Direct *versus* indirect facilitation (herbivore mediated) among woody plants in a semiarid Chaco forest: A spatial association approach

ANDRÉS TÁLAMO,[1],* ALICIA BARCHUK,[2] SILVANA CARDOZO,[3] CARLOS TRUCCO,[3] GUSTAVO MARÁS[3] AND CAROLINA TRIGO[1]

[1]*Instituto de Bio y Geociencias del NOA (IBIGEO), Facultad de Ciencias Naturales, Universidad Nacional de Salta – Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Salta Avenida Bolivia 5150, CP 4400, Salta, Argentina (Email: andrestalamo@gmail.com),* [3]*Facultad de Cs. Naturales, Universidad Nacional de Salta, Salta, and* [2]*Ecología Agrícola, Facultad de Cs. Agropecuarias, Universidad Nacional de Córdoba, Córdoba, Argentina*

Abstract In arid environments, direct facilitation (microhabitat amelioration) and indirect facilitation ('associational resistance' via protection from herbivory) among plants of different species may act simultaneously. Little is known about their relative effects. One way to disentangle the effects is by evaluating spatial associations. We examined the relative importance of these two mechanisms of facilitation in the semiarid Chaco vegetation of north-central Argentina, through an eight-way observational study in which we quantified the degree of spatial association between saplings of each of two key tree species, *Schinopsis lorentzii* (Anacardiaceae) and *Aspidosperma quebracho-blanco* (Apocynaceae), with shrub neighbours either possessing spines or without spines and in both an ungrazed site and a site with a long history of cattle grazing. We analysed data across 400 subparcels at each site with spatial analysis by distance indices. Saplings of both tree species showed positive spatial associations with spiny shrubs in the grazed site but not in the ungrazed site, and never with non-spiny shrubs. This result suggests that spiny shrubs may indeed provide associational resistance for saplings of key tree species in grazed habitats in these dry subtropical forests, that is, that indirect facilitation may predominate over direct facilitation. If confirmed by experimental studies, this result can have implications for the silvopastoral management of rapidly expanding ranches in the semiarid Chaco, where current practice includes the near elimination of native shrubs.

Key words: associational resistance, Chaco, facilitation, grazing, spiny shrub.

INTRODUCTION

Due to high levels of abiotic stress and herbivore pressure in arid environments, facilitation often prevails over competition in interactions among plants of different species (Callaway & Walker 1997). Facilitation results when some plants modify, directly or indirectly, the physical and/or biological environment such that the survival or growth of other individuals (often juveniles) in their proximity is enhanced (Callaway 1995; Callaway *et al*. 2005). Several possible mechanisms for facilitation exist. These could operate simultaneously and give rise to the same pattern of spatial association among 'benefactor' and 'beneficiary' plants. Direct facilitation results when the presence of some plants ameliorates stressful physical conditions for juveniles or adults of others and enhances their establishment and survival, thus becoming 'benefactors' or 'nurse plants' (Brooker *et al*. 2008). Indirect facilitation

results when the presence of some plants ameliorates negative effects of animal herbivores (Milchunas & Noy-Meir 2002; Rebollo *et al*. 2002) or yet other plant species (Levine 1999) on 'beneficiaries'. For example, the presence of individuals of a plant species unpalatable to herbivores due to chemical or physical defences may end up benefiting juveniles or adults of other species growing nearby, by decreasing the probability of their consumption and/or trampling by herbivores (McAuliffe 1986; Callaway 1995; Milchunas & Noy-Meir 2002; Rebollo *et al*. 2002; Garcia & Obeso 2003; Baraza *et al*. 2006).

