Facilitation within Species: A Possible Origin of Group-Selected Superorganisms

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ABSTRACT: Facilitation (positive interactions) has emerged as a dominant ecological mechanism in many ecosystems. Its importance has recently been expanded to include intraspecific interactions, creating the potential for higher-level natural selection within species. Using multiple lines of evidence, we show that conspecific facilitation within the southern beech tree, *Nothofagus pumilio*, appears to overcome competition in two life phases. In a seedling experiment addressing stress and planting-density effects, we found that mortality was lowest (~0%) where there was no stress and was indistinguishable across densities. Furthermore, in mature forests (45 years old), genetically variable, merged individuals had lower mortality (−50%) than unmerged individuals in locations without identifiable stress. Thus, a full understanding of the occurrence of facilitation may require a more general model of resource improvements than the commonly cited stress gradient hypothesis. Additionally, the merged trees showed a density-dependent mortality pattern at the level of the group. These data demonstrate a potential mechanism (facilitation) driving natural selection at this higher level, via stem merging. These merged "superorganisms" would confirm theoretical predictions whereby facilitation acts as an ecological mechanism driving group selection.

Keywords: multistemmed trees, *Nothofagus pumilio*, Patagonia, positive interactions, positive density dependence, stress gradient hypothesis.

Introduction

Positive, same trophic level interactions among organisms—often known as "facilitation"—have become formally included in community ecology theory (Bruno et al. 2003; Lortie et al. 2004*a*) and are known to increase local community diversity (Cavieres and Badano 2009). They are sufficiently well understood to affect conservation and restoration efforts (Gómez-Aparicio et al. 2004; Halpern et al. 2007), yet the evolutionary consequences of facilitation have just begun to be explored (Brooker et al. 2008; Bronstein 2009; Kikvidze and Callaway 2009). In virtually all cases to date, facilitation has been observed and tested between unrelated species (Callaway 2007 and citations therein) or between individuals of the same species that are of dramatically different size (such as large individuals protecting small seedlings; e.g., Dickie et al. 2005; Fajardo et al. 2006; Eränen and Kozlov 2008). Consequently, there has been the implicit assumption that facilitation dominates where niche overlap is low or does not exist and that competition for common resources otherwise dominates. Thus, intraspecific facilitation is not expected to dominate in genetically unrelated individuals of the same cohort (Eränen and Kozlov 2008) because this condition would likely have the strongest resource-mediated competition.

A small set of studies, however, have shown intraspecific, same-cohort plant facilitation (Harley and Bertness 1996; Miller 1996; Bertness et al. 1998; Chu et al. 2008; Goldenheim et al. 2008; Fajardo and McIntire 2011). Although these previous studies laid some groundwork for conspecific facilitation (Fajardo and McIntire 2011), the special nature of intraspecific interactions was not explicitly addressed. First, facilitation becomes a population ecology phenomenon whose implications are not at all understood. Second, competition is supposed to be particularly strong among conspecifics of the same cohort (Silvertown and Charlesworth 2001). In trees, for example, forest-stand development in temperate latitudes has shown strong and ubiquitous competitive exclusion (Oliver 1981; Fajardo and McIntire 2007). Thus, numerous questions remain unanswered: Are there longer-term implications when conspecific facilitation occurs? Are the ecological conditions promoting facilitation within conspecific cohorts always the same as for other positive interactions? For example, does the stress gradient hypothesis (SGH; Bertness and Callaway 1994; Bruno et al. 2003; Callaway 2007; Brooker et al. 2008; Maestre et al. 2009), which states that

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