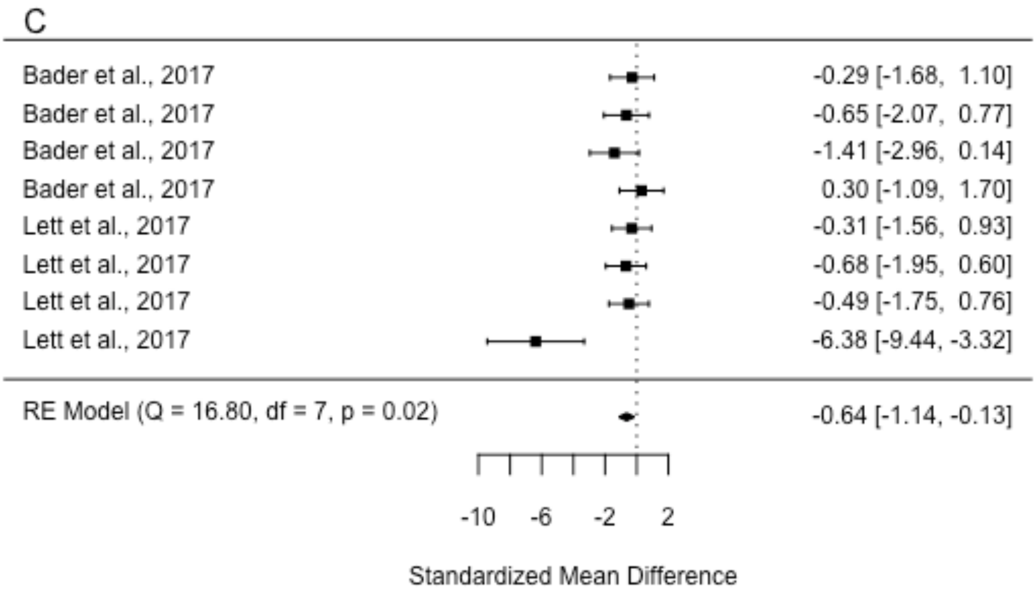


Global drivers of tree seedling establishment at alpine treelines in a changing climate

Lett S and Dorrepaal E





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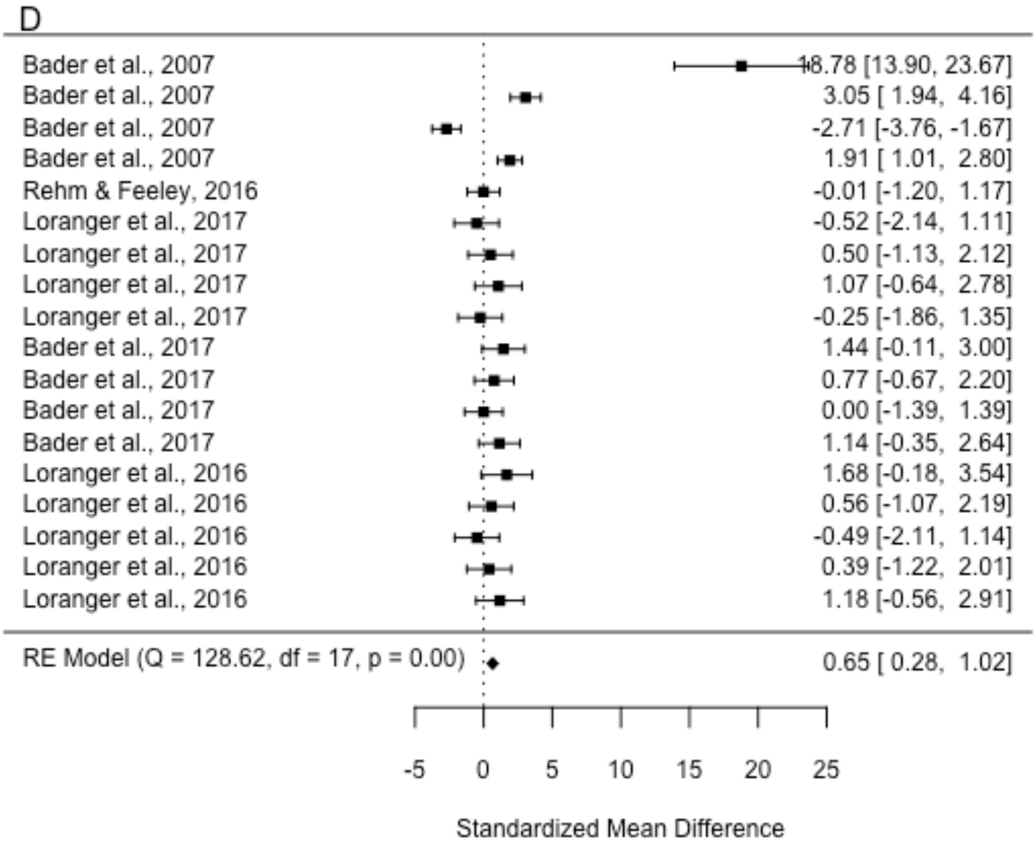