Indirect facilitation mediated by herbivores exemplifies 'associational resistance' (henceforth AR), originally proposed by Root and colleagues to emphasize the importance of interactions among neighbouring plants of different species in determining the likelihood that a given plant will be detected by, or vulnerable to, herbivores (Tahvanainen & Root 1972; Root 1973). As Barbosa *et al*. (2009) discussed in a recent revision, the effectiveness of AR, of course, may depend on many factors among which the most

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obvious are the specific traits of the 'nurse' or 'benefactor' plants and the intensity of herbivore pressure. Indeed, numerous works on this theme propose that the highest net facilitative effect (AR most notable) tends to occur in areas with high but not extreme consumer pressure (Rebollo *et al.* 2005; Michalet *et al.* 2006; Brooker *et al.* 2008; Levenbach 2009; Smit *et al.* 2009; Verwijmeren *et al.* 2013) and with 'benefactor' plants possessing conspicuous herbivore-deterrent traits such as spines, thorns or extreme chemical defences (Milchunas & Noy-Meir 2002; Rebollo *et al.* 2002, 2005; Callaway *et al.* 2005; Smit *et al.* 2005; Graff *et al.* 2007; Barbosa *et al.* 2009).

The relative importance of direct and indirect facilitation (AR) has received little research attention in arid environments, and to our knowledge, no study has assessed the occurrence and importance of each of these two mechanisms in Latin American tropical and subtropical dry forests. Theoretical models predict that microhabitat amelioration will be the predominant facilitation mechanism at sites with pronounced abiotic stress whereas AR will predominate at sites with pronounced herbivory by native animals at least (Boulant *et al.* 2008). The importance of herbivory by native animals tends to increase with ecosystem productivity, which leads to the general expectation that indirect facilitation will be important chiefly in places with less physical stress. This generalization might explain the low number of investigations that have separated and evaluated the two mechanisms in a single habitat where plants experience both physical stress and herbivore stress imposed by domestic livestock (Boulant *et al.* 2008). Results of these studies are mixed. In arid grasslands grazed by domestic livestock in France, the two mechanisms were equally important (Boulant *et al.* 2008). In a mixed pine forest in Spain, direct facilitation predominated (Gomez-Aparicio *et al.* 2008). In Chilean evergreen scrub, AR predominated over direct facilitation in explaining the spatial distribution of 'beneficiary' plants (Jaksic & Fuentes 1980). In short, for the world's arid and semiarid habitats, a clear pattern of the relative importance of the two mechanisms in arid habitats does not emerge. Gómez-Aparicio *et al.* (2008) propose that their relative importance would simply depend on the relative magnitudes of biotic and abiotic stress.

Direct facilitation and AR can be evaluated experimentally through long-term studies, or through shorter-term studies on spatial associations between potential benefactor and beneficiary plants. The latter provides a valid alternative approach to investigating the net effects of interactions at the community level, using observed patterns to infer the underlying process. Positive spatial associations between target plants and their neighbours imply facilitation whereas negative associations imply any one of several negative

plant–plant effects such as competition for water or nutrients, allelopathy or herbivore attraction (Tirado & Pugnaire 2005).

The Gran Chaco of subtropical South America, occupying more than 1 200 000 km² of low-relief landscapes in Paraguay, Bolivia and Argentina (Prado 1993), is characterized by high levels of solar radiation, extreme summertime temperatures and widespread livestock grazing. Such a combination of abiotic and biotic stress is not at all new to the native vegetation of the Chaco, thorny subtropical dry forest which at the close of the Pleistocene hosted an astounding array of large mammalian herbivores (Bucher 1987) that undoubtedly exerted effects on the vegetation at least as profound as those that their counterparts exerted on Central American dry forests (Janzen & Martin 1982).

Despite the vast expanse of the Gran Chaco (about 320 000 km² in Argentina alone), to our knowledge, no previous studies have examined plant–plant facilitation there with respect to livestock grazing. In fact, the dynamics of natural regeneration in this seriously threatened vegetation formation (Gasparri & Grau 2009; Hansen *et al.* 2013) have not been closely examined to date outside of the most arid sector (annual precipitation 400 mm). In this dry Chaco, Barchuk *et al.* (2008) found that shrubs facilitated the regeneration of the principal tree species (*Aspidosperma quebracho-blanco*), the spatial distribution of whose juveniles was positively associated with that of certain shrub species. For the great expanse of semiarid Chaco (annual precipitation 700–800 mm), no studies exist on patterns and mechanisms of the regeneration of characteristic tree species. Such knowledge is critical to the conservation and sustainable management of this rapidly deteriorating ecosystem (Gasparri & Grau 2009; Hansen *et al.* 2013).

