

Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level

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Summary

1. Competition among conspecifics of the same cohort has been traditionally thought to be a main process driving population dynamics. In this classical view, however, the role of facilitation in stressful conditions has rarely been considered. Here, using a transplant experiment across a forest–prairie gradient, we test whether the stress gradient hypothesis (SGH) extends to individuals thought to be strongly competing.

2. We transplanted 2-year-old seedlings of *Nothofagus pumilio* at two different densities (clusters of 10 and isolated) and at different distances from the forest edge (from 30 m inside the forest up to 50 m outside the forest in the prairie). We further stem-mapped all seedlings belonging to the clusters and computed a competition index (CI). After 3 years of growing, survival and increment growth in diameter and height were measured and analysed using mixed-effects models. We conducted a nearest-neighbour analysis using seedlings' CI and growth and computed model fit using the *area under the curve* (AUC) method.

3. Seedlings planted in dense clusters had significantly higher survival than solitary seedlings at the stressful end of the gradient. This trend was reversed at the opposite end of the gradient, supporting the SGH at the intraspecific level. Pursuing this at the level of the individual, we found that higher CIs (more neighbours) in seedlings predicted higher probabilities of their survival (facilitation) in stressful conditions.

4. Seedlings diameter and height increment growth were not affected by planting density and only diameter varied along the stress gradient; seedlings had higher diameter increments in growth outside the forest. Finally, when compared with conceptual models, our results mostly support predictions of a higher facilitation at intermediate position along the gradient.

5. *Synthesis*. We showed that facilitation overrides competition among tree seedlings even at locations under moderate stress; the facilitation process occurs in resource-mediated interactions (niche overlapping). These results represent an important shift in our way to understand the density-dependent mortality process, and calls for a model reformulation including positive interactions even when competition is expected to be strongest (conspecifics of the same cohort).

Key-words: area under the curve method, competition, *Nothofagus pumilio*, Patagonia, plant–plant interactions, positive density-dependence, stress gradient hypothesis

Introduction

Bertness & Callaway's (1994) seminal review suggested that positive interactions or facilitation can play a more important role than competition in stressed and resource-limited environments, introducing this concept into community ecology

(Bruno, Stachowicz & Bertness 2003). It was also initially proposed that positive and negative interactions may act simultaneously and that the balance between them would depend on the harshness of the physical environment (Bertness & Callaway 1994; Callaway & Walker 1997; Holmgren, Scheffer & Huston 1997; Holzapfel & Mahall 1999). These studies rooted the conceptual model specifications and expectations on how facilitation *should* work and resulted in the formulation of the

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stress gradient hypothesis (SGH). The SGH predicts that with increasing physical harshness of the environment (e.g. abiotic stresses), facilitative interactions among plants become more dominant than competitive interactions, i.e. some species can mitigate potentially limiting stressors to create more favourable habitat for other species (Bertness & Callaway 1994; Callaway & Walker 1997; Maestre *et al.* 2009). Although myriad studies have supported the SGH (e.g. Brooker & Callaghan 1998; Choler, Michalet & Callaway 2001; Holzapfel *et al.* 2006; Callaway 2007), Maestre, Valladares & Reynolds (2005) showed that this process formulation is by no means a general pattern, particularly in water-stressed conditions (see also Tielbörger & Kadmon 2000), which has led to refined versions of the SGH covering certain gaps and exceptions to the rule (Michalet *et al.* 2006; Brooker *et al.* 2008; Maestre *et al.* 2009). One of the gaps, however, not covered thus far by the SGH is intraspecific, same-cohort facilitation, i.e. facilitation among exact niche competitors.

The study of positive plant–plant interactions is constantly maturing. More insightful hypotheses about facilitation, its origins and its evolutionary consequences, are being explored and needed (e.g. Brooker *et al.* 2008; Valiente-Banuet & Verdú 2008; Kikvidze & Callaway 2009). For example, studies investigating facilitation have commonly focused on responses at the community level, disregarding the possibility for facilitation processes at the population level (Malkinson & Jeltsch 2007). Support for this bias comes from niche theory, i.e. intraspecific competition must be stronger than interspecific competition for species to coexist (Silvertown & Charlesworth 2001). Accordingly, the regulation of populations becomes a function of negative density dependence, i.e. higher densities can increase mortality through greater competition for resources and easier detection by consumers (Connell & Slatyer 1977; Stachowicz 2001). There has therefore been the implicit assumption that facilitation mostly occurs where niche overlap is low or does not exist, otherwise competition for common resources would arise. The consequence of this assumption is that facilitation among conspecifics (i.e. complete niche overlapping) should not happen.

