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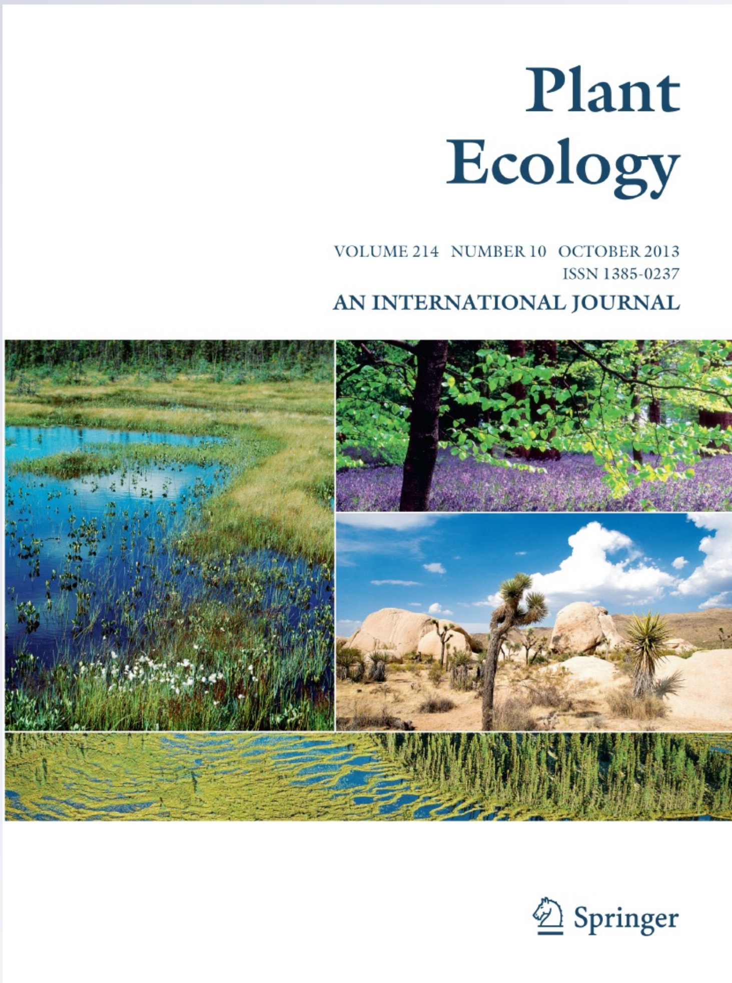
Plant Ecology
An International Journal

ISSN 1385-0237
Volume 214
Number 10

Plant Ecol (2013) 214:1287-1297
DOI 10.1007/s11258-013-0251-5



Springer

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Herbivore-mediated facilitation alters composition and increases richness and diversity in ruderal communities

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Received: 24 April 2013 / Accepted: 9 August 2013 / Published online: 19 August 2013

Abstract Little is known about positive interactions among members of herbaceous plant communities initiating secondary succession (i.e., ruderal communities). Here, we explored the possibility that *Euphorbia schickendantzii* (*Euphorbia*), a latex-containing herb, facilitates other ruderals by protecting them from herbivores in recently plowed and overgrazed sites in central Argentina. To test this hypothesis, we compared plant number, height, reproductive output, and herbivore damage for four species when associated with *Euphorbia* versus in adjacent open zones without *Euphorbia*. Additionally, we classified species in the community according to their palatability, and compared community composition, richness, and diversity between *Euphorbia* and open zones. Dominant (66 % relative abundance) and highly palatable species exhibited increased plant number, size, and fecundity, and decreased herbivory when associated with *Euphorbia* relative to non-*Euphorbia* zones. In contrast, a physically and chemically well-defended species showed greater number of individuals in the open and no differences in herbivory between sampling zones. In detrended correspondence analysis, ordination scores of most palatable species were closer to *Euphorbia*, while those of most unpalatable species were closer to the open. Community composition differed between areas, with six species (25 % of the community) occurring exclusively with *Euphorbia* and three other species occurring only in open zones. Additionally, richness and diversity were greater in communities associated with *Euphorbia* than in those associated with non-*Euphorbia* zones. These results support our hypothesis, highlight the importance of facilitation in altering community-level responses, and indicate that positive interactions can play a more significant role in organizing terrestrial ruderal communities than previously recognized.