The vegetation of Copo National Park, the largest protected area in the semiarid Chaco of Argentina, consists of sites with highly variable grazing histories but similar plant species composition. Juveniles (seedlings and saplings) of dominant tree species are vulnerable to grazing and trampling. Certain shrub species have highly visible, and effective, physical protection (spines and thorns) and are quite invulnerable to domestic livestock grazing, especially by cattle. Others, though, are palatable and vulnerable to mammalian herbivores. This set of features – variation in grazing pressure from site to site, variation in physical protection among shrubs at a given site and tree species whose juveniles are vulnerable to grazing and trampling by cattle – enabled us to address the relative importance of direct (habitat amelioration) and indirect (AR) facilitation, in a rarely studied type of vegetation (tropical dry forest with a very dense and spiny shrub stratum). If habitat amelioration (direct facilitation) is the main mechanism of facilitation, the expected result is a positive spatial association of

juvenile plants with any kind of shrubs in sites without livestock grazing. On the other hand, if AR (indirect facilitation) is the main mechanism of facilitation, the expected result is a positive spatial association of juvenile plants with spiny shrubs, but not with shrubs lacking spines, in the presence of livestock. If both mechanisms are acting simultaneously, the expected result is a positive spatial association of juvenile plants with any kind of shrubs in sites with and without livestock, but a stronger spatial association with spiny shrubs in presence of livestock. To test these predictions, we compared the spatial association between saplings of the trees *Schinopsis lorentzii* and *A. quebracho-blanco* and shrubs with and without conspicuous physical defences (spines and thorns) in a region of Copo National Park subjected to livestock for decades, and repeated the comparison in an otherwise similar site without livestock.

METHODS

Study sites

Copo National Park is an expanse of 114 000 ha of semiarid Chaco in Santiago del Estero province, Argentina (25°56′18″S; 61°56′50″W). We worked in two sites, each approximately 80 ha, in the southeastern section of the park, the ancient riverbed of Juramento River (Morello & Adámoli 1974). Climate in Copo is markedly seasonal, with 80% of the 700 mm annual rainfall occurring between October and March. The open tree canopy of the semidedicuous thorn forest is dominated by *S. lorentzii*, *A. quebracho-blanco* and *Ziziphus mistol* (Rhamnaceae) (Tálamo *et al.* 2012). The dense shrub stratum (10933 ± 898 shrubs per hectare, mean ± SE) contains non-spiny species such as *Capparis* spp. (Capparaceae) and *Achatocarpus praecox* (Achatocarpaceae), but over 50% of individuals pertain to notably spiny species such as *Acacia praecox* (Fabaceae), *Celtis ehrenbergiana* (Ulmaceae) and *Schinus polygamus* (Anacardiaceae) (Tálamo & Caziani 2003).

Evaluation of habitat use by livestock

We selected two study sites on the basis of informal interviews with local ranchers intimately familiar with the current and historical movements of their animals. The 'grazed' site has had livestock continuously since 1940 ('grazed' signifies potential effects of trampling, not only herbivory, on the vegetation). The grazed site in our study experienced relatively low biotic stress given that it consisted of open range with approximately one cow per 10–12 hectares, a low-intermediate stocking rate for the Chaco forest (Quiroga *et al.* 2009). The 'ungrazed' site has not experienced grazing within the memory of local people. In each site (grazed and ungrazed), we independently evaluated present-day intensity of habitat use by domestic livestock by recording animal tracks along two 1-km transects each consisting of 20 track traps (1 m²) spaced at 50-m intervals (Simonetti & Huareco 1999). The two transects in each site were at least 1 km apart. Transects to characterize intensity of use by cattle involved a scale much larger than that of the vegetation study plots per se because the wanderings of free-ranging cattle also involve a large scale (home ranges with radii of around 8 km). Each track trap was cleared of vegetation and the soil sifted so as to better detect tracks. We checked transects once per day, recording the number of livestock tracks in each track trap, for 5 consecutive days. This procedure was repeated five times in the grazed site and three in the ungrazed site. We calculated intensity of habitat use by livestock as the number of livestock tracks × 100 track traps⁻¹ × day⁻¹. We evaluated differences in central tendency with a non-parametric test using R software (R Development Core Team 2012).

