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Indirect facilitation becomes stronger with seedling age in a degraded seasonally dry forest

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ABSTRACT

In seasonally dry forests direct facilitation by woody species due to amelioration of harsh abiotic conditions could be important during germination and early establishment of tree seedlings, and under some species but not others. Recent research suggests that at later stages facilitation by woody species may be indirect due to protection of saplings from herbivores, implying that under absence of herbivores reforestation programs may plant saplings in unprotected open sites. We used the native tree *Lithraea molleoides* from central Argentina as a model species to test this hypothesis. We performed a seeding and planting experiment simulating early and late establishment respectively, which included 234 study plots situated in herbaceous, shrub and tree patches of differing species composition and under two herbivore treatments (grazed and ungrazed) and replicated at three sites. Seedling counts averaged 0.82% of the sown seeds after 6 months, were highest under shrubs and lowest in open patches, and were influenced by woody species composition only in tree patches (all P values < 0.05). At seedling stages we detected no influence of herbivory ($P = 0.4$) nor of indirect facilitation due to herbivory (herbivory × patch type $P = 0.7$). Survival of planted saplings was 53% after 3 years and over winter dieback affected 76% of the saplings. At sapling stages we found an increasing importance of indirect facilitation through protection from herbivores, as we recorded the highest sapling survival and growth at tree and shrub patches and the lowest in open patches (all P values < 0.001), and a negative effect of livestock ($P < 0.001$) mainly on the open patches (herbivory × patch type $P = 0.07$ and $P = 0.001$ for survival and growth, respectively). We found no significant influence of woody species composition on sapling survival and growth (all P values > 0.05). We conclude that direct facilitation is involved at all studied stages while indirect facilitation becomes increasingly important at the sapling stage.

1. Introduction

Facilitation processes are an important topic in ecological studies as they are essential to understanding ecological succession and species distributions, and at present discussions are focussing in understanding the mechanisms of facilitation and variation underlying facilitation processes (Filazzola and Lortie, 2014; He and Bertness, 2014). In seasonally dry forests and degraded sites woody vegetation is well known for providing a direct facilitative effect on the establishment of tree species through amelioration of the harsh abiotic environment. Shrubs and other woody vegetation types provide shade, soil moisture retention and protection from wind, reducing seed and seedling desiccation and ameliorating the effect of winter frost and soil loss (Vieira and Scariot, 2006; review by Gómez-Aparicio, 2009). However, several facilitation studies have found that the degree of facilitation often depends on the identity of the nurse plant (e.g. Siles et al., 2010), and often thorny or un-palatable shrubs and other woody vegetation provide an indirect facilitative effect by protecting tree regeneration from trampling and browsing of large herbivores and to a lesser degree from the harsh abiotic environmental factors (del Moral et al., 2010; Papachristou and Platis, 2010). Woody patches can also provide an indirect facilitative effect by trapping seeds dispersed by wind or birds that perch in the woody patches (Bullock and Moy, 2004; Aerts et al., 2006). Thus, the causes of a spatial association

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between tree saplings and nurse plants cannot be assigned to direct facilitation without careful experimentation, and the relative importance of the mechanisms underlying facilitation are still poorly explored in seasonally dry forests (Tálamo et al., 2015a, 2015b).

The relative importance of direct and indirect facilitation may also change at different stages of the regeneration process (Vieira and Scariot, 2006; Renison et al., 2015). The amelioration of harsh abiotic conditions by woody plants could be more important than the protection from herbivores at early stages when seedlings are too small to be browsed but more vulnerable to wind, strong radiation and lack of moisture (Fenner and Thompson, 2005). Conversely, the protection from herbivore damage can be more important than the amelioration of abiotic conditions at later stages of the regeneration process when seedlings grow and become accessible to herbivore browsing (Renison et al., 2015).

Determining the relative importance of the mechanisms underlying facilitation has important implications for forest restoration. If facilitation is mainly determined by indirect effects of protection from herbivores and not by amelioration of harsh abiotic microenvironment conditions, in unprotected sites forest encroachment may be accelerated through livestock exclusion without need of planting nurse shrubs. If facilitation by woody plants is mainly determined by indirect effects of seed trapping, forest restoration of open sites may be improved through sowing and fixation of seeds. Instead, this may not be feasible if nurse plants mainly ameliorate harsh abiotic conditions, as proposed by the review of Gómez-Aparicio (2009).

According to the only three studies that we are aware of, in the vast region of the Grand Chaco (1,200,000 km^2), indirect herbivore-mediated facilitation appears to be far more important than direct facilitation (Tálamo et al., 2015a, 2015b; Torres and Renison, 2015). However, the previous studies were performed on target species which are presumed to be sun tolerant and did no evaluations regarding the relative importance of seed trapping and of the identity of the potential "nurse" plants. Clearly we need more case studies to be able to establish generalizations, mainly in target species with a different ecological status regarding shade tolerance and the influence of shrub identity.

