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Research article

Community attributes determine facilitation potential in a semi-arid steppe

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ABSTRACT

Studies on positive plant–plant relations have traditionally focused on pair-wise interactions. Conversely, the interaction with other co-occurring species has scarcely been addressed, despite the fact that the entire community may affect plant performance. We used woody vegetation patches as models to evaluate community facilitation in semi-arid steppes. We characterized biotic and physical attributes of 53 woody patches (patch size, litter accumulation, canopy density, vegetation cover, species number and identity, and phylogenetic distance), and soil fertility (organic C and total N), and evaluated their relative importance for the performance of seedlings of *Pistacia lentiscus*, a keystone woody species in western Mediterranean steppes. Seedlings were planted underneath the patches, and on their northern and southern edges. Woody patches positively affected seedling survival but not seedling growth. Soil fertility was higher underneath the patches than elsewhere. Physical and biotic attributes of woody patches affected seedling survival, but these effects depended on microsite conditions. The composition of the community of small shrubs and perennial grasses growing underneath the patches controlled seedling performance. An increase in *Stipa tenacissima* and a decrease in *Brachypodium retusum* increased the probability of survival. The cover of these species and other small shrubs, litter depth and community phylogenetic distance, were also related to seedling survival. Seedlings planted on the northern edge of the patches were mostly affected by attributes of the biotic community. These traits were of lesser importance in seedlings planted underneath and in the southern edge of patches, suggesting that constraints to seedling establishment differed within the patches. Our study highlights the importance of taking into consideration community attributes over pair-wise interactions when evaluating the outcome of ecological interactions in multi-specific communities, as they have profound implications in the composition, function and management of semi-arid steppes.

Introduction

Biotic interactions determine community assembly and ecosystem functioning. Competition has been traditionally considered as the main driver in structuring plant communities (Grime, 1974). However, over the last decades, an increasing number of studies have emphasized the importance of facilitation as a major ecological interaction (Bertness and Callaway, 1994; Callaway, 1995, 2007; Brooker et al., 2008). Studies on plant–plant relations have traditionally focused on pair-wise interactions, paying scarce attention to other co-existing species (Brooker et al., 2008). This topic was reviewed by Jones and Callaway (2007), where they discussed the context-dependency of plant interactions and emphasized the role of third species. When many benefactor and beneficiary species co-occur, a complex network of interactions arises, leading to indirect effects, such as indirect facilitation (Callaway, 2007; Brooker et al., 2008; Gross, 2008). Thus, the net outcome of multi-species interactions may not necessarily be the additive effect of pair-wise relationships (Weigelt et al., 2007; Zhang et al., 2011).

In recent years, there have been an increasing number of studies employing the community approach to study facilitation (Verdú and Valiente-Banuet, 2008; Cavieres and Badano, 2009; Gilbert et al., 2009; Soliveres et al., 2011a; Granda et al., 2012). However, most of those studies are either extrapolations of individual responses to a community scale, or studies focused on the effect of nurse species on biodiversity, but not on the opposite, i.e., on the

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capacity of species assemblages to act as nurses (but see Castillo et al., 2010 for an analysis of the effect of phylogenetic distance of the nurse community on seedling establishment). Drylands are not the exception and pairwise approaches dominate the study of positive interactions (Pugnaire et al., 2011). However, species in drylands do not occur in isolation. Harsh conditions, especially water scarcity, promote spatially aggregated vegetation patterns (Aguiar and Sala, 1999).

In drylands, vegetation is frequently arranged in multi-species patches where direct and indirect facilitation promotes species coexistence (Flores and Jurado, 2003; Callaway, 2007). Attributes defining the physical and biotic structure of these patches, such as patch size, litter accumulation, canopy structure, and species number and identity may affect seedling establishment. Communities of putative benefactor species in vegetation patches may promote species coexistence by favoring seedling performance. As not all species co-occurring in a patch act as nurses, patches with high species richness are more likely to contain benefactor species than those with fewer species (i.e., sampling effect), and thus species richness may enhance the recruitment of new individuals. Conversely, as species richness increases, the probability that species with contrasted functional traits co-occur may also increase. Due to niche saturation, patch biotic and physical dimensions may be limited, and the establishment of new individuals may be hindered with patch size and age (MacArthur and Levins, 1967; Case, 1991). In this case, increased species richness would reduce patch potential to accept new individuals. The positive and negative relationship between species richness and community capacity to accept further species, together with the influence of spatial scale, has been discussed around the theory of the invasion paradox (Levine, 2000; Stohlgren et al., 2003; Fridley et al., 2007). According to this theory, community diversity and invasibility should be negatively related at small spatial scales. However, facilitation often promotes invasive species richness (Von Holle, 2005; Fridley et al., 2007; Vellend, 2008; Altieri et al., 2010), and accordingly, we would expect increased establishment rates in species-rich patches, particularly under the stressful conditions of semi-arid areas (Von Holle, 2005). Species identity may also be crucial for the establishment of new individuals, because of similarity of ecological niches, species competitive ability and species capacity to enhance microclimate conditions for the newcomers. Phylogenetic distance between species may directly affect the net outcome of the interaction, as closely related species are likely to share important ecological traits and therefore to compete among each other (Webb et al., 2002; Valiente-Banuet and Verdú, 2007). However, in multi-specific assemblages, phylogenetic composition of the entire community, rather than the phylogeny of a dominant species, may control seedling establishment. The mechanisms of competition in multi-species communities in dry grasslands showed that non-additive effects of pair-wise interactions drive the net outcome of the interaction (Weigelt et al., 2007). However, to our knowledge, no study has evaluated the facilitative effect of whole communities in seedling establishment in drylands. Neither the attributes of communities that are involved in seedling recruitment have been explored. Still, species identity, patch composition and the physical structure of woody vegetation patches may be crucial for seedling establishment.