Community structure of woody vegetation

Within each site, grazed and ungrazed, we delimited one 50 × 50 m plot in a location randomly selected from representative areas of woody vegetation. In each parcel, we identified every shrub and every juvenile tree, defined as a sapling of between 0.5 and 5.0 cm diameter measured at 10 cm above the ground. From these data, we calculated the number of spiny shrubs as a whole, of non-spiny shrubs as a whole and of saplings of each tree species studied per parcel.

Spatial association

We divided each of the two 50 × 50 plots whose vegetation composition we examined into 400 subplots each 2.5 × 2.5 m, approximately the spatial scale of adult shrubs. Within each subplot, we counted the number of tree saplings (as defined above) of each of the two focal tree species (*S. lorentzii* and *A. quebracho-blanco*); the total number of shrubs without spines; and the total number of shrubs with spines.

We performed four association analyses on the data set of each site (with and without grazing): association of saplings of each of the two focal tree species with each of the two classes of shrubs (shrubs with spines and shrubs without spines). The analysis used was spatial analysis by distance indices (Perry *et al.* 1996, 1999; Perry 1998). This analysis first calculates a 'local cluster index' v_{ij} for each subplot of the grid, for each of the two data sets whose association is to be evaluated (e.g. saplings of *S. lorentzii* and spiny shrubs in the ungrazed site), where values of $v_{ij} > 1.5$ indicate 'patches' and values < 1.5 indicate 'gaps'. Next, the analysis detects areas of positive and negative association between the two data sets by first calculating local association indices X_{ij} for each subplot. Values of X_{ij} relate values of v_{ij} for the two data of a given subplot or coordinate, revealing whether or not 'patches' and 'gaps' of the two coincide (positive covariance and association, $X_{ij} > 0$) or not (negative covariance and association, $X_{ij} < 0$). Finally, the global association index X is calculated. After analysing the observed data set, we applied resampling procedures (1000 spatial randomizations) for each of the four pairs of data sets per site to estimate the probability of encountering values of X as extreme as, or

more extreme than, the observed values. Because we made four simultaneous analyses per site across two sites, to adjust the probability of committing type I statistical errors, we used a simple Bonferroni procedure (0.05/4 = 0.0125) to achieve a conservative α of 0.05. Thus, observed P values < 0.006 indicate a statistically significant positive association, values > 0.994 a statistically significant negative association.

We emphasize here that the associational study involved two sites, one grazed and one ungrazed, rather than replicate grazed and ungrazed sites across a much larger scale. The latter, while theoretically ideal, is unrealistic given the necessity of making a detailed examination of spatial patterning (recording all shrubs and tree juveniles within 2500 m^2 of nearly impenetrable thorn forest) across a large number of subplots at a single site. In fact, we know of no analogous study, in any vegetation type, that has achieved replication at the larger scale and know of only a few that have dealt with more than a single site (Graff & Aguiar 2011; Saiz & Alados 2012). The limitation of our study to two particular sites, though, signifies that we should exercise great caution in generalizing our results beyond that scope.

RESULTS

Habitat use by livestock

The present-day intensity of habitat use differed notably between sites selected as 'grazed' and 'ungrazed', supporting the information on grazing history obtained through interviews with local ranchers. We recorded 13.7 ± 5.78 livestock tracks $\times$ 100-track plots$^{-1} \times$ day^{-1} on the grazed site and none whatsoever on the ungrazed site (W = 21; P = 0.0313).

Community structure of woody vegetation

Celtis ehrenbergiana dominated both sites (23% of total shrub density in both sites, Table 1). Five infrequently encountered species were exclusive to the grazed site and two to the ungrazed site (Table 1). Total shrub density on the ungrazed site was nearly 28% greater than on the grazed site, but the proportion of spiny shrubs differed by only 7% (Table 2). Combined density of saplings of the two tree species was nearly identical between sites but the proportion of *A. quebracho-blanco* saplings was higher on the ungrazed site (Table 2).