Keywords Community-level facilitation · Disturbance · Early-secondary succession · *Euphorbia* · Indirect interactions · Latex

Electronic supplementary material The online version of this article (doi:10.1007/s11258-013-0251-5) contains supplementary material, which is available to authorized users.

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Introduction

Positive and negative interactions among plant species occur simultaneously, with the net result depending on the relative strength of the contrasting forces involved in the interplay (Holmgren et al. 1997). Thus, plants facilitate other plants when, for example, positive effects derived from direct habitat amelioration or indirect herbivore protection overcome concurrent negative effects for resource competition. While much debate surrounds the conditions under which facilitative effects are more likely to prevail over competitive effects (Bertness and Callaway 1994; Michalet et al. 2006; Maestre et al. 2009; Holmgren and Scheffer 2010; Holmgren et al. 2012; He et al. 2013), there is ample consensus regarding the significance of facilitation as a major organizer of plant communities (Bruno et al. 2003; Lortie et al. 2004; Callaway 2007; Thorpe et al. 2011).

The importance of facilitation was recognized early in the context of temporal changes in communities. Here, positive interactions were regarded as modulating transitions in primary succession, as early colonists can contribute to soil formation, ameliorate harsh initial conditions, and pave the way for other species (Connell and Slatyer 1977; Harris et al. 1984). In contrast, positive interactions among members of herbaceous plant communities initiating secondary succession (i.e., ruderal communities, Grime 1977) have traditionally been deemed of much lower importance. Rather than facilitation, dominant perspectives on plant community ecology propose that attributes that maximize colonization and site preemption (Grime 1977; Bazzaz 1979), interactions such as competition (Huston and Smith 1987, Tilman 1987) and consumption (Bach 1994; Carson and Root 1999), and random processes such as dispersal (Seabloom et al. 2003) shape communities soon after disturbance in secondary succession (Rees et al. 2001). This view and the fact that herbs often have negative effects on their neighbors (Gómez-Aparicio 2009; He et al. 2013) may help to explain the paucity of work on facilitation in ruderal communities.

A notable exception to this gap in knowledge is research from plant communities in salt marshes. Early studies in these systems focused on facilitated succession driven by direct amelioration of physical stresses (Bertness 1991; Bertness and Shumway 1993; Huckle et al. 2000). More recent work has advanced that indirect positive interactions can also play a role in the temporal dynamic of early marsh communities (Alberti et al. 2008). Indeed, in a comprehensive assessment of interspecific processes in Argentinean marshes, Alberti et al. (2008) have shown that the colonizing plant *Sarcocornia perennis* facilitates the latter establishment of *Spartina densiflora* by protecting it from the herbivory of the crab *Chasmagnathus granulatus*. This work raises the possibility that facilitation similarly affects the structure and function of plant communities at the onset of secondary succession in terrestrial ecosystems.

Here, we explored positive interactions in ruderal communities in the semiarid forest of central Argentina (Caldenal). *Euphorbia schickendantzii* Hieron (Euphorbiaceae; hereafter referred as *Euphorbia*) is a common member of these communities in exceptionally sandy and dry soils of the Caldenal. As for many species in the family, this native and short-lived perennial herb is rich in latex, a well known anti-herbivore substance that confers defense via toxicity or anti-nutritive effects and stickiness (Agrawal and Konno 2009). Under grazed conditions, ruderals growing in zones occupied by *Euphorbia* appear to exhibit increased size and fecundity as compared to those growing in open zones without *Euphorbia* (Plate 1). Consequently, we explored the possibility that *Euphorbia* facilitates co-occurring ruderal species by protecting them from grazing. The alternative that *Euphorbia* preferentially occurs in zones already occupied by larger and more fecund plants is unlikely because *Euphorbia* and the other ruderals simultaneously colonize recent disturbed sites in this system. We assessed the herbivore-mediated facilitation hypothesis by comparing plant number with and without signs of herbivory, height, and reproductive output for species growing in zones occupied by *Euphorbia* individuals versus species in adjacent open zones free of *Euphorbia*. Additionally, we examined community-level responses by comparing species composition, richness, and diversity between zones with and without *Euphorbia*.