In its simplest definition, facilitation or positive interactions are encounters between organisms that benefit at least one of the participants and cause harm to neither (Stachowicz 2001; Bruno, Stachowicz & Bertness 2003; Callaway 2007), i.e. one species facilitates other species by providing primary living space and/or modifying environmental conditions. This implies the absence of niche overlap when facilitation occurs, because competition necessarily induces the detrimental performance of one of the competitors (Keddy 2001). However, intraspecific facilitation may occur, particularly when different life stages of the same species are neighbours, e.g. adult trees causing *nurse effects* to recruitment (e.g. Niering, Whittaker & Lowe 1963; Callaway 1995, 1998; Tielbörger & Kadmon 2000; Fajardo, Goodburn & Graham 2006; Anderson 2009). Recently, intraspecific same-cohort facilitation has been explicitly (i.e. experimentally) addressed in a couple of studies and results are mixed: tree seedlings of *Betula pubescens* subsp. *czerepanovii* growing in subarctic stress

gradients in north-western Russia showed that competition prevailed at the more stressful end of the gradients (Eränen & Kozlov 2008); however, annual forbs (*Suaeda linearis*) growing on cobble beaches did show intraspecific facilitation (Goldenheim, Irving & Bertness 2008). In spite of this example and one other with passing mention to intraspecific facilitation (Miller 1996), positive density dependence is still largely absent in current models of population dynamics. In particular, intraspecific facilitation has not yet been shown in tree species of the same cohort (see above), where it is expected the strongest resource-mediated competition happens. Furthermore, the ecological conditions that influence the appearance of intraspecific facilitation and the circumstances under which neighbourhood interactions between conspecifics switch from negative to positive interactions are poorly known.

The broadleaf southern beech tree species, *Nothofagus pumilio*, dominant in Patagonian forests solely forms multi-stemmed mature trees at the outer edge of second-growth post-fire forests (Fajardo & McIntire 2010). Based on field observations, we think that pervasive strong Patagonian winds negatively influenced the establishment of second-growth forests originated after fire occurrence, mostly affecting early regeneration survival at the outermost limit of the forest. Here, seedlings would be able to overcome desiccation and physical inhibition by wind at the soil surface only by growing in groups and eventually forming merged multi-stem individuals. For this sequence of events to be a consistent explanation of the existence of multi-stemmed trees, individuals in early life stages should exhibit net positive density dependence under physical stress conditions. In other words, positive effects of neighbours, in terms of reducing wind desiccation effects, are greater than negative effects produced by competition for resources.

The general objective of this study was to determine whether density-dependence processes are related to the balance between positive and negative plant–plant interactions at the intraspecific level. Our predictions are based on the SGH; we first predict that (P1) survival and growth of seedlings will increase with seedling density and with distance from the forest edge where seedlings are planted as a result of increasing environmental stress. Secondly, we predict that (P2) facilitation will no longer be the dominant process and will switch to competition as we get closer to the forest edge where abiotic conditions are more benign. Further, if facilitation is occurring at the population level, this trend should be reflected at the individual level as well and thus our third prediction is that (P3) survival probability of seedlings in stressful conditions is higher at the core of the cluster (more protective neighbours, thus facilitation prevails), and lower at more benign abiotic conditions for seedlings located at the border of the cluster (fewer neighbours, thus competition prevails). Chu *et al.* (2008) previously explored the balance of facilitation and competition among conspecifics; however, they studied clonal plants and thus tested resource allocation with limited inference to ecological facilitation. Our study focuses explicitly on conspecific facilitation for a long-lived perennial.

Materials and methods

STUDY SITE AND EXPERIMENTAL DESIGN

We conducted our experiment in two forest–grassland ecotones (gradients) in the protected area Reserva Coyhaique (45°52' S and 72°00' W, 900 m a.s.l.), in Coyhaique province, Patagonia, Chile. Annual precipitation there is *c.* 1350 mm, most of which falls as snow from May to October (Informe Meteorológico de Chile, Dirección General de Aguas, 2008). The study area has a southern aspect with a slope of < 5%. The current forest–grassland ecotone constitutes a sharp and directional stress gradient in wind intensity and, possibly, radiation. Measurements of wind speed taken in other ecotones in the region have recorded an exponential increase from the forest edge (1.5 m s⁻¹) up to 50 m away from it (spring mean wind speed of 11 m s⁻¹) (Fajardo, unpublished data). We took the distance to the forest edge as a surrogate for wind speed, i.e. the longer the distance from the edge the higher the wind speed and hence the harsher the abiotic conditions. We propose that this gradient of wind speed constitutes a consistent stress gradient, which most probably reduces plant productivity (Grime 1977; Lortie *et al.* 2004). We suspect that the most likely mechanism involved here is seedling desiccation that would occur via evaporation from the wind gradient. *N. pumilio* is likely to suffer from wind desiccation and it is believed that many large-scale planting initiatives where seedlings of this species were grown in the open have failed because of this reason (Howorth & Truscott 2007).