Spatial association

Saplings of both *A. quebracho-blanco* (Fig. 1) and *S. lorentzii* (Fig. 2) showed positive spatial associations with spiny shrubs on the grazed site but not on the ungrazed site. In neither site did saplings of either tree species display notable positive associations with non-spiny shrubs (Figs 1,2).

Table 1. Relative abundance of the woody plant species encountered in the two study sites (grazed and ungrazed) in semiarid Chaco forest, Argentina, with total number of individuals at foot of table

Species	Spiny	Grazed	Ungrazed
Shrubs			
Acacia furcatispina	Yes	0	0.012
Acacia praecox	Yes	0.041	0.082
Castela coccinea	Yes	0.043	0.018
Celtis ehrenbergiana	Yes	0.228	0.231
Maytenus spinosa	Yes	0.016	0.021
Mimosa detinens	Yes	0.025	0
Schinus poligamys	Yes	0.006	0.069
Ximena americana	Yes	0.001	0
Achatocarpus praecox	No	0.023	0.094
Bouganvillea praecox	No	0	0.001
Caesalpinia paraguariensis	No	0.002	0
Capparis atamisquea	No	0.058	0.041
Capparis retusa	No	0.043	0.200
Capparis saliscifolia	No	0.030	0.008
Capparis speciosa	No	0.053	0.001
Capparis tweediana	No	0.065	0.002
Trees			
Aspidosperma quebracho-blanco		0.107	0.119
Jodina rhombifolia		0.004	0.007
Prosopis elata		0.006	0
Prosopis nigra		0.001	0
Schinopsis lorentzii		0.127	0.062
Ziziphus mistol		0.101	0.030
Total number of individuals		1591	1647

Table 2. Species richness and densities of woody plants encountered in the two study sites (grazed and ungrazed) in semiarid Chaco forest, Argentina

Attributes	Grazed	Ungrazed
Species richness (no. species in 2500 m^2)	20	17
Shrub density (no. plants in 2500 m^2)		
Spiny	610	868
Non-spiny	395	415
Total	1005	1283
Tree sapling density (no. plants in 2500 m^2)		
Aspidosperma quebracho-blanco	77	97
Schinopsis lorentzii	72	56
Total	149	153

