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Positive effects of shrubs on plant species diversity do not change along a gradient in grazing pressure in an arid shrubland

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Abstract

Facilitative or positive interactions among species are driven mainly by the environmental amelioration or protection from grazing provided by nurse plants. Some studies have suggested that protection from grazing is inconsequential in water-limited environments because of low herbivore densities and their grazing effects. Others, however, argue that herbivores have a major effect on semi-arid plant communities, and that protection from grazing is a significant factor driving positive plant–plant interactions in such environments. We identified a gradient in grazing pressure in a semi-arid shrubland in south-eastern Australia along which we compared soil condition, incident radiation and plant composition beneath two nurse shrub species with open (shrub-free) interspaces. Our aim was to assess the degree of microclimatic amelioration provided by both shrubs, and changes in the interactions (intensity, importance and frequency) between both nurse shrubs and their understorey species, and their effects on species richness at the community level. Both the relative interaction intensity (RII) and interaction importance (I_{imp}) indices of plant–plant interactions were generally positive and independent of grazing pressure. Soil beneath both nurse plants had significantly greater indices of nutrient cycling and infiltration, and contained more C and N than soil in the open. Almost twice as many species occurred under the canopies of both shrubs (44 species) than in the open (23 species), and the composition of species differed significantly among microsites. Fifty-four percent of all perennial plant species occurred exclusively under shrubs. Our results suggest that environmental amelioration is a stronger driver of the facilitatory effect of shrubs on their understorey species than protection from grazing. Our conclusions are based on the fact that the substantial effect of plant–plant interactions on plant species richness was largely independent of grazing pressure. Irrespective of the underlying mechanism for this effect, our study illustrates the ecological role of shrubs as refugia for understorey plants in semi-arid environments and cautions against management practices aimed at reducing shrub populations.

Zusammenfassung

Positive oder fördernde Interaktionen zwischen Arten beruhen hauptsächlich auf einer Verbesserung der Umwelt oder auf dem Schutz vor Beweidung, der durch Ammenpflanzen zur Verfügung gestellt wird. Einige Untersuchungen ließen vermuten, dass der Schutz vor Beweidung in Umwelten mit einer begrenzten Verfügbarkeit von Wasser ohne Konsequenzen bleibt, weil die Herbivorendichten und ihr Beweidungseffekt gering sind. Andere argumentieren jedoch damit, dass die Herbivoren einen ausschlaggebenden Effekt auf semiaride Pflanzengemeinschaften haben und dass der Schutz vor Beweidung ein signifikanter Faktor

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ist, der positive Pflanzen-Pflanzen-Interaktionen in diesen Umwelten vorantreibt. Wir untersuchten einen Gradienten im Beweidungsdruck in einem semiariden Buschland im süd-östlichen Australien und verglichen die Bodenbeschaffenheit, die einfallende Strahlung und die Pflanzenzusammensetzung unter zwei Ammenstraucharten mit offenen (buschfreien) Zwischenräumen. Unser Ziel war es, den Grad der mikroklimatischen Verbesserung, der durch die beiden Straucharten zur Verfügung gestellt wurde, und die Veränderungen in den Interaktionen (Intensität, Bedeutung und Häufigkeit) zwischen den beiden Straucharten und ihren Unterwuchsarten sowie ihre Effekte auf den Artenreichtum auf der Gemeinschaftsebene abzuschätzen. Sowohl die Indizes der relativen Interaktionsintensität (RII) als auch der Bedeutung der Interaktionen (limp) waren im Allgemeinen positiv und unabhängig vom Beweidungsdruck. Der Boden unter beiden Ammenpflanzen besaß signifikant höhere Indizes in Bezug auf den Nährstoffkreislauf und die Durchlässigkeit und enthielt mehr C und N als der Boden in offenen Bereichen. Unter dem Dach der beiden Straucharten kamen fast doppelt so viele Arten vor (44 Arten) wie in den offenen Bereichen (23 Arten) und die Zusammensetzung der Arten unterschied sich signifikant zwischen den Mikrostandorten. 54% der perennierenden Arten kamen ausschließlich unter Büschen vor. Unsere Ergebnisse lassen vermuten, dass die Verbesserung der Umwelt ein Faktor ist, der für die fördernden Effekte von Büschen auf ihre Unterwuchspflanzen eine größere Bedeutung hat als der Schutz vor Beweidung. Unsere Schlussfolgerungen basieren auf der Tatsache, dass der substantielle Effekt der Pflanzen-Pflanzen-Interaktionen auf den Pflanzenartenreichtum im Großen und Ganzen vom Beweidungsdruck unabhängig war. Unabhängig von den zugrundeliegenden Mechanismen für diesen Effekt, zeigt unsere Untersuchung anschaulich die ökologische Rolle der Büsche als Refugien für Unterwuchspflanzen in semiariden Umwelten, und sie warnt vor Managementpraktiken, die darauf abzielen die Strauchpopulationen zu verringern.

