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Vital rates in early life history underlie shifts in biotic interactions along bioclimatic gradients: An experimental test of the Stress Gradient Hypothesis

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Abstract

Question: The Stress Gradient Hypothesis (SGH) predicts that competition and facilitation shift along stress gradients. We ask if the underlying mechanisms operate at specific points in plant life history, and if patterns are consistent along different stress gradients.

Location: Boreal, sub-alpine and alpine grasslands in southern Norway.

Methods: We test the SGH through ontogeny along stress gradients by monitoring seedlings in intact vegetation vs bare-ground gaps across a climatic grid of temperature and precipitation gradients. We follow one seedling cohort over two years and quantify four vital rates; emergence, survival, establishment success, and growth rate, to determine if biotic interaction effects (intact vs removed vegetation) on each of these stages shift along gradients in accordance with the SGH.

Results: We find competitive effects early in ontogeny, reflected in increased probability of seedling emergence in gaps. The magnitude of competition increases with temperature and precipitation, in line with the SGH. Growth rate of alpine seedlings was higher in intact vegetation vs gaps, indicating facilitation, and in accordance with the SGH, these effects decreased towards warmer climates. The net outcome of these processes occurring in early life history are reflected in the seedling community, where richness of emerging and surviving species is higher in bare-ground gaps than in intact vegetation, with increasing effect toward warmer but not toward wetter sites.

Conclusion: Our results support the SGH for the earliest stages in plant life, predicting shifts from competitive to neutral or facilitative interactions toward colder climates. The biotic interaction effects on vital rates vary over ontogeny, with competition dominating for emergence whereas facilitation was more evident for seedling growth. The patterns along the precipitation gradient indicate stress at both the dry and the wet end. We highlight the importance of studies across ontogeny and along different gradients to disentangle the mechanisms underlying the SGH.

1 | INTRODUCTION

Understanding how the role, strength, and even direction of biotic interactions may change along environmental stress gradients is crucial for understanding plant species and community responses to environmental change (Brooker et al. 2008). The Stress Gradient Hypothesis, which predicts a shift from competitive to facilitative interactions along gradients from relatively benign to environmentally stressful environments (SGH; Bertness and Callaway 1994), is broadly confirmed (Brooker et al. 2008; He et al. 2013; Michalet et al., 2014a,2014b; but see Maestre et al. 2005). While most of these studies focus on a single life-history stage, other studies show that the role of facilitation and competition may also change over the plant life history (i.e., affecting different vital rates; Gurevitch, 1986; De Steven 1991; Goldberg et al. 2001; Schiffers & Tielbörger, 2006; Valiente-Banuet & Verd, 2008; Bullock, 2009). Survival, for example, has been found to be more likely to be facilitated than emergence or growth (Goldberg et al. 1999; Howard & Goldberg, 2001; He et al. 2013), and establishment has been suggested to be more vulnerable to competition than seedling emergence (Olsen & Klanderud, 2013).

However, it is not clear to what extent these shifts in interaction effects between different life-history stages and processes reflect and contribute to the broader-scale community-level patterns described by the SGH. In this study, we ask how the magnitude and direction of interactions changes across productivity/stress gradients for multiple stages of plant life history. In addition, as called for by Brooker et al. (2008), we assess robustness of these patterns within a single system by examining the entire community rather than one or a few selected species, and by comparing responses to plant–plant interactions across multiple sites spanning different types of stress gradients. Whether the stress factor is non-resource-related, such as temperature or wind, or resource-related, such as water or nutrients, may affect plant interactions and how they shift between competition and facilitation along the gradients (Kawai & Tokeshi, 2007; Maestre et al. 2009).

To address these questions, we use removal experiments to examine the effects of biotic interactions from the mature vegetation on a key demographic process, recruitment from seed, at the community level, and we replicate these experiment across orthogonal gradients of temperature and precipitation. Removal experiments are the standard approach for revealing plant–plant interactions (Díaz et al. 2003), and our experimental design consisted of intact alpine grassland vegetation and experimentally created gaps where all vegetation, i.e., all potential competitors or facilitators, was removed. To resolve variation in interaction effects over the ontogeny, we followed a seedling cohort over a two-year period by individually marking each seedling, and registering and measuring their size over time. This allowed us to assess their progression through three life

stages and calculate three vital rates and growth rates during seedling establishment. To examine if such biotic interaction effects on seedling recruitment change consistently along bioclimatic gradients, we replicated the experimental design across twelve sites that differ systematically in productivity and environmental stress because they are laid out in a systematic "climatic grid" across broad-scale temperature and precipitation gradients (Klanderud et al. 2015).