DISCUSSION

This comparative study enabled us to distinguish the relative importance of direct facilitation (microhabitat amelioration) and indirect facilitation (AR mediated by herbivores) on the saplings of two tree species in semiarid Chaco. Spatial analyses showed clear patterns: positive associations of juveniles
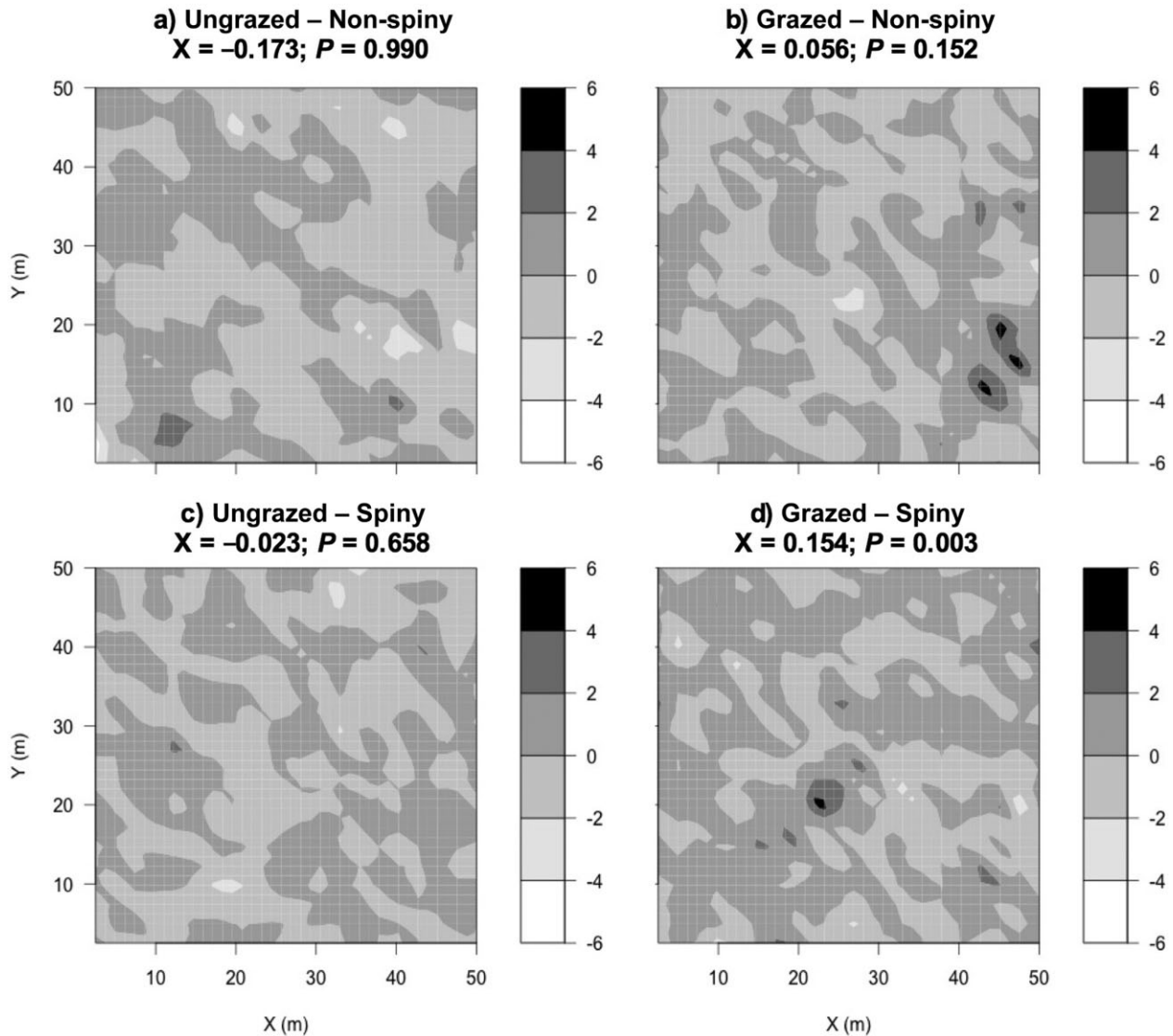
Fig. 1. Spatial association between juveniles of *Aspidosperma quebracho-blanco* and shrubs with (c, d) and without spines (a, b), in a grazed (b, d) and an ungrazed site (a, c). The grey scale indicates the local association index (X_{ij}) for each subplot. Darker tones indicate positive spatial association, lighter tones negative association. X is the index of overall association, with probability level P (probability of encountering values of X as extreme as or more extreme than the observed values). Positive association is significant when $P < 0.006$, negative association when $P > 0.994$.

of both tree species with spiny shrubs and only in the grazed site, suggesting that in this dry subtropical forest indirect facilitation (AR) likely plays a much more important role than direct facilitation in influencing spatial patterns.

Assessments of the relative importance of indirect and direct facilitation are few and far between, perhaps in large part because conceptual models suggest that each mechanism predominates in a different environment. In sites with low levels of abiotic stress, high productivity and high pressure from native herbivores, AR is expected to predominate (Rebollo *et al*. 2002; Graff *et al*. 2007; Soliveres *et al*. 2012). In sites