To promote the most likely conditions found at the foundation of the second-growth forest, we transplanted 2-year-old seedlings of *N. pumilio* in each of four stress gradient transects the first weeks of March 2006 (end of growing season). Seedlings were planted from inside the forest up to 50 m away from the forest edge: -30, 0, 15, 30 and 50 m into the open prairie, where abiotic conditions are harsher (e.g. wind speed, insolation). We assumed that these five locations would allow us to correctly assess the variation in the net interactions between individuals due to the continuous underlying rate of change in abiotic factors. At each of these five locations, we removed vegetation and planted seedlings either in dense clusters of 10 individuals (planted as densely as physically possible) or as single isolated individuals. This setting (Fig. 1) was replicated at three scales: multiple plantings within a plot (2 clusters, 4 singles), two transects in a single forest–prairie ecotone and two different ecotones (total plot level $N = 120$, total number of seedlings $N = 480$) at equally spaced grid intersections in a 2 × 3 m rectangle (the location). The forest edge here is constituted by second-growth post-fire forest stands of *N. pumilio*. Bare-root seedlings (10–15 cm tall) were obtained from the same area where the experiment was set up (Las Lengas nursery, CONAF, Coyhaique). The seedling cluster density planted into the experimental plots (mean of 265 seedlings m⁻², SE = 11.06, $n = 40$) was greater than the density of small seedlings (≤30 cm tall) found in

a set of forest gap plots (50 × 50 cm: mean of 152 seedlings m⁻², SE = 18.51, $n = 80$). Collar diameter and total height of each seedling were measured once they were planted. We also stem-mapped (mm-scale) all seedlings taking horizontal distances among them and then converting these measurements to actual coordinates using trigonometric functions. At planting, we erected 0.6-m high chicken wire fencing (2.5 cm mesh) to prevent hares, the dominant wild mammalian herbivore, from clipping the seedlings. Cattle and guanaco (*Lama guanicoe*), which occasionally browse *N. pumilio* regeneration (Cavireres & Fajardo 2005), are not a concern in Reserva Coyhaique, as the former are fenced out and the latter do not occur in this province. During each re-measuring period, we also assessed whether and confirmed that there was extremely little apparent herbivory by insects or vertebrates. Finally, after we had established the experiment we watered the seedlings for 3–5 days to minimize transplant shock. At the beginning of the next growing season (October 2006) all seedlings were alive. We conducted a 3-year census in March 2009. Seedlings were qualified as being dead or alive and the collar diameter and the height of the stem was measured for all live seedlings.

The extent of canopy openness for each plot, defined as the percentage of the upper hemisphere compared with open sky, was quantified using hemispherical photography. We used a 7-mm Nikon f 7.4 fisheye lens (the lens has an orthographic projection of 180° angle of view), mounted on a Nikon Coolpix 5000 digital camera (Nikon Corporation, Tokyo, Japan) and GLA (Gap Light Analyzer ver. 2) software (Frazer, Canham & Lertzman 2000). Also, at each plot we determined wind speed at 20–30 cm above ground with a pocket weather metre (Kestrel 3000) multiple times at the beginning of the growing season (spring), where wind speed is expected to be stronger.

NEIGHBOURHOOD ANALYSIS

We recognize that, according to theory, it is likely that individuals in dense clusters growing in stressful conditions might still compete with each other for resources, but that such costs do not outweigh the benefits of group living. Thus, we also predicted a probability of seedling survival based on a density-dependent Hegyi competition index (CI, Hegyi 1974) at planting time of seedlings growing in clusters. For this, we used individually mapped seedling coordinates and assessed the relationship between CIs and growth variables (i.e. collar diameter and height at planting time) of survivor seedlings after 3 years. The Hegyi CI is computed by summing distance-weighted ratios of competitor diameter (or height) to subject seedling diameter (or height):

$$CI_i = \sum_{j=1}^{N_i} \left(\frac{d_j}{d_i} \right) \left(\frac{1}{D_{ij}} \right), \text{ for } i \neq j,$$

where CI_i is the Hegyi competition index for the subject seedling i , d_j is the diameter of the competitor seedling j , d_i is the diameter of the