The resulting detailed individual-level performance data from manipulative experiments replicated across regional-scale stress gradients provide a powerful test of the SGH over the plant ontogeny and along multiple stress gradients. In our study region in southern Norway, precipitation increases from the continental inner fjords to the oceanic west (Hanssen-Bauer et al. 2003), whereas temperature increases from high to low elevations (Tveito & Førland, 1999). Thus, environmental stress increases towards colder alpine sites, and we therefore predict that (a) more seedlings will recruit in vegetation removal plots than in intact vegetation in the most productive and climatically benign warm sites, while the reverse effect will occur in the least productive and climatically harshest cold sites. (b) The strength of this pattern will differ throughout ontogeny; survival will be facilitated (i.e., respond negatively to vegetation removal) to a greater degree than either emergence or growth. Along the precipitation gradient, environmental stress is typically predicted to increase toward drier eastern sites, as water is a limiting resource for plant growth in most systems (e.g., Maestre et al. 2005). However, our study is conducted in an oceanic region where the wetter sites receive very high precipitation (>2,000 mm/yr), and in such very wet systems, precipitation can be a source of environmental stress such as water-logged soils and large amounts of snow resulting in late snowmelt and a shorter growing season (Tingstad et al. 2015; Klanderud et al. 2016). We therefore predict that (c) the patterns along the precipitation gradients will be more complex, as both the dry and the wet end may be stressful for plants.

2 | METHODS

2.1 | Study sites

The study area extended from the continental east to the oceanic west and from the alpine to the lowlands in the fjord landscapes of southern Norway. In this region, twelve sites were selected on a climatic grid where three levels of mean summer temperature (7.5°C [alpine], 9.5°C [sub-alpine], 11.5°C [boreal]) were replicated along four levels of annual precipitation (~600 mm [level 1], ~1,200 mm [level 2], ~2,000 mm [level 3], ~2,700 mm [level 4]) with all other environmental factors held as constant as possible (Appendix S1; see also Klanderud et al. 2015). The climate data were interpolated

with 100-m resolution (see Tveito et al. 2000, 2005 for methods description) from the normal period 1961–1990 (met.no, 2009). All sites were southwest-exposed with slopes of approximately 20 degrees, with one exception (alpine 2, which was exposed to the east). The interpolated temperatures correlated with on-site temperature measurements in 2009 and 2010 (Pearson correlation > 0.93, $n = 12$; Meineri et al. 2013) and the climate grid shaped by the sites remained similar when based on 2009–2013 gridded data (Vandvik et al. 2020). The study sites are moderately grazed intermediate-rich grasslands associated with phyllite or other calcium-rich bedrock (see Klanderud et al. 2015 for more details).

2.2 | Seedling recruitment experiment

At each site, we placed four replicate blocks in homogenous grassland vegetation. In June 2009, two 25 cm × 25 cm plots were placed within each of the blocks, one in intact vegetation and one where we removed all below- and above-ground vegetation to create a bare-ground gap. We used a 4-mm mesh sieve to separate soil and plant remains, thereby keeping soils and soil seed banks in situ while removing the roots. We recorded seedling emergence (the 2009 cohort) in all intact and vegetation removal plots (96 in total) in the climate grid in August 2009. Each emerging seedling was id-tagged using a numbered plastic toothpick and assigned a spatial coordinate using a 5 cm × 5 cm subplot grid overlain on each plot. Marked seedlings were classified into forbs, graminoids, and woody species, and identified to species level when possible. Survival and establishment of the cohort of seedlings were monitored over three years (2010–2012), in spring (early June, recording winter survival from the previous autumn census) and in early autumn (late August, recording summer survival from the spring census). A total of 2,946 seedlings were marked in August 2009; of these, 77% were forbs, 23% graminoids and 0.2% woody seedlings. Of the marked seedlings, 64% were identified to at least genus level and 55% to species level (64% of the forbs, 23% of the graminoids and 100% of the woody seedlings) during the course of the study. Nomenclature follows Lid and Lid (2007).

2.3 | Seed rain data

To enable calculation of seedling emergence rates, we collected seed rain at each site during winter (September 2009 to June 2010) and summer (June 2010 to September 2010) seed deposition. We trapped seeds using a 25 cm × 25 cm artificial turf mat placed in a vegetation gap in each of four blocks at each site, for a total of 48 seed traps across all sites. Seeds were extracted from the turfs by flushing them with water over 500 and 125 μm diameter sieves to discriminate seeds by size and remove debris, and seeds were counted and identified taxonomically using a stereomicroscope. We included fruits, bulbils (e.g., *Bistorta vivipara*) and viviparous seeds (e.g., *Festuca vivipara*), but not spores (e.g., *Polytrichum* spp.). For

additional details about seed rain data, see Boixaderas (2012) and Guittar et al. (2020).