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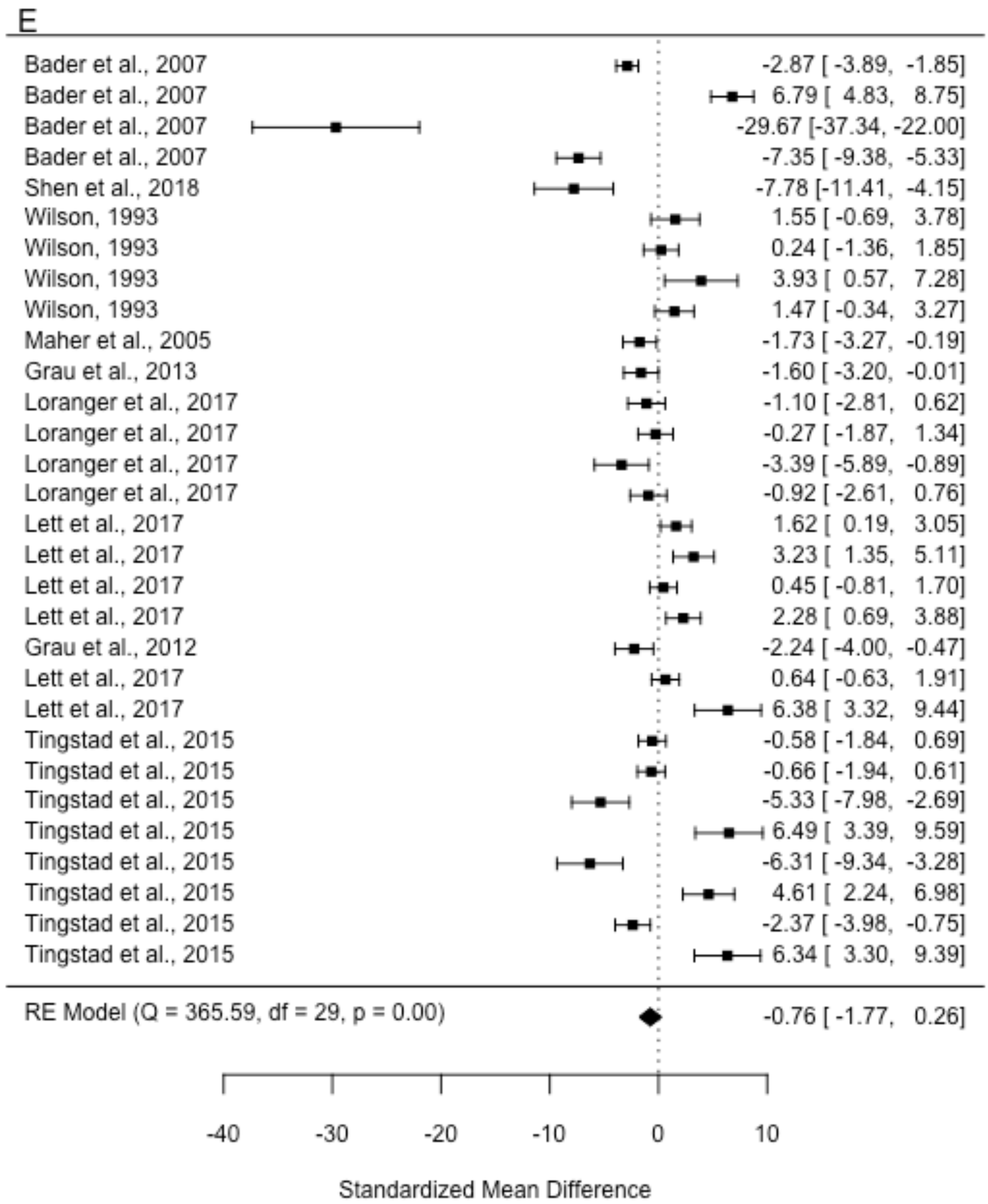

Forest plots for individual meta-analyses of environmental factor (A: temperature, B: water, C: Snow, D: Light and E: Vegetation) effects on tree seedling survival at the alpine or Arctic treeline. In brackets of each plot is the output of the test for heterogeneity (Q-test). Studies are ordered according to approximate latitude (10 degree intervals) with studies from lowest latitudes placed highest in the plot.