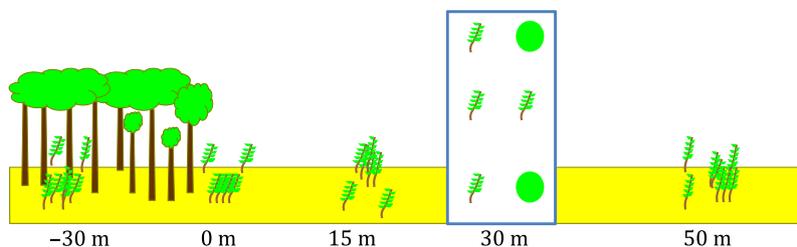


Fig. 1. Depiction of the experimental setting showing one of the four transects, forest–prairie ecotones in Patagonia, Chile. At each transect, seedlings of *Nothofagus pumilio* were transplanted at five different distances (plots) from the forest edge (including within the forest, e.g. -30 m). Within each plot (2 × 6 m) four solitary seedlings and two clusters of 10 seedlings (circles) were planted in a random arrangement.

subject seedling i , D_{ij} is the distance between subject seedling i and competitor seedling j , and N_i the number of competitor seedlings for subject seedling i . With this spatially explicit analysis we wanted to determine, first, how interactions among individuals of the same cohort within the cluster influence patterns of survival and, therefore, impact population dynamics, and second, predict at the individual level where the switch between facilitation and competition occurs. To ensure that we had planted seedlings at consistent densities at all distances and used a random arrangement of seedling sizes (a potential source of error in our assessment of the role of CI), the CI of seedling clusters at planting time did not vary with distance ($F_{4,12} = 0.65$, $P = 0.48$) and therefore it is unlikely that any initial variation in planting density influenced the final survivorship level.

STATISTICAL ANALYSIS

Plot-level seedling survival and growth (P1) data were analysed using mixed-effects (logistic for survival and normal linear regression for growth) models, with random effects for plot and transect and fixed effects for location along gradient (as a categorical factor) and planting density. All analyses were performed using R (R-Development 2009), 'lme4' (Bates & Maechler 2009) and 'nlme' (Pinheiro *et al.* 2009) packages. To assess significance of terms for these generalized mixed-effects models, several challenges in calculating P -values would have to be overcome (Pinheiro & Bates 2001). Instead, we use the recommended approach of using the Akaike Information Criterion corrected for small sample size (AICc) and Likelihood Ratio Tests for all nested models (Bolker *et al.* 2009). For growth, determining the significance of terms was done using the more traditional approach of assessing P -values for main factor and interaction effects (ANOVA function on lme object, R). Because of unbalanced designs, all means we report are marginal means from these linear models that take into account the other effects in the model. In testing whether there is a shift between positive and negative plant-plant interactions across the forest-prairie gradient (P2), we computed net effects of facilitation and competition by comparing survival levels (logit scale on planned contrasts) between seedlings growing in clusters and growing solitary.

For individual-level response to growth conditions (P3), we fit a model assessing the relationship between survival and planted Hegyi CI. The first model had three predictors: initial CI, location along the gradient (as a categorical factor) and their interaction. We included the same random effects as above. This model differed from the previous models in that we used the individual as the unit of response (not the cluster), since each individual that we planted had its unique CI based on how many neighbours it had, how close they were and the neighbours' dimensions (e.g. collar diameter and height). Thus, we explicitly tested whether the effect of planting density is strictly due to spatial proximity. In other words, we were able to determine whether the individuals who survive are the solitary ones, those on the outside of a cluster (fewer neighbours, thus competition prevails), or the ones on the inside of a cluster (more neighbours, thus facilitation prevails). This represents a fine-scale assessment of the facilitation-competition balance. For this, we also included solitary seedlings in the analysis, representing a CI of zero. To provide an absolute indicator of model fit, we used the area under the curve (AUC) in a receiver operator function (Hanley & McNeil 1982). This AUC is a number constrained between 0 and 1 commonly used for binomial prediction where models with values above 0.8 are considered 'good' and above 0.9 are considered 'excellent'. The AUC represents the proportion of randomly drawn pairs of seedlings (one dead and one alive) which the model correctly classifies.

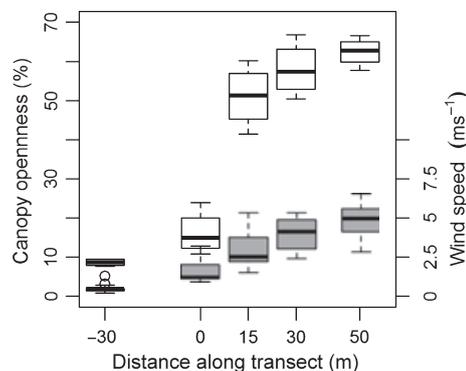


Fig. 2. Mean (\pm SE) canopy openness (white boxes) and wind speed (grey boxes) as a function of distance from the forest edge in the forest-prairie ecotone of *Nothofagus pumilio*, Patagonia, Chile.