2.4 | Calculation of vital rates and growth rate proxies

We estimated three vital rates between emergence and establishment of seedlings: emergence rate, survival rate to 15 months, and rate of establishment as juveniles; each calculated at the plot level. Emergence rate was calculated as the probability of a seed germinating from the seed rain and emerging as a visible seedling above the soil surface (number of emerged seedlings/ number of seeds recorded in the seed rain). Survival rate was calculated as the probability of surviving at least 15 months (number of surviving seedlings/ number of emerged seedlings). We considered a seedling to have established when it had at least two fully grown leaves or leaf pairs and plant height >2 cm. Establishment rate was calculated as the probability of a seedling surviving from the emergence stage (see above) to the establishment stage (number of established seedlings/number of surviving seedlings). Because we defined the establishment phase based on size, we also use the time for a seedling to reach this stage as a proxy of growth rate.

Some of these data are reported elsewhere to ask questions comparing particular groups of species rather than community totals. Klanderud et al. (2016) compared the raw numbers of emerging seedlings in removal vs intact vegetation plots between alpine, boreal, and generalist species across the grid. Guittar et al. (2020) used data from the removal plots in combination with a number of other data sets to compare performance of locally persistent vs locally transient species across the grid.

2.5 | Statistical analysis

First, we used logistic generalized linear mixed-effects models (GLMM with binomial error distribution) to test the effects of biotic interactions (vegetation removal) on the three vital rates along temperature and precipitation gradients. Vegetation removal, temperature, and precipitation were used as fixed explanatory variables. Intercepts were set as intact vegetation plots, alpine temperatures, and the driest precipitation level. Significant positive interactions between vegetation removal and either temperature and/or precipitation would be consistent with the SGH; i.e., less competitive (or more facilitative) effects in more stressful habitats.

To explore whether climate influences growth rate (indicated by the time to achieve establishment after emergence), we analysed whether the association between probability of establishment and time (in months since the first census) differed between intact vegetation and vegetation removal plots for each temperature and precipitation level. For these analyses, we used a logistic GLMM (binomial distribution) including establishment probability as response variable, and time (sampling date), treatment (intact vs removed

vegetation plots), temperature, precipitation and interactions among these variables (up to three ways) as explanatory variables. In these models, interactions between time and other explanatory variables indicate that the time to establish as a juvenile shifts as a function of the interacting variable (treatment, temperature or precipitation). An autoregressive error structure of order 1 (AR1) was used for the residuals to account for temporal auto-correlation.

To assess the overall consequences of trends in the vital rates and growth rates for the seedling community, we tested the effects of biotic interactions (vegetation removal) on the abundance and species richness of seedlings at each stage (emergents, survivors to 15 months, established juveniles) along temperature and precipitation gradients using log-linear GLMM (with Poisson error distribution). This analysis indirectly takes into consideration climatic effects on previous life stages because the number of seedlings reaching a specific life stage is directly impacted by the number of seedlings that have reached the previous life stage, which may have been impacted by climate. To visualize the effects of vegetation removal, we calculated the effect of biotic interactions on abundances and richness as (ln [intact/removal]) for seedling emergence, 15-month survival, and establishment within each block, and plotted site means across the temperature and precipitation gradients. Because of multiple zeros in the data set, we added 1 to each of the values for abundance and richness before calculation of these effect sizes. This approach is not appropriate for vital rates, so we do not visualize effect sizes for these.

In all models, blocks nested within sites were included as random factors. A backward stepwise selection based on Maximum Likelihood tests was applied to all models (significance level = 0.1). The data were analysed in the software package R version 3.4.0 (21 Apr 2017; R Foundation for Statistical Computing, Vienna, Austria). We used the libraries *lmerTest* (Kuznetsova et al. 2017) to

fit models on the different vital rates, the library *MASS* (Venables & Ripley, 2002) to fit the model on growth rate (including temporal auto-correlation). R^2 and partial R^2 were extracted using the library *r2glmm* (Edwards et al. 2008; Jaeger, 2017). Note that partial R^2 may not be reliable for single-term effects involved in interaction terms because they are computed in the absence of the interaction. Furthermore, R^2 was not calculated for growth rates due to the high complexity of the model (penalized quasi-likelihood mixed-effect model including three-way interaction and time correlation structure).

3 | RESULTS

Emergence rate increased in the vegetation removal plots (partial $R^2 = 0.55$), and this effect increased with increasing temperature and precipitation (Table 1). Specifically, in intact vegetation, the rate of emergence was relatively low across all climates, and declined with increasing temperature, ranging from an average of 4.9% emerging seedlings per plot in alpine sites to 2.4% emerging seedlings in the boreal (significant temperature effect in Table 1, Figure 1). In contrast, in plots were vegetation was removed, the rate of emergence was overall higher, and sharply increased toward warmer climates, from 8.7% in the alpine to 23.3% in the boreal sites (significant positive $R \times T$ effect in Table 1, Figure 1, partial $R^2 = 0.26$). The consequence of these two opposing trends with temperature is that the magnitude of removal effects is smallest in the alpine and increases with temperature, consistent with the SGH.