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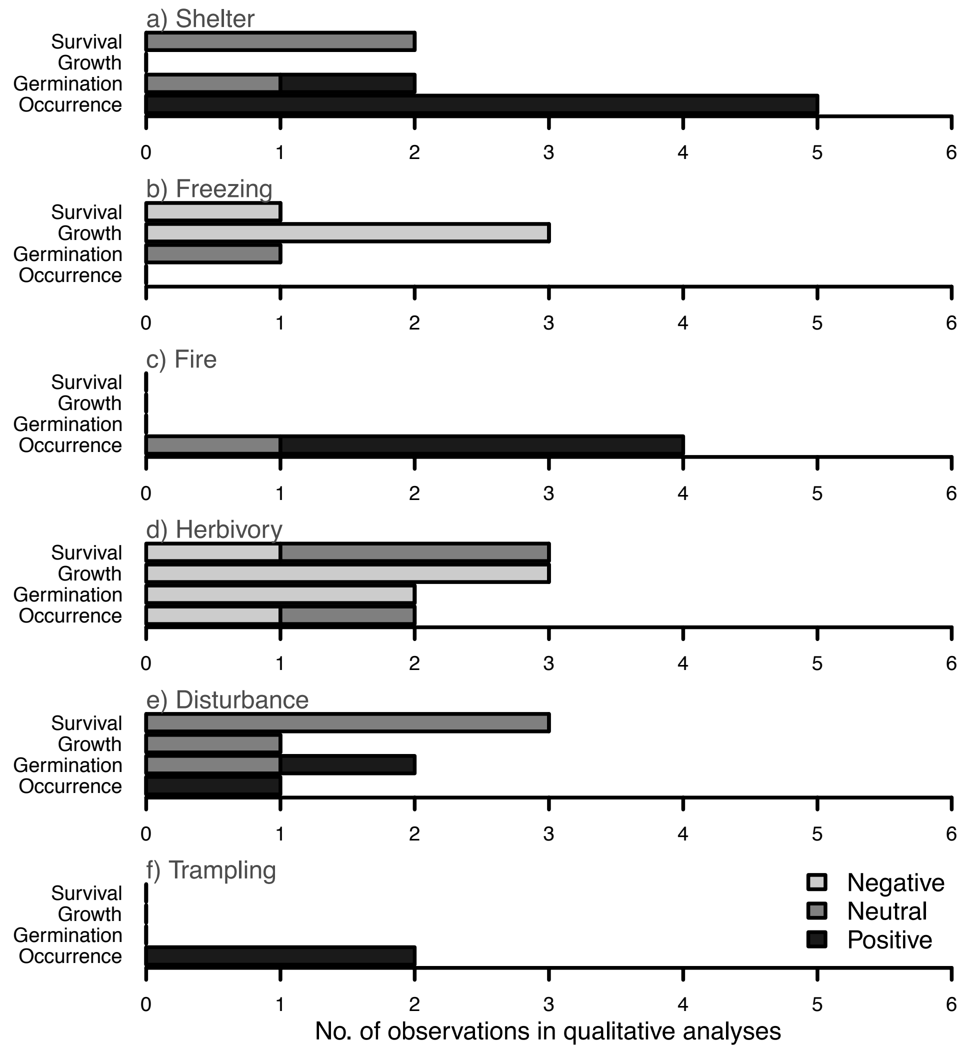
Appendix S2 Distribution of effects of "other factors"



Distribution of observations investigating effects of environmental factors on germination or seedling survival, growth or occurrence of tree seedlings at the alpine or arctic treeline, and obtaining negative, neutral, positive or complex impacts of the investigated factor.

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Appendix S3 Overview of relative effects and interactions between warming and other factors

Appendix S3 Overview of observations investigating the effect of warming and one other environmental factor on tree seed germination and tree seedling survival and growth at the alpine or Arctic treeline. It is indicated if the response of warming (W) and the other factor (OF) is positive (+), neutral (0) or negative (–) and if the warming response is larger (>), smaller (<) or the same (=) as that of the other factor. It is also shown if the two factors interact (Y) or not (N), if this was not tested (NA) and what the outcome of the interaction is.