Materials and methods

Study area

The study was conducted at Parque Luro Provincial Reserve in La Pampa Province, Argentina (36°54’33″S, 64°15′38″W). Parque Luro covers 7,500 ha, and is the only natural reserve protecting the Caldenal vegetation type. Mean annual precipitation and temperature for Santa Rosa (30 km N to Parque Luro) are 638 mm (1911–2010; G. Vergara,

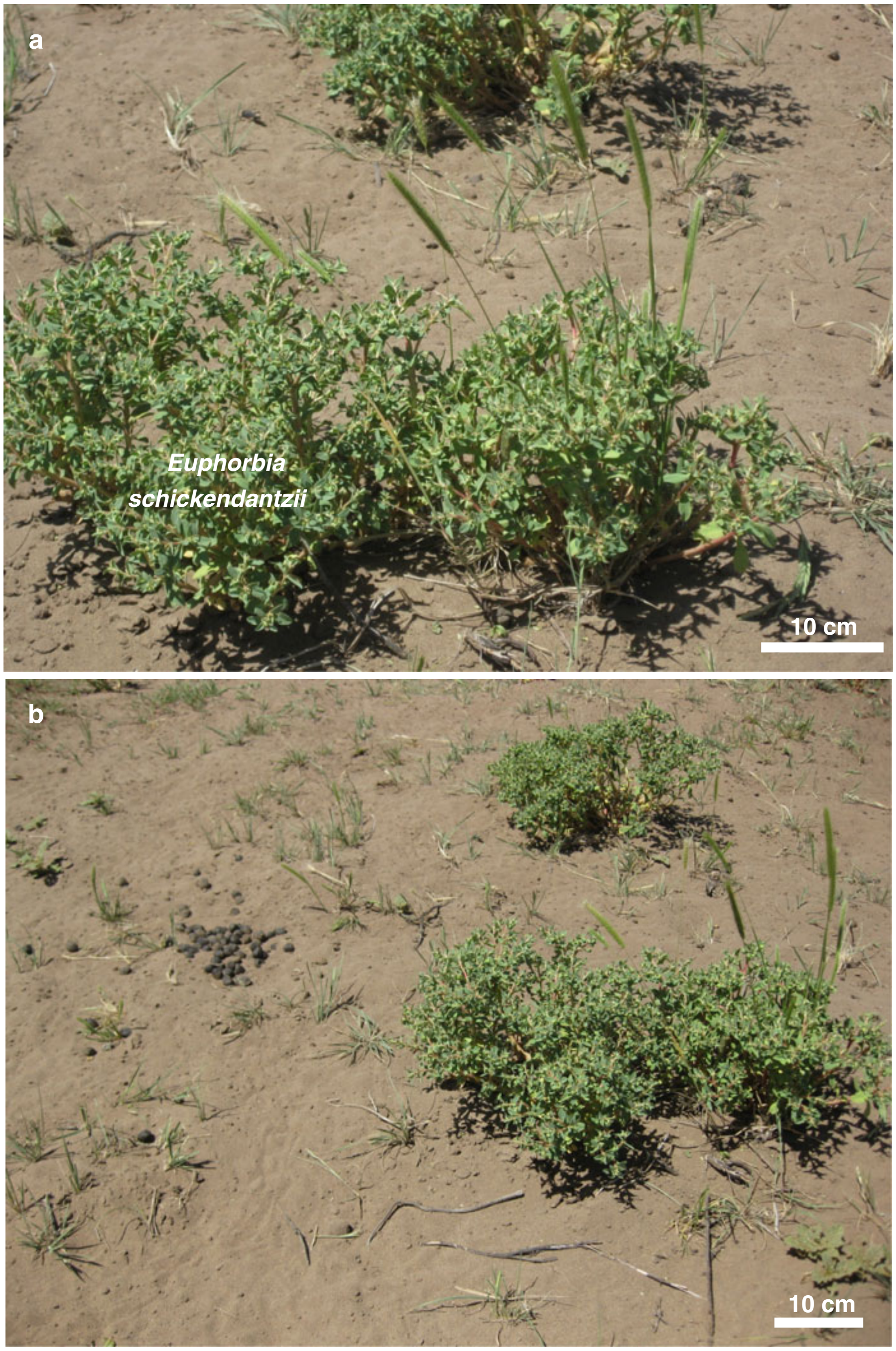

Plate 1 Ruderal communities in semi-arid forest of central Argentina (Caldenal). Plants growing inside zones occupied by *E. schickendantzii*, a native herb rich in latex, appear to exhibit increased size and fecundity as compared to those in open zones (**a**). These communities are intensively grazed by large herbivores, as indicated by the presence of tracks, feces, and plant consumption (**b**)