Woody patches may affect seedling establishment in various ways, including microclimate regulation, changes in water and nutrient availability, and the presence of symbiotic fungi, to mention a few (Vetaas, 1992; Nara and Hogetsu, 2004; Smith and Read, 2008; Cable et al., 2009; Soliveres et al., 2011a; Anthelme et al., 2012). Their combined effect cannot be easily predicted, as interactions are common and complex. For example, nutrient and organic matter accumulation, and the formation of a thick litter layer depend on plant size and species identity (Vivanco and Austin, 2006). However, whilst higher soil fertility may enhance seedling establishment, litter frequently hinders seed germination and rooting (Rotundo and Aguiar, 2005; B. Amat, pers. obs.). The outcome of the interaction between established patches and seedlings may also depend on the particular location within the patch where the new individual thrives. For example, the relative importance of aboveground interactions (e.g., competition for light, excess radiation, herbivory) vs. belowground interactions (allelopathy, competition for nutrients and water, mycorrhizae) may substantially change if seedlings germinate underneath the patches or on their periphery.

We studied the facilitative potential of whole communities of woody vegetation patches on the establishment of a key-stone species in *Stipa tenacissima* L. steppes. These semi-arid steppes show a combination of bare soil, *S. tenacissima* tussocks and woody patches, formed by large resprouting shrubs (hereafter 'dominant species'), accompanied by small shrubs and perennial grasses (hereafter 'accompanying species'). These woody patches improve ecosystem functionality, and favor the presence of frugivorous birds and vascular plants (López and Moro, 1997; Maestre and Cortina, 2004a; Maestre et al., 2009). Positive interactions between *S. tenacissima* and large woody species have been widely described (Maestre et al., 2001, 2003a; Soliveres et al., 2011a), and dominant species of woody patches act as benefactors in other areas (Castro et al., 2004), but little is known about the facilitative potential of patch forming species and patch communities in these semi-arid steppes. As woody patches in *S. tenacissima* steppes form spatially delimited plant communities, they are suitable environments to test the facilitative effects of communities and explore the role of different community attributes in that interaction. The aims of our study are (1) to evaluate how patches modify their immediate environment, (2) to assess the net effect of woody patches on the performance of new individuals, (3) to quantify the relative importance of physical and biotic community (patch) attributes as drivers of seedling recruitment, and (4) to explore the underlying mechanisms of such interactions. To achieve this, we characterized biotic and physical attributes of multi-specific woody vegetation patches in *S. tenacissima* steppes, and evaluated the performance of shrub seedlings planted underneath them compared to seedlings planted in open areas. We expected substantial differences in aboveground and belowground interactions in different parts of the patch. To take this into account, we evaluated seedling performance in three different locations within the patch.

Materials and methods

Study site

Our study was established in a semi-arid area in southeastern Spain. Mean annual temperature is 18 °C and mean annual precipitation ranges between 286 and 330 mm (Ninyerola et al., 2005). Soil is Lithic Calciorthid developed from marl and limestone (Soil Survey Staff, 1994). The area is covered by *S. tenacissima* steppes with sparse patches of woody vegetation (Fig. S1). We considered a woody patch any combination of adults of the species *Pistacia lentiscus* L., *Quercus coccifera* L., *Rhamnus lycioides* L., *Juniperus oxycedrus* L., *Ephedra fragilis* Desf. and *Osyris lanceolata* Hochst. & Steud. (the dominant species) whose physiognomy was different from the adjacent matrix (Fig. S1). We selected 8–13 patches in five independent sites (53 patches in total). Patches were selected to provide a balanced representation of number and identity of dominant species.