with greater abiotic stress, lower productivity and (presumably) lower pressure from native herbivores direct facilitation is expected (Boulant *et al*. 2008; Smit *et al*. 2009; Verwijmeren *et al*. 2013). Nevertheless, arid or semiarid environments with introduced livestock, simultaneously experiencing significant abiotic and biotic stress, are widespread. These environments provide opportunities to evaluate the importance of both mechanisms (Boulant *et al*. 2008) under a wide range of herbivore pressures. As stated previously, on a much larger scale the results of the few isolated studies that exist, undertaken in very different habitats, vary with the life form of the dominant vegetation, from
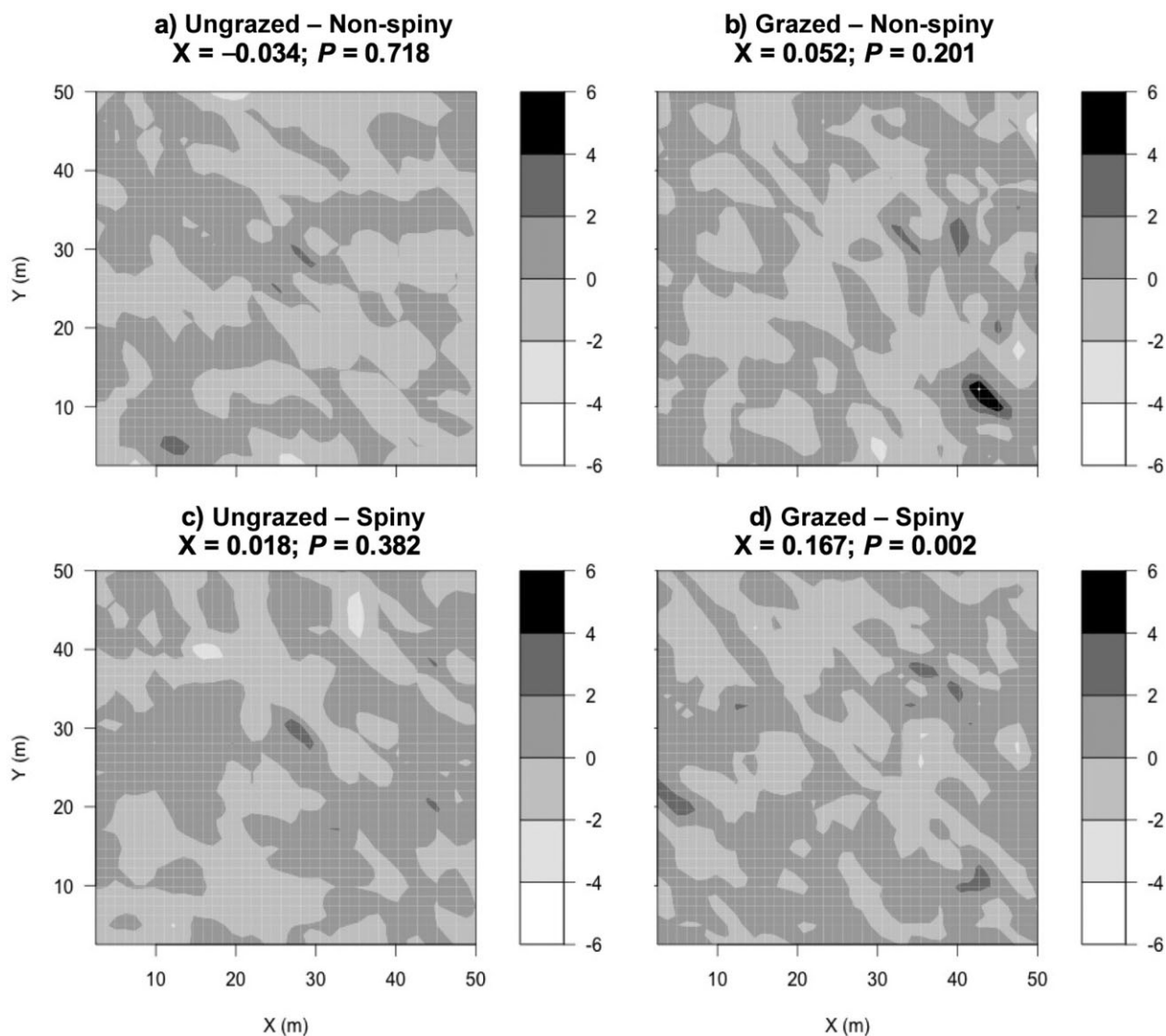
Fig. 2. Spatial association between juveniles of *Schinopsis lorentzii* and shrubs with (c, d) and without spines (a, b), in a grazed (b, d) and an ungrazed site (a, c). The grey scale indicates the local association index (X_{ij}) for each subplot. Darker tones indicate positive spatial association, lighter tones negative association. X is the index of overall association, with probability level P (probability of encountering values of X as extreme as or more extreme than the observed values). Positive association is significant when $P < 0.006$, negative association when $P > 0.994$.