In contrast, vegetation removal did not significantly affect survival rate, although a positive tendency suggested competitive release independent of climate ($p < 0.1$; Table 1, Figure 1). Precipitation alone, on the other hand, had a significant negative main effect on

TABLE 1 Coefficients of selected generalized linear mixed-effects models (GLMMs) testing the effect of removal of vegetation, temperature (°C), and precipitation (100 mm) on the vital rates of seedling emergence, survival to 15 months (two growing seasons) and establishment (seedling reaching >2 cm and more than two pairs of adult leaves), and on the number of seedlings within each of these stages

	Vital rates			Number of seedlings		
	Emergence	Survival	Establishment	Emergence	Survival	Establishment
Variables	$n = 78$	$n = 73$	$n = 56$	$n = 78$	$n = 73$	$n = 73$
Intercept	−3.863***	−0.046	1.776**	1.526***	0.752***	−0.568+
Removal	2.025***	0.314+	0.445	1.799***	1.893***	2.532***
Temperature	−0.261**	-	1.419***	−0.098	−0.118	0.185
Precipitation	−0.072***	−0.029*	-	−0.059**	−0.051**	−0.105*
$R \times T$	0.594***	-	−0.778*	0.523***	0.519***	0.269+
$R \times P$	0.037***	-	-	0.035**		0.064*

Abbreviations: P, Precipitation; R, Removal; T, Temperature.

Plots with no survival or establishment were not included in analyses of survival and establishment, respectively. *N* is the number of observations entered in the model. '-' indicates variable factored out during stepwise backward selection. See full tables in Appendices S2 and S3.

+$p < 0.1$.

*$p < 0.05$.

**$p < 0.01$.

***$p < 0.001$.

FIGURE 1 Vital rates recorded at the 12 alpine, sub-alpine, and boreal sites replicated along a precipitation gradient from dry (1) to wet (4) climates. Rates of seedling emergence (a), survival until the end of the second growing season (b), and establishment (c), given as means per 25 cm × 25 cm plot + *SE*, assuming a binomial error distribution. 0 means a vital rate of 0 (e.g., 0% survived out of the emerged seedlings or 0% established out of surviving seedlings), NA: no data (0 individuals reached the previous and the current life stage)
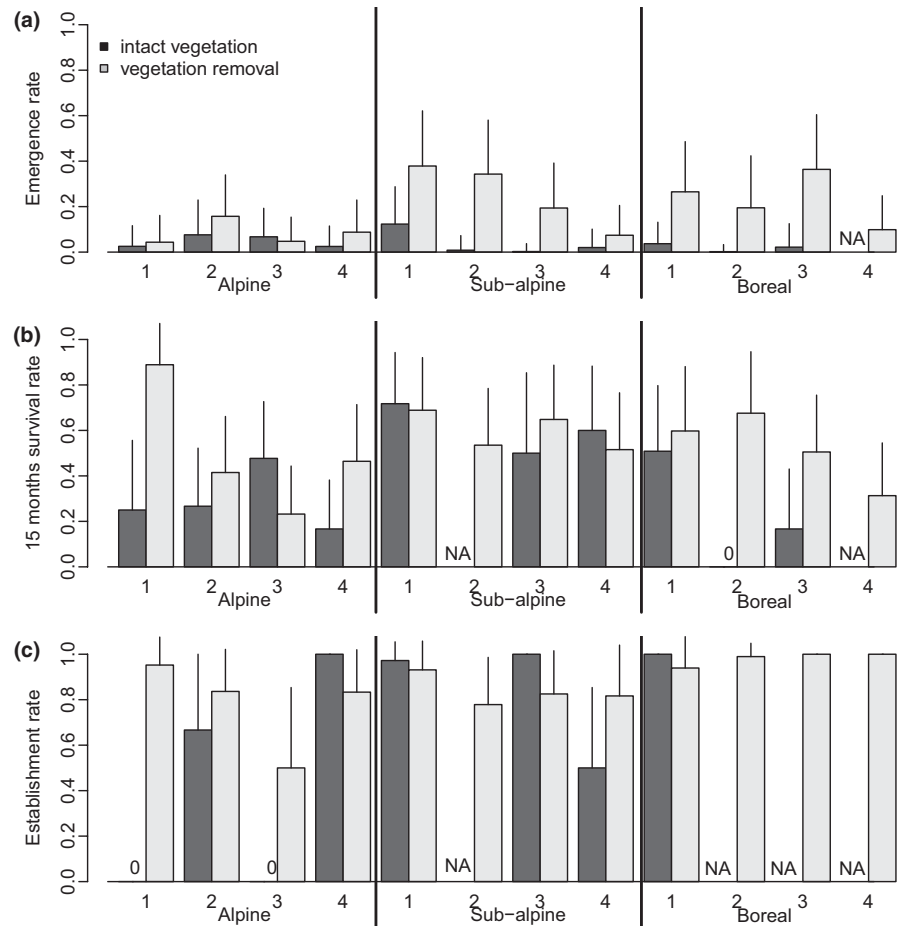