Keywords: Facilitation; Shrubland; Encroachment; Interactions; Nurse plant; *Eremophila*; *Senna*

Introduction

Positive or facilitative interactions among plant species are strongly dependent on environmental conditions and play a major role in structuring communities in most biomes (Callaway 2007; Brooker et al. 2008). Most studies of the relationships between plant–plant interactions and environmental conditions have been inspired by the seminal 'stress–gradient hypothesis' (SGH; Bertness & Callaway 1994), which suggests that the frequency of facilitative species interactions increases monotonically with increases in abiotic or consumer stress. Although facilitative interactions between plants are common under harsh conditions such as water limitation (e.g. Holzapfel, Tielbörger, Parag, Kigel, & Sternberg 2006), their monotonic increase with increasing abiotic stress has recently been questioned (e.g. Maestre, Valladares, & Reynolds 2005). The outcome of plant–plant interactions depends largely on the nature and level of the stressors involved (Maestre, Callaway, Valladares, & Lortie 2009; Smit, Rietkerk, & Wassen 2009), the ecological strategy of the interacting species, the performance measure or the interaction indicator used (Brooker et al. 2005; Maestre et al. 2005) and the interaction among different stressors (Baumeister & Callaway 2006; Soliveres, García-Palacios, et al. 2011). Disentangling the relative importance of these multiple factors as drivers of plant–plant interactions is an important part of understanding how these interactions will behave along environmental gradients or under changing climatic conditions, and how they might influence plant community dynamics (Brooker et al. 2008).

Abiotic constraints and consumer pressure often co-occur in arid and semi-arid ecosystems, and are particularly important in defining the dynamics of vegetation communities (McNaughton 1985; Hendricks, Bond, Midgley, & Novellie 2005). However, the relative importance of these stressors in structuring arid and semi-arid plant communities, and more specifically, their joint effects on plant–plant interactions, remains poorly understood (Gómez-Aparicio, Zamora, Castro, & Hódar 2008). Recent theory predicts a relatively low importance of grazing protection by nurse plants in water-limited environments (Smit et al. 2009). The logic underpinning this prediction is that herbivores in such environments are sparsely distributed, and abiotic constraints such as limited water or nutrients are more important for vegetation and therefore for plant–plant interactions than herbivory (Ellis & Swift 1988). Moreover, plant species adaptations to drought such as hairy and thick leaves, are also related to grazing resistance (Smit et al. 2009). Drought-adapted and therefore herbivory-resistant plant species are expected to be a major component of plant communities under arid and semi-arid conditions (e.g. Grime 1973; McNaughton 1985). Under harsh environmental conditions therefore, we would expect a relatively lower importance of grazing protection for most species at the community level (Smit et al. 2009). Conversely, other studies have demonstrated contrasting results and have shown how herbivores exert substantial pressure on vegetation and soils in water-limited environments (e.g. McNaughton 1985; Lunt, Eldridge, Morgan, & Witt 2007). Accordingly, grazing protection has been shown to be a crucial mechanism underlying plant–plant interactions in arid and semi-arid environments, with shifts from negative to positive interactions under high grazing pressure (Graff, Aguiar, & Chaneton 2007; Soliveres, García-Palacios, et al. 2011). Furthermore, the ability of plants to recover after herbivore damage is directly influenced by the availability of resources (Wise & Abrahamson