Results

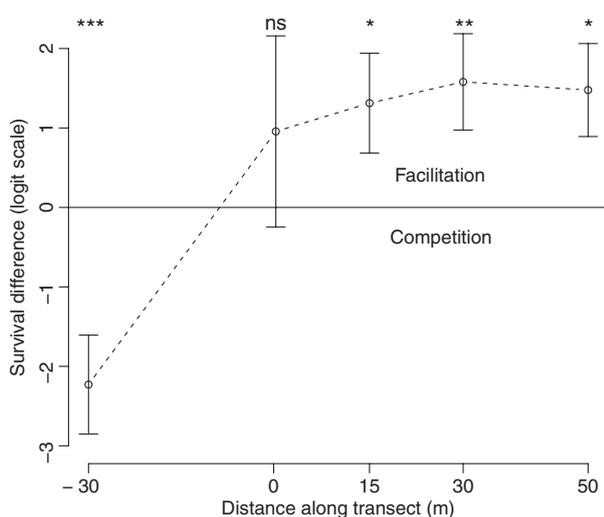
In support of the existence of an environmental gradient in our forest-prairie ecotones, we found a gradient in both canopy openness and mean wind speed from inside the forest (-30 m) to 50 m distance from the forest edge (Fig. 2) in the prairie. Canopy openness (or radiation) and wind speed increased monotonically from inside the forest to the prairie. Accordingly, we found that after 3 years of growing, seedlings strongly differed in survival (Table 1, Fig. 3) and in growth rate (Fig. 4) depending on where they were planted along the stress gradient. Survival was severely modified depending on whether they were planted in clusters or in solitary fashion (Table 2). Most importantly, the interaction between abiotic stress (location along the gradient) and planting density was clearly the best model (Tables 1 and 2). Thus, solitary seedlings had decreasing survival from the forest edge (0 m) towards the open prairie end of the gradient (50 m, Table 1).

The net effects of facilitation and competition agreed with our expectations of facilitation dominating in the open and competition dominating under the canopy (Fig. 3). At one end of the stress gradient (50 m from the forest edge in the prairie) seedlings growing in dense clusters had a significantly greater survivorship than isolated planted seedlings (1.45 on the logit scale, $P = 0.04$, planned contrasts); i.e. facilitation was more important than competition. This pattern persisted at mid distances from the forest edge, 30 and 15 m, but became reversed 30 m within the forest (-2.25 , $P = 0.004$), i.e. seedlings growing alone had significantly higher survivorship than seedlings growing in clusters.

By the end of the third growing season, collar diameter increment of alive seedlings increased across the gradient (location: $F_{4,13} = 12.97$, $P < 0.001$), but not by planting density (density: $F_{1,13} = 2.63$, $P = 0.106$, Fig. 4). Mirroring the observed survival patterns, higher-density plants had higher diameter growth rates in the open prairie and the reverse was true inside the forest, although this interaction was not significant ($F_{4,13} = 2.60$, $P = 0.175$). Height increment of living seedlings, however, was neither affected by location ($F_{4,13} = 2.05$, $P = 0.146$) nor by planting density ($F_{1,13} = 0.91$, $P = 0.342$, Fig. 4).

Table 1. *Nothofagus pumilio* seedlings survivorship mean values and confidence intervals around the mean after 3 years as a function of treatments: growing at five different distances in forest–prairie ecotones and at two different densities (clusters of 10 seedlings and isolated) in Patagonia, Chile

Stress gradient						
	Under canopy		Forest edge		Prairie	
Distance (m)	-30	0	15	30	50	
Survival (%)						
Cluster	24.94 9.99–49.87	97.80 88.56–99.62	90.19 73.12–96.88	77.84 53.24–91.55	76.88 52.15–91.03	
Single	76.25 40.60–93.78	94.45 62.16–99.44	70.67 35.17–91.45	42.25 14.18–76.41	42.62 14.42–76.32	

**Fig. 3.** Differences in 3-year survival (on the logit scale) between seedlings of *Nothofagus pumilio* growing in clusters and growing alone at each distance of the stress gradient. Where the difference is positive, growing in clusters is better (facilitation); where difference is negative, growing alone is better (competition). *, **, and *** indicate planned comparisons significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively.