TABLE 2 Coefficients of selected generalized linear mixed-effects models (GLMMs) testing the effect of time, removal of vegetation, temperature (°C), and precipitation (100 m) on probability of establishment (a proxy for growth rate)

Explanatory variables	Coeff	Std Err	DF	T value	p value
Intercept	−4.64	1.22	254	−3.791	<0.001
Time	0.331	0.082	254	4.065	<0.001
Removal	1.470	1.302	254	−1.128	0.260
Temperature	−0.143	0.300	9	−0.476	0.646
Precipitation	−0.041	0.019	9	−2.216	0.053
Time × R	0.080	0.087	254	0.912	0.362
Time × T	0.305	0.029	254	1.064	0.288
Time × P	-	-	-	-	-
Time × R × T	0.048*	0.024	254	2.006	0.046
Time × R × P	-	-	-	-	-

Note: Abbreviations: P, Precipitation; R, Removal; T, Temperature.

*$p < 0.05$.

n= 300 (number of observations entered in the model); '-' indicates variable was factored out during stepwise backward selection; Coeff, model coefficients; Std Err, standard error of coefficient; DF, degrees of freedom.

survival, which decreased at higher precipitation (Table 1, Figure 1; partial $R^2 = 0.09$). Establishment rate generally increased with temperature (Table 1, Figure 1; partial $R^2 = 0.25$). In addition, there was an effect of vegetation removal depending on temperature, although in opposite ways from seedling emergence. Vegetation appeared to have competitive effects on establishment rate in the alpine sites (Figure 1), and a negative interaction with temperature indicating that removal effects become negative, suggesting facilitation, with increasing temperature, which is inconsistent with the prediction of the SGH (Table 1, Figure 1; partial $R^2 = 0.09$). Because only four

intact vegetation plots had any seedlings in the boreal that could have established, we redid the analyses for establishment without the boreal and found that this significant interaction effect remained (result not shown).

Vegetation removal also affected growth rate, with different responses in alpine, sub-alpine and boreal sites (three-way interaction between time, removal and temperature; Table 2). In the coldest alpine sites, seedlings reached the established plant stage about ten months faster in the intact plots than in plots where the vegetation was removed, suggesting facilitation from the neighboring vegetation (Figure 2). In contrast, growth rate was similar in intact vegetation and where vegetation was removed in the sub-alpine and boreal sites (Figure 2). Growth rate also appeared to slow down in wetter conditions, although there was no interaction with the removal treatment (negative precipitation effect in Table 2, Appendix S2).

The consequences of the strong but variable competitive effects of vegetation on emergence are reflected in the seedling community across all three life stages, with a higher number of seedlings or juveniles in plots where vegetation has been removed compared to intact vegetation, especially in warm sites (Table 1, Figure 3, Appendices S3 and S4). Similarly, the trends for interactions between removal and temperature in emergence rate (Figure 1) drive the trends in abundance across all three stages (Table 1, Figure 3, Appendices S3 and S4). While competitive effects on abundances are stronger in the warmer boreal sites, vegetation effects in the colder alpine are also largely competitive, with only one site (precipitation level 3) having small facilitative effects on abundance. Although removal does significantly interact with precipitation for two of the stages, the effect sizes are quite small (partial R^2 0.04 and 0.06 for number of emerged and established seedlings, respectively). No obvious trends are visible in removal effects with precipitation, although negative responses (competitive effects) seem to be most pronounced at intermediate precipitation levels in sub-alpine and boreal sites (Figure 3). Species richness of the seedling community shows largely similar patterns to those for seedling abundance at all three stages (Appendices S5–S7).

