

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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