The fitted neighbourhood model can be considered a ‘good’ model in absolute terms as its AUC is 0.805. Plotting the fitted values of probability of survival as a function of initial CI and location along the gradient, the highest survival was found at the forest edge and was constant across all initial CI values (Fig. 5). However, there was a highly significant interaction whereby seedlings with high initial CI (more neighbours) received the greatest survival benefit in the open prairie and the greatest survivors in the forest were seedlings with the lowest CIs (fewer neighbours).

Discussion

Consistent with our first prediction, we show here that positive interactions occur among conspecific seedlings of the same cohort at relatively stressful sites, both at the coarser community level and at the individual-level, in direct contrast to

expectations derived from niche concepts of competition. We found that for a non-clonal perennial species, the balance between facilitation and competition was positive, i.e. densely growing seedlings had higher survival than single-planted seedlings, when growing in open, more stressful locations. Since all vegetation was removed from the plots upon planting and there was no herbivory due to the erected fence, mortality in open locations of single planted seedlings is likely not due to biotic factors but to abiotic factors that cause stress and eventually lead to mortality. Before this study, it would have been difficult to expect a process other than competition structuring populations of individuals of the same tree species and cohort (but see Chu *et al.* 2008 and discussion below). Our results then suggest that conspecific aggregation brings benefits due to habitat amelioration, which, at the same time, compensates for expected negative effects of competition when growing at high densities. What is striking is that facilitation overrides competition at locations that are relatively stressful, but not very stressful on an absolute scale (survival $>40\%$ at all prairie plots – including single-planted seedlings). Additionally, the observed switch in the direction of density dependence (P2) occurred predictably along a physical stress gradient (Figs 2 and 3), supporting the SGH, which suggests greater strength and frequency of positive interactions with increasing abiotic stress (Bertness & Callaway 1994; Callaway & Walker 1997; Holmgren, Scheffer & Huston 1997; Callaway 2007), in this case, for individuals of the same species and cohort. This ultimately widens the spectrum and consequences of positive plant–plant interactions.

Previously, positive interactions were mostly overlooked partly due to the uncritical acceptance by ecologists of negative interaction (e.g. competition) as the driving force in community structuring or due to their alleged idiosyncratic character (Callaway 1997; Stachowicz 2001; Michalet *et al.* 2006). Nowadays, the greater relative importance of positive plant–plant interactions in high-stress sites can be attributed either to decreasing competition intensity (Grime 1977), to an increase in facilitative effects – habitat amelioration (Bertness & Callaway 1994; Callaway 2007), or to both (Michalet *et al.* 2006). Contrary to traditional models of positive plant–plant interactions (Michalet *et al.* 2006; Maestre *et al.* 2009) that expect facilitation to peak at intermediate stressful conditions and

Fig. 4. Experimental responses of *Nothofagus pumilio* seedlings' collar diameter and height growth increment (mean \pm SE) in the forest–prairie ecotone (stress gradient). Solid lines indicate seedlings growing in clusters while dashed lines indicate seedlings growing alone. There were significant effects of distance in diameter increment only.

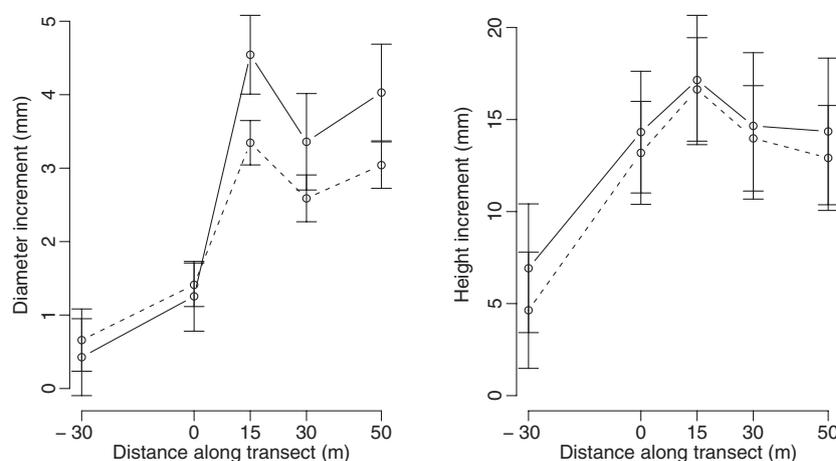


Table 2. Summary of AICc selection models, Akaike differences (Δ_i) and Akaike weights (w_i) for describing survivorship based on Distance (distance in the stress gradient), Density (density of seedlings planting) and the interaction of both for seedlings of *Nothofagus pumilio* growing in forest–prairie ecotones in Patagonia, Chile

Model support			
	AICc	Δ AICc	w_i
Distance	459.8	25.5	0.00
Density	478	43.7	0.00
Distance + Density	459.6	23.3	0.00
Distance \times Density	438.3	0	0.99

Note: AICc stands for Akaike Information Criterion corrected for small sample size and K parameters, including each theoretical model, intercept and error term; Δ AICc stands for differences in AICc with respect to the best model (i.e. model with the lowest AICc); w_i is the Akaike weight which is similar to the relative likelihood of each model.