4 | DISCUSSION

Our study of seedling recruitment in alpine and boreal grasslands show that biotic interaction effects can change both along bioclimatic gradients and through the early stages of plant ontogeny. Our results illustrate how biotic interactions may operate through different vital rates during the early plant life history, shifting from more competitive effects on seedling emergence and survival early on, to less negative or even facilitative effects on establishment and growth as the seedlings age. While only two out of four vital rates consistently supported the specific predictions of the SGH, these produce a net community-level outcome in support of the SGH, and our findings are also in line with our prediction that biotic interaction effects may change through early ontogeny.
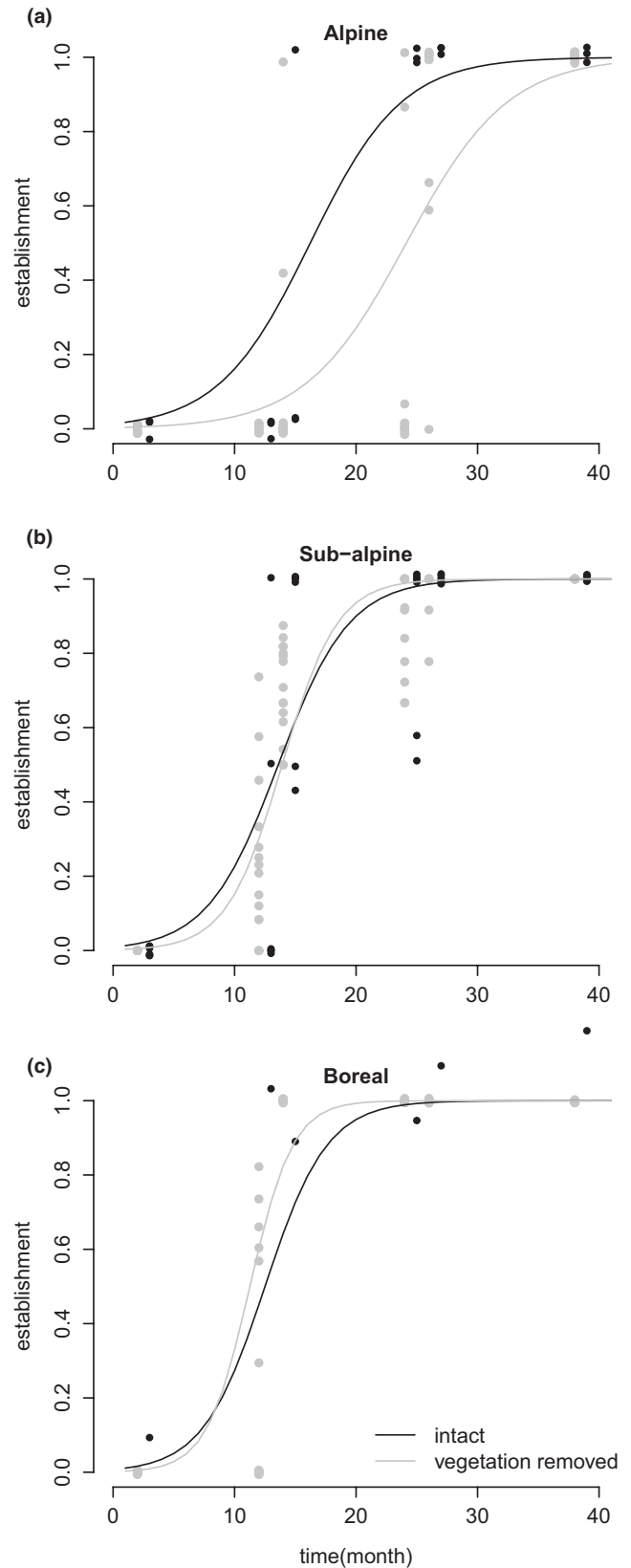

FIGURE 2 Seedling growth rate (expressed as time from emergence to establishment to the juvenile stage) in intact vegetation and in plots where the vegetation was removed in alpine (a), sub-alpine (b), and boreal (c) sites

