Journal of Vegetation Science **24** (2013) 417–418

COMMENTARY

Life at the edge, cooperation in Antarctica

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Abstract

In a current article in the *Journal of Vegetation Science*, Molina-Montenegro and colleagues extend the study of plant–plant interactions on stress gradients to extremes – the moss and lichen-dominated communities of Antarctica. They found that the importance of facilitation at this extreme end of a 'cold–harsh continuum' was similar to that reported at the extreme ends of alpine gradients around the world. In other words, in contrast to recent theory and case studies in other systems, facilitative effects did not wane in extremely stressful conditions.

Extreme environments have fascinated people for a long time. Ecologists have been particularly interested in how life adapts to conditions that are very dry, cold, salty, toxic or otherwise inimical to homeostasis. Thus a predominant perspective on the distribution and abundance of life in extreme abiotic conditions is that it is controlled by appropriate adaptations and much less by interactions among the tough organisms that can live at the edge. For example, biodiversity in extreme environments would seem more likely to be regulated by how many taxa can evolve tolerance than by the exclusion of weak competitors. But in the last 20 yr other ideas have emerged. Among these is the perspective that in extreme environments cooperative, or facilitative, interactions among species and individual organisms become more important (Bertness & Callaway 1994; Anthelme & Michalet 2009). One line of support for this comes from a number of studies in arctic and alpine ecosystems, which have explored shifts in the nature of interactions among vascular plants. These studies show that competitive interactions are stronger or more frequent in higher productivity systems at lower elevations, and that they shift towards facilitative interactions in more abiotically stressful conditions at higher elevations (Callaway et al. 2002; Fajardo et al. 2008; Cavieres & Badano 2009; Yang et al. 2010; McIntire & Fajardo 2011; Cranston et al. 2012; Butterfield et al. 2013; but see Cavieres et al. 2006).

This body of work has been substantially extended by a paper in a recent issue of the *Journal of Vegetation Science* (2013) from Marco Molina-Montenegro and a group of his Chilean colleagues who take the study of inter-specific interactions in extreme conditions to a new extreme by exploring interactions among mosses and lichens in northern Antarctica. Antarctic environments are among the most stressful on Earth for plants, possessing only two native vascular plant species, and so Molina-Montenegro et al. (2013) focused on mosses and lichens, taxa that are often associated with conditions too harsh for vascular plants. They observed that one widespread, abundant and large lichen species, *Usnea antarctica*, formed a 'cushion' morphology similar to that of many species of alpine vascular plants, and found that of the 14 moss and other lichen species that they sampled, three occurred only within *Usnea* cushions, and the abundance of six species was highly skewed toward co-occurrence with *Usnea*. They also found that transplanted *Deschampsia antarctica*, one of the two native Antarctic species, roughly doubled its rate of survival inside *Usnea* cushions compared to outside cushions. In other words, some of the most stress-tolerant organisms on Earth still benefitted from the facilitative effects of other species in one of the most stressful places on Earth.

A fascinating aspect of Molina-Montenegro et al.'s findings is that even in what 'represent[s] the most extreme end of a cold–harsh continuum as can be found on Earth,' the importance and intensity of general facilitative process did not wane. My back-of-the-envelope calculations of relative importance indices (see Armas et al. 2004) for Molina-Montenegro et al.'s sites yielded values of +0.66 and +0.54 (based only on total plant density), and these values are very similar to those found at the extreme ends of alpine gradients around the world (L. Cavieres and the Alpine Pals, http://plantecology.dbs.umt.edu/People/alpine_pals.html, unpubl. data). This is important because some ecologists have speculated about whether or not some aspects of facilitation might not increase linearly to the extreme ends of gradients (Michalet et al. 2006) and this is clearly the case in some systems (Kitzberger et al. 2000; Forey et al. 2010; Verwijmeren et al. 2013). It is

Doi: 10.1111/jvs.12070

quite reasonable to think that at the extreme ends of gradients, most species might not be able to survive even with the cooperation of the strongest facilitators, thus erasing any pattern that might demonstrate facilitation. This would render facilitation 'unimportant' (see Brooker et al. 2005), no matter how 'intense' it might be. The fact that Molina-Montenegro et al.'s results do not indicate a dip in the importance of facilitation at the extreme end suggests that, at least for whatever factors drive this particular gradient, facilitation remains an important organizing principle of life, even to the point where vascular plants begin to drop out of communities altogether.

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Doi: 10.1111/jvs.12070