Values in bold stand for the lowest AICc and hence the best model fitting the data.

ultimately disappear at the more stressful end of the gradient (where competition prevails), we found that the net positive effect of seedling interaction remained high. Assuming that we might have not covered the entire length of the stress gradient (Lortie 2010), we may have missed the expected pattern of facilitation being sharply reduced at stress levels higher than the ones we considered (Michalet *et al.* 2006; Maestre *et al.* 2009). Although this last expectation is based on the assertion that competitors sustain high rates of resource uptake under stress (Grime 1977), competition has been documented to prevail at high stress levels only in semi-arid conditions (Tielbörger & Kadmon 2000; Maestre & Cortina 2004), but there is no empirical support yet for this to occur in other stressful conditions (e.g. Goldenheim, Irving & Bertness 2008). In our opinion, negative biotic interactions (competition) under high levels of abiotic non-resource-based stress in this particular system may occur only after survival mediated by positive biotic interactions (facilitation) has been assured. In other words, competition may prevail in highly stressful conditions when

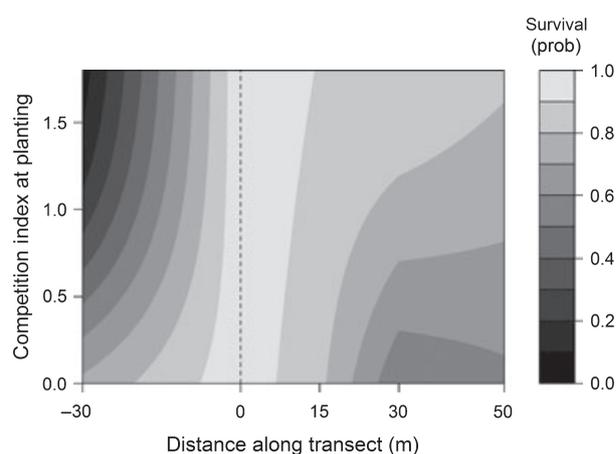


Fig. 5. Effects of distance in the forest–prairie ecotone (stress gradient) on the probability of survival after 3 years of *Nothofagus pumilio* seedlings depending on the number and size of neighbours at planting time (competition index, CI). The scale on the right indicates a continuum from low (dark grey) to high probability of survival (light grey). Note the benefit of high CI for seedlings growing in the open.

time (as a gradient of stress) is considered and facilitation is not needed anymore. However, in a companion study we have found that adult trees of *N. pumilio* have the ability and tendency to merge with their immediate neighbours (McIntire & Fajardo unpublished results), demonstrating that competition did not occur. Regarding the community level, Michalet *et al.* (2006) propose that under very stressful conditions facilitation disappears and competition prevails, mainly because only stress-tolerant species will occur, i.e. absence of stress-intolerant species to facilitate. In our case, we hypothesize that the potential mechanism behind the increase of facilitation with increasing stress here includes harsh habitat amelioration via wind shelter (Carlsson & Callaghan 1991; Baumeister & Callaway 2006; Eränen & Kozlov 2008), and probably a reduction in radiation, both of which may lead to reductions in evapotranspiration and improved water retention capacity of the soil, reducing water losses. At the other end of the gradient, competition prevailed most probably because of competition for light. Further studies need to be conducted to clarify the

specific physiological mechanisms responsible for the higher survival of seedlings when living in groups at stressful conditions as found in this experiment.

Positive interactions at the interspecific level derived from the ability of neighbours to protect the target species from extreme abiotic factors (Sthultz, Gehring & Whitham 2007). At the intraspecific level, we found that CI was a strong predictor of survival. In accordance with our third prediction, we found that at the stressful location neighbour seedlings *protected* the centrally located seedlings in the cluster as these seedlings are the ones with the highest CI (more neighbours). This particular circumstance, i.e. having a higher CI predicting higher chance of facilitation, helps to exemplify the non-sensical meaning of a traditional index that accounts for competition but actually results in facilitation under stressful conditions. This situation shifts completely under canopy where seedlings without neighbours (single-planted seedlings) had the higher survival. This transition clearly shows the facilitation–competition interplay is mediated by the mix of both, abiotic and biotic factors (Holmgren, Scheffer & Huston 1997). In general, it is expected that the fiercer competition occurs between individuals of the same species and same cohort because the presence of an absolute niche overlapping (there is no resource partitioning). Here, in relatively stressful conditions, we found the contrary to happen: strong competitors do not compete but help each other to survive.