FIGURE 3 Difference in seedling abundance between intact vegetation (control) and plots where vegetation was removed (gap) at the 12 alpine, sub-alpine and boreal sites replicated along a precipitation gradient from dry (1) to wet (4). (a) Number of emerging seedlings recorded in August 2009; (b) seedlings surviving for at least two growing seasons (15 months); and (c) number of seedlings successfully establishing to juveniles. All entries are means per plot ± *SE*, assuming a Poisson error distribution. Bars above the zero line indicate facilitation, bars below indicate competition
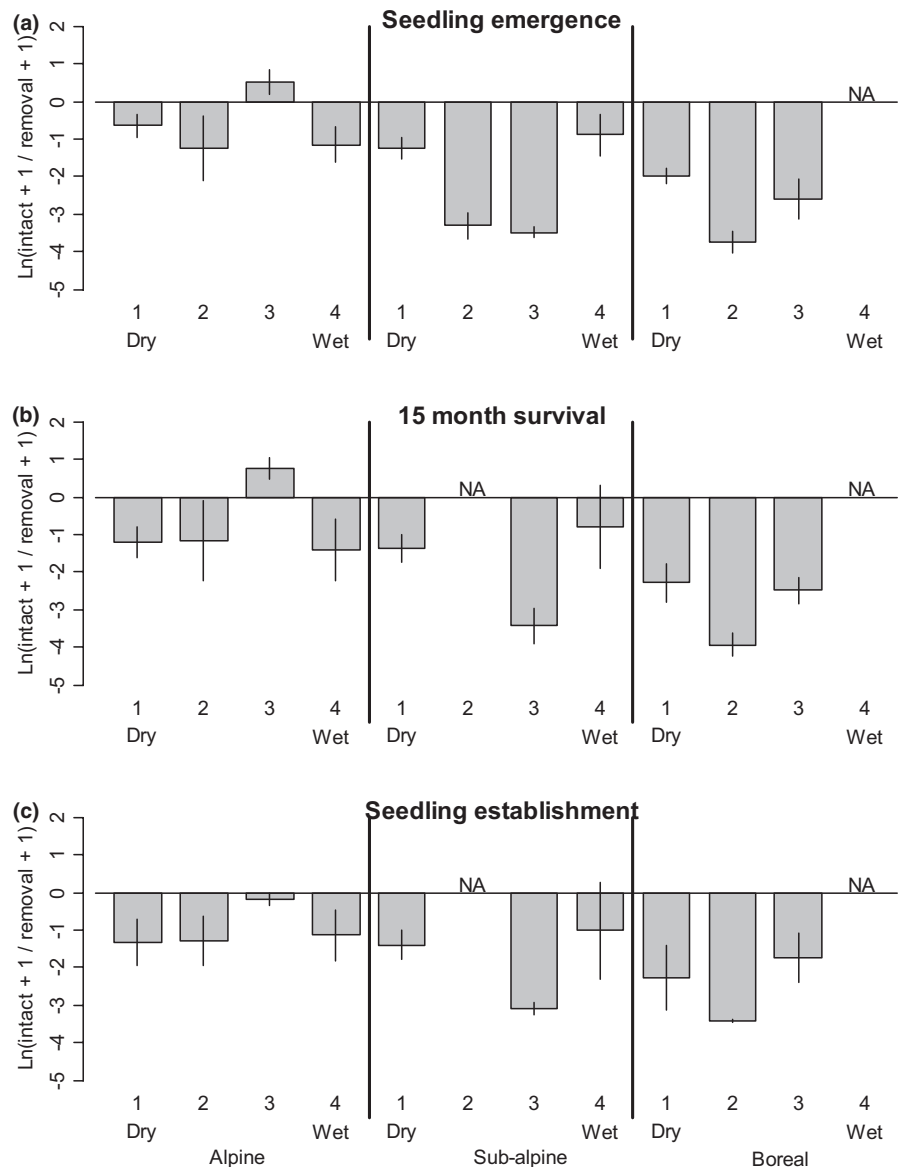
The strong positive effect of vegetation removal on seedling emergence compared to weaker effects on survival and establishment in our study, suggests that this earliest vital rate is more prone to plant–plant interactions than the later life-history transitions. Overall, this is in line with previous studies suggesting that early life-history stages in general are more susceptible to competition than later life stages (Goldberg et al. 2001; Bullock, 2009). Quantitatively, the competitive effects of neighbor vegetation on seedling emergence increased towards warmer sub-alpine and boreal sites in our study. In these sites, productivity is higher than in the alpine (Klanderud et al. 2015), with taller and denser vegetation that might suppress seedling emergence through shading and lack of open soil. Paterno et al. (2016) also showed that plant–plant interaction effects were stronger in the earliest ontogenetic stages, with seed germination responding more consistently to facilitation by benefactor plants than seedling establishment and growth in a seed sowing experiment of different tree species. Although we did

not see much facilitation on seedling emergence along the gradients in our study, there is a clear decrease of the positive effects of vegetation removal toward colder alpine sites. This suggests that facilitation could become important at the highest elevations if the gradient was extended, although facilitation may also be non-linear, or even collapse in the most severe environments (Butterfield, 2009; Michalet et al., 2014a,2014b). Facilitation was evident only for seedling growth rate in our study, with seedlings developing faster in intact alpine vegetation than in gaps where vegetation was removed. Indeed, this was in contrast to our second hypothesis and to previous meta-analyses (Goldberg et al. 1999; He et al. 2013), suggesting that facilitation would be more important for early-stage survival than for later growth. However, although He et al. (2013) concluded that survival was more facilitated than growth across ecosystems, they found slightly stronger facilitation on growth than on survival when alpine and arctic areas were analysed separately (although sample size for survival was low), in line with our results. Vegetation may