Authors	Genus	Other factor	W	vs	OF	Interaction effects
Germination						
Munier et al. 2010	Picea	Disturbance (D)	+	=	+	Y: larger W effect with OF
Munier et al. 2010	Picea		+	<	+	NA
Munier et al. 2010	Picea	D + herbivore excl.	+	<	+	NA
Munier et al. 2010	Picea		+	<	+	Y: W effect decreases with OF
Loranger et al. 2016	Sorbus	Soil moisture	–	>	0	Y: OF effect decreases with W
Loranger et al. 2016	Pinus		0	<	–	Y: OF effect decreases with W
Kueppers et al. 2017	Pinus		0	=	0	N
Loranger et al. 2016	Picea		0	=	0	N
Kueppers et al. 2017	Picea		0	<	+	N
Loranger et al. 2016	Larix		0	<	+	N
Loranger et al. 2016	Pinus		+	>	+	Y: W effect increases with OF
Growth						
Munier et al. 2010	Picea	Disturbance (D)	+	>	0	NA
Munier et al. 2010	Picea	D + herbivore excl.	+	=	+	NA
Grau et al. 2013	Pinus	Fertilization	+	<	0	N
Grau et al. 2012	Betula		+	=	+	Y: Positive OF effect with W
Hofgaard et al. 2010	Betula	Herbivore exclusion	0	<	+	NA
Okano & Bret-Harte 2015	Picea	Neighbour removal	+	>	X	Y: OF positive with W and negative without
Grau et al. 2013	Pinus		+	=	–	Y: W response with OF
Grau et al. 2012	Betula		+	>	0	N
Hobbie & Chapin 1998	Populus		0	=	–	N
Hobbie & Chapin 1998	Populus		+	=	+	Y: VT(*) x W x OF (complex)
Hobbie & Chapin 1998	Picea		+	<	+	N
Hobbie & Chapin 1998	Betula		+	<	+	N
Hobbie & Chapin 1998	Alnus		+	na	+	NA
Bader et al. 2017	Larix	Snow addition	0	=	0	N
Bader et al. 2017	Picea		0	=	0	N
Bader et al. 2017	Pinus		0	=	0	N
Bader et al. 2017	Pinus		0	=	0	N
Bader et al. 2017	Sorbus		0	=	0	N
Bader et al. 2017	Larix		0	=	0	N
Bader et al. 2017	Picea		0	=	0	N
Bader et al. 2017	Pinus		0	=	0	N
Bader et al. 2017	Pinus		0	=	0	N
Bader et al. 2017	Sorbus		0	=	0	N
Lazarus et al. 2018	Pinus	Soil moisture	–	=	+	Y: OF removes W response
Lazarus et al. 2018	Picea		–	=	+	Y: OF removes W response
Lazarus et al. 2018	Pinus		0	=	+	Y: OF removes W response
Moyes et al. 2015	Pinus		+	=	+	Y: W induced water stress
Survival						
Munier et al. 2010	Picea	Disturbance (D)	0	=	0	NA
Munier et al. 2010	Picea	D + herbivore excl.	0	<	+	NA
Grau et al. 2012	Betula	Fertilisation	0	=	0	N
Grau et al. 2013	Pinus		0	=	0	N
Grau et al. 2012	Betula	Neighbour removal	0	=	0	N
Grau et al. 2013	Pinus		0	=	0	N
Lett et al. (in press)	Betula		0	=	0	N
Lett et al. (in press)	Pinus		0	=	0	N
Hobbie & Chapin 1998	Populus		–	>	0	N
Hobbie & Chapin 1998	Alnus		–	>	0	N
Hobbie & Chapin 1998	Picea		–	>	0	N
Hobbie & Chapin 1998	Betula		–	>	0	N
Hobbie & Chapin 1998	Populus		0	=	0	N
Lett et al. (in press)	Betula		0	=	0	N
Lett et al. (in press)	Pinus		0	=	0	N

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Lett et al. (in press)	Betula		0	=	0	N
Lett et al. (in press)	Pinus		0	=	0	N
Bader et al. 2017	Larix	Snow addition	0	=	0	N
Bader et al. 2017	Picea		0	=	0	N
Bader et al. 2017	Pinus		0	=	0	N
Bader et al. 2017	Pinus		0	=	0	N
Bader et al. 2017	Sorbus		0	=	0	N
Bader et al. 2017	Larix		0	=	0	N
Bader et al. 2017	Picea		0	=	0	N
Bader et al. 2017	Pinus		0	=	0	N
Bader et al. 2017	Pinus		0	=	0	N
Bader et al. 2017	Sorbus		0	=	0	N
Lett et al. (in press)	Betula		0	<	+	Y: W removes OF effect
Lett et al. (in press)	Pinus		0	<	+	Y: W removes OF effect
Loranger et al. 2016	Sorbus	Soil moisture	–	>	0	N
Kueppers et al. 2017	Picea		–	=	+	N
Kueppers et al. 2007	Pinus		0	<	–	N
Kueppers et al. 2017	Pinus		0	=	0	N
Loranger et al. 2016	Picea		0	=	0	Y: OF positive with W and negative without
Loranger et al. 2016	Pinus		0	=	0	N
Loranger et al. 2016	Larix		0	<	+	N
Moyes et al. 2013	Pinus		0	<	+	NA

* VT = vegetation type.