This phenomenon of intraspecific facilitation at harsh environmental conditions changes our way to see how density-dependence processes (e.g. self-thinning) may work at the population level. Deng *et al.* (2006) already mentioned that populations (and communities) living in environments characterized by a high degree of abiotic stress, such as ecotones, may show different size–density relationships. Current theories based solely on models of resource competition may not hold in even moderately stressful environments, where facilitation plays a more important role in inter- (Bruno, Stachowicz & Bertness 2003; Callaway 2007; Maestre *et al.* 2009) and intraspecific interactions (Goldenheim, Irving & Bertness 2008). As higher densities are not increasing mortality, what can we expect to occur in the future stand under a scenario of weak self-thinning? We observed the presence of adult multi-stemmed trees at the edge of second-growth forests of *N. pumilio*, which, we hypothesized, is the consequence of successful establishing in groups (Fajardo & McIntire 2010), so aggregation may be maintained through time, and thus the negative relationship between individual size and density might not apply here.

To our knowledge, there are only two other studies showing intraspecific facilitation and the SGH in plants: Goldenheim, Irving & Bertness (2008) found the same facilitation–competition switching pattern for an intertidal annual forb (*Suaeda linearis*) in cobble shores in New England, USA; Chu *et al.* (2008) claimed to have experimental support for positive intraspecific interaction at low-to-intermediate densities (stressful conditions were constant) in alpine meadows of the Tibetan Plateau, though they worked with genetically related clonal ramets of an annual species (*Elymus nutans*), which con-

founded physiological resource allocation with positive interactions among individuals. Eränen & Kozlov (2008, 2009) did not find facilitation to occur in subarctic stress gradients in north-western Russia when working with tree seedlings of *Betula pubescens* subsp. *cazerepanovii*; on the contrary, they found that competition prevailed at the more stressful end of the gradient. They used, however, seedling–seedling distances of 25 cm for which we expect that facilitation process (e.g. absence of wind barrier effect) might not happen yet (as they recognize), and what prevailed was not competition but the action of stress only. Ours is then the first known study showing intraspecific facilitation for a perennial non-clonal species. We have at least two possible explanations for the lack of examples of positive conspecific interactions. First, for trees, a large fraction of forests near humans have been planned, planted or actively thinned leaving very few opportunities to observe this phenomenon for reasons other than survival (e.g. straight trunks). Secondly, it may be a feature of this species because of its ability and tendency to merge with its immediate neighbours later in development (Fajardo & McIntire 2010; McIntire & Fajardo *in review*), so the antagonism that should be present was selected against.

Finally, neither collar diameter nor height increments of the survivor seedlings were correlated with seedlings density, although diameter increment showed a significant and positive trend along the gradient. Consequently, after 3 years of growing, the balance between positive and negative seedling–seedling interactions affected survivorship of seedlings but not growth, which suggests that growth rates depend chiefly on abiotic conditions at establishment, i.e. open conditions are better for growth, if the seedling can survive the drought. Thus, at stressful conditions we found that facilitation promoted higher survival with no loss in growth rates of seedlings growing in clusters when compared with solitary seedlings. According to Goldberg *et al.* (2001) the different response of density-dependence between survival and growth may be explained in terms of fundamental differences between processes affecting both survival and growth, e.g. resource retention vs. resource uptake. Survival is priority; any resource will be first used to assure survival (retention) and much later for growth (uptake), generating different responses. Another explanation might be methodological; survival is an all-or-nothing phenomenon, hence it is easily accounted for and creates high variation, while growth is only measured in live seedlings thus variation is necessarily reduced because of sample size.

Conclusions

Studies about competition have primarily focused on resource-mediated interactions between species; facilitation studies have often found their examples in non-resource-mediated interactions. Here, we found, for the first time, empirical evidence for facilitation processes occurring in resource-mediated interactions (niche overlapping) of tree seedlings. The fact that facilitation overrides competition of tree seedling conspecifics of the same cohort represents a fundamental shift in our way

to understand density-dependence mortality (e.g. self-thinning) processes. Thus, intraspecific facilitation may need to be included in common models of population and community dynamics, improving predictions, particularly when the environment is not stable and varies along gradients, a situation that is not so exceptional. We finally assert that the findings of our study will have broader consequences from plant population biology – a probable extension of the Allee effect (Ferdy & Molofsky 2002) – to ecological restoration, e.g. we could predict an *ideal* planting density for which survival would be assured (highest) in different environmental conditions (the stress gradient).

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