buffer temperature extremes in harsh alpine areas (Kjær et al., 2018; van Zuijlen et al., 2019), and our results suggest that this may be more crucial for seedling growth than for other early vital rates, such as seedling survival. Temperatures on open alpine ground can be very high (Körner, 1999), and may hamper seedling photosynthesis due to overheating or drought. Optimal conditions for seedling growth are a balance between light and moisture (Holmgren et al. 1997), and interaction effects of neighbor vegetation may depend on vegetation density (Bullock, 2009). Thus, protection by relatively open alpine vegetation may mitigate temperature extremes and drought, and at the same time provide enough light and open soil for seedling growth. Vegetation surrounding seedlings may also provide nutrients through decomposing litter, which may facilitate seedling growth. This is also shown in other studies where neighbor vegetation provides resources in the early ontogenetic stages of facilitated plants, until they grow bigger and may start competing with the previous facilitators resulting in a shift from facilitation to competition as plants grow (Miriti, 2006; Nunez et al. 2009; Paterno et al. 2016). Thus, the balance between neighbor vegetation offering protective structure and competing for resources is a key mechanism to understand shifts in plant–plant interactions (Bullock, 2009; Paterno et al. 2016).

In line with our third prediction, changes in the magnitude of biotic effects were not consistent between non-resource- and resource-related stress gradients, as effects tended to be stronger along temperature than along precipitation gradients, as shown by the smaller effect sizes and fewer significant interactions between precipitation and vegetation removal. However, along our precipitation gradient, competition appeared to be most pronounced at intermediate levels in sub-alpine and boreal sites. This is in line with previous studies in this system suggesting that productivity, and thus competition peak at the highest temperatures, but at intermediate precipitation levels (Fariñas, 2011; Klanderud et al. 2015). Furthermore, studies on individual species in the same system suggested that depending on the species, both the dry and the wet end can be more stressful than at intermediate precipitation, resulting in unimodal biotic interaction effects along the precipitation gradient (Tingstad, 2015; Klanderud et al. 2016). A similar pattern, but with the opposite direction of the interactions, has been shown in a semi-arid system, where facilitation peaked at intermediate levels, with competition at the two ends (Maestre & Cortina, 2004). In arid desert, on the other hand, facilitation increased with increasing precipitation, in contrast to the SGH (Tielbörger & Kadmon, 2000; Filazzola et al. 2020). Our results, together with these studies, suggest that biotic interaction effects along precipitation gradients may be more complex and context-dependent than along temperature gradients. This is also in line with inconsistent patterns of biotic interaction effects along soil moisture gradients (Maestre et al. 2005; Lortie & Callaway, 2006; Butterfield et al. 2016), where multiple environmental factors, such as soil substrate and interactions with temperature in warm sites likely play a role (Mod et al. 2014).

Thus, in our test of the SGH across multiple sites in a single system, we do not find general support for the SGH across early stages of ontogeny and in response to different environmental gradients, although it is supported for some system components. Where results are consistent with the SGH, they were driven primarily by the difference between alpine and sub-alpine sites, whereas the sub-alpine and boreal sites were often similar. Interestingly, we found that emergence rates, rather than survival and establishment rates, were the key drivers of seedling community abundance and richness across the landscape. Moreover, the number and species richness of the seedling communities were primarily driven by variation in emergence rates, which was the variable most consistent with the SGH. This shows that sorting of the seedling community is occurring very early in plant life history, and the net outcome of this sorting is reflected in the abundance and species richness of the seedling community later on (Klanderud et al. 2016). Thus, our results highlight the importance of biotic interaction effect studies on plant performance across ontogeny and along different productivity gradients to disentangle the mechanisms underlying the SGH.

DATA AVAILABILITY STATEMENT

The data codes are stored and available at https://osf.io/62fvb/.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Site information including bioclimatic zone, geographic coordinates, elevation, annual precipitation, and summer temperature

Appendix S2. Generalized linear mixed-effects model details and R^2 values of removal and climate effects on vital rates of seedling emergence, survival and establishment

Appendix S3. Generalized linear mixed-effects model details and R^2 values of removal and climate effects on the abundance of emerging, surviving and established seedlings

Appendix S4. Bar plots of abundance of emerging, surviving, and established seedlings in alpine, sub-alpine and boreal sites replicated along a precipitation gradient

Appendix S5. Generalized linear mixed-effects model details and R^2 values of removal and climate effects on the species richness of emerging, surviving and established seedlings

Appendix S6. Bar plots of species richness of emerging, surviving, and established seedlings in alpine, sub-alpine and boreal sites replicated along a precipitation gradient

Appendix S7. Difference in species richness of emerging, surviving and established seedlings between intact vegetation and plots were vegetation was removed at alpine, sub-alpine and boreal sites replicated along a precipitation gradient