Here, we focused on the identity of the potential "nurse" plants and *Lithraea molleoides* as a target species which has traditionally been mentioned as shade tolerant at early stages of regeneration and a late successional species in the Chaco Serrano forest where it is considered a foundation species of high conservation value. In this ecosystem *L. molleoides* dominates old-growth stands a (Luti et al., 1979), but no formal studies exist to determine whether the species is facilitated by other woody vegetation and to what extent this facilitation is direct or indirect due to protection from herbivory. Our aims were to (1) evaluate changes in the relative importance of direct and indirect herbivore-mediated facilitation during target species ontogeny (2) determine the importance of woody patches as seed traps for natural regeneration, (3) evaluate the influence of nurse identity and target tree species ontogeny on the facilitation. We tested the hypothesis that at early stages woody patches facilitate establishment mainly through the amelioration of harsh abiotic conditions and because they serve as seed traps. At late stages we hypothesized that woody vegetation facilitate establishment mainly due to the protection from herbivores. We predicted that the number of seedlings developed from seeds (early stage), will be lower in open patches, intermediate under shrub patches and higher under tree patches (with variability depending on "nurse" species) with no differences in grazed and ungrazed sites. Whereas the survival and growth of planted saplings (late stage) will be lower in open patches than under protection of woody plants only in grazed sites, with few or no differences between patch types in ungrazed sites.

2. Materials and methods

2.1. Study area

The vegetation of the mountains of central Argentina corresponds to the Chaco Serrano district (Cabrera, 1976) of the Gran Chaco Region. The climate is warm-temperate to subtropical, with mean temperatures of 13.9° C and annual precipitations of 780 mm, concentrated during the warm season, from September to March (Colladon et al., 2014). By the late 20th century the remnant forests of the Gran Chaco were lost at an annual rate of 2.2%, mainly due to the expansion of agriculture (Zak et al., 2004). Most of the remaining Chaco forests persist in areas where agriculture is not feasible, such as mountain areas. However, particularly in mountain areas, Chaco forests are being rapidly degraded by repeated wildfires and replaced by non-native tree plantations, housing developments, and foci of invasive non-native species (Hoyos et al., 2010; Giorgis et al., 2011; Torres et al., 2014). Less than 12% of the mature native forests still remain in the mountains of central Argentina (Zak et al., 2004), and soils are being lost at very high rates in the most susceptible areas (Cingolani et al., 2013).

The vegetation in the experimental area (S −31.48° W −64.54°, 700 m a.s.l.) is open woodland dominated by pioneer woody species that grow in patches. Shrubs and trees include *Acacia caven*, *Geoffroea decorticans*, *Condalia buxifolia*, *Schinus fasciculatus*, *Celtis ehrenbergiana*, *Lippia turbinate*, *Aloysia gratissima* and several non-native species, mainly *Ulmus pumila*, *Gleditsia triacanthos* and *Pyracantha angustifolia*. The area has been affected by fires and livestock presence since at least the 1950s, and is fairly representative of the present state of Chaco Serrano forests of Córdoba. Our target study species, *Lithraea molleoides* (Vell.) Engler (Anacardiaceae), is an evergreen tree up to about 8 m tall, distributed in Argentina, Brazil, Bolivia, Uruguay and Paraguay. In the Córdoba Mountains it often dominates the canopy of mature stands, where it is considered a foundation species, and ranges from 500 to 1600 m a.s.l. Its fruit is a drupe of 4–8 mm in diameter (Carmello-Guerreiro and Sartori Paoli, 2005).

2.2. Field experimental setup

In a large paddock of 300 ha we selected three sites separated by at least 500 m from one another. At each site we built fences

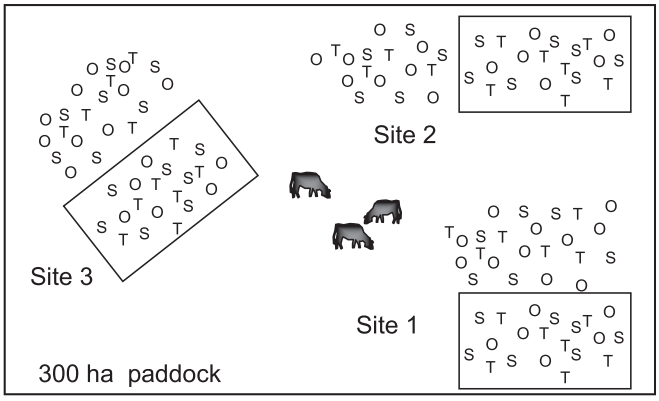

Fig. 1. Diagram showing the three study blocks within the 300-ha study paddock. Letters represent plots in open (H), shrub (S) and tree (T) patches. Letters inside the inner rectangles indicate plots in ungrazed exclosures and letters outside rectangles indicate plots in grazed sites.