arid French grasslands (both indirect and indirect facilitation, Boulant *et al.* 2008) and Spanish pine woods (direct facilitation, Gomez-Aparicio *et al.* 2008), to evergreen Chilean scrub (AR or indirect facilitation, Jaksic & Fuentes 1980). Our study adds to this heterogeneous collection, with its evidence that AR predominates over direct facilitation in a dry tropical forest with cattle grazing. It is worth remembering that while grazing pressure from cattle and domestic livestock may be a recent phenomenon in the Gran Chaco and other dry forests in the Americas, historically these habitats experienced significant grazing pressure from numerous native large mammalian herbivores (Janzen & Martin 1982; Bucher 1987). We

speculate that AR might have left off playing a central role in vegetation dynamics in the Gran Chaco and similar habitats only during the relatively short time span between the extinction of the Pleistocene megafauna and the introduction of Old World domestic livestock.

Inferences on causal mechanisms such as AR drawn from spatial association studies have had their critics for many years, given that a variety of mechanisms and ecological processes aside from facilitation in the face of grazing pressure could lead to similar results (McIntire & Fajardo 2009). Nevertheless, the triple comparison of our study – not only between otherwise similar grazed and ungrazed sites but also between

saplings of two tree species and between shrub neighbours with and without spines – removes some of the uncertainty from our interpretation of the underlying process. It is highly unlikely that the variation between the two sites in some factor other than grazing pressure – for example, resource concentration, allelopathy, microclimate – would have been of sufficient magnitude to account for the observed differences in spatial pattern (McIntire & Fajardo 2009). The similarity in community structure of woody plants between the two sites (Tables 1,2 and see Tálamo & Caziani 2003) as well as the similarity in community structure between grazed and ungrazed sites in an earlier study carried out a few kilometre from the present study (Tálamo *et al.* 2009) reinforce our proposal that AR to grazing pressure is the most likely causal mechanism for the spatial patterns we found (Figs 1,2). Still, we strongly suggest that to better evaluate these conclusions, this observational study should be followed by field experiments.

Other researchers have encountered similar results (evidence for AR) in a variety of arid and semiarid habitats and with a variety of species (McAuliffe 1986; Rebollo *et al.* 2002, 2005; Graff *et al.* 2007; Anthelme & Michalet 2009; Graff & Aguiar 2011; Saiz & Alados 2012). These studies taken as a whole suggest that AR provided by spiny shrubs, or in some cases chemically unpalatable neighbouring plants, may be determining factors in regeneration success and consequently in spatial patterning of plants in arid and semiarid environments with grazing pressure. Our study provided no evidence for a role of chemical unpalatability, given that (i) the comparison was between spiny and non-spiny shrubs; (ii) there was no significant evidence for AR with non-spiny shrubs; and (iii) 100% of the non-spiny shrubs studied are consumed by livestock (Scarpa 2007), although it is of course possible that some spiny shrubs were also unpalatable. In a different habitat (arid Chaco with 400 mm of rainfall, *versus* the semiarid Chaco of this study), saplings of *A. quebracho-blanco* displayed positive spatial association not only with the spiny shrub *Mimozyganthus carinatus* (Fabaceae) but also with another shrub lacking spines and at least somewhat palatable to livestock, *Larrea divaricata* (Zygophyllaceae) (Barchuk *et al.* 2008). This finding suggests that the severe physical stress of the truly arid Chaco may indeed induce direct as well as indirect facilitation, a suggestion corroborated experimentally (Barchuk *et al.* 2005).

Should further studies confirm the conclusions based on the two sites of the current work, this study in basic ecology also has potential management implications. Our findings suggest that AR could be used as a potential strategy in restoring grazed rangelands. Where livestock still roam, seedlings and saplings of key tree species could be planted under the shade of spiny shrubs, potentially increasing the likelihood of successful establishment – but only after this management strategy is verified by a highly replicated study comparing survival of plantings under spiny shrubs, under non-spiny shrubs and in the open, away from shrubs. Such studies may be essential to management given that land management policies associated with the rapid expansion of silvopastoral systems of livestock production in the semiarid Chaco include the virtual elimination of the shrub stratum. Results of this preliminary, non-experimental study already suggest that ranchers and natural resource managers should consider the potential value of shrubs in the natural regeneration of these and other key tree species.

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