UNLPam, *unpublished data*) and 15.4 °C (1941–1990; www.worldclimate.com), respectively. Precipitation falls mainly in the form of rain during the spring and summer. Soils are sandy and the vegetation is characterized by xerophytic woodland, dominated by *Prosopis caldenia*. Less abundant woody vegetation includes

P. flexuosa, Geoffrea decorticans, Condalia microphylla, and *Schinus fasciculatus.* The herbaceous layer is dominated by perennial bunchgrasses, such as *Piptochaetium napostaense*, *Poa ligularis*, *Jarava ichu, Nassella tenuisima,* and *N. tenuis*. The largest herbivore in the reserve is the exotic red deer (*Cervus elaphus*), which occurs at high densities (0.36 deer/ha; Salomone 2005).

Lightening and human-induced fires are common in the Caldenal (Medina et al. 2000). To prevent damages from fire, Parque Luro has an extensive net of fire-breaks, covering 3 % of the reserve (González-Roglich et al. 2012). These fire-breaks are plowed yearly before the fire season (December to March, summer time in the southern hemisphere), leading to the establishment of native and exotic ruderal species, including *Euphorbia*, on the breaks (Chiuffo 2009). The main emergence pulse of ruderals in the Caldenal occurs in the fall (March–April). Red deer commonly graze on these ruderal plants. *Euphorbia* resembles the shape of a prolate spheroid, reaches 0.40 m high, 0.40 m long, and 0.35 m width, and occurs in discrete patches (Online Resource 1).

Sampling design

Sampling was conducted in six populations of *Euphorbia* located in a 1,500 × 40 m area (6 ha) along fire-breaks plowed in December 2008. The shortest distance between populations ranged from 100 to 750 m. Vegetation sampling was conducted at the peak flowering time of most species in the spring (November) of 2009. In each population, co-occurring ruderal plants were sampled within the zone occupied by 30 randomly selected individuals of *Euphorbia* and outside this zone (hereafter referred as open), except for one of the populations, for which 31 *Euphorbia*-open pairs were selected. The open zone was located adjacent to and at a random direction from each *Euphorbia* individual and covered an area equal to that of *Euphorbia* (Online Resource 2). Response variables measured in *Euphorbia* and open zones included plant number with and without signs of vertebrate herbivory, height, and reproductive output (number of flowers/inflorescences and/or fruits/infructescenses, Table 1) of all species. Plant height and reproductive output were measured on a maximum of three individuals per species per zone. The mean of these three individuals was introduced into the analyses. Plant counts were used to estimate herbivory as the proportion between number of plants with signs of vertebrate consumption and total number of plants present in each zone, as well as to determine species richness, diversity (Shannon index; Shannon 1948), and relative abundances. Species were classified as palatable or unpalatable based on published sources of their chemical and physical characteristics. Finally, feces in the sampling zones were counted and identified.

Data analyses

Species-level comparisons between *Euphorbia* and open zones were performed on species common enough to apply statistical tests on the different variables (four species, representing 17 % of species and 77 % of relative abundance in the community; see Results). Number of individuals and herbivory were analyzed using Generalized Linear Mixed Models (GLMMs) with a Poisson error distribution and log link function and a Binomial distribution and logit link function, respectively. In turn, size and reproductive output were assessed with Linear Mixed Models (LMMs). In both cases, population was entered as a random factor, zone as a fixed factor, and zone pairing as a blocking factor into the model. Except for height in *Hordeum euclaston*, which did not require transformation, height and number of flowers and fruits were transformed with the logarithmic function to meet test assumptions (Bolker et al. 2009).

Plant counts in all 362 sampling units were used to conduct community-level comparisons between *Euphorbia* and open zones with detrended correspondence analysis (DCA, Hill and Gauch 1980). Following Callaway et al. (2000, 2005), differences between communities were assessed by comparing the degree of overlap of 95 % confidence intervals of ordination scores, and assemblages were considered different if they did not overlap in at least one of the ordination axis (Cavieres and Badano 2009). In addition, totals counts per species were used to visually explore the association between species and zone types also with DCA. Finally, species richness and diversity were compared in and out *Euphorbia* with a GLMM (Poisson distribution and log link function) and LMM, respectively. As before, population was considered as a random factor, zone a fixed factor, and zone pairing a blocking factor.

Table 1 Species recorded in the studied ruderal community along with information on their relative abundances, palatability, life cycle and form, type of reproductive output assessed, and origin

Species	Relative abundance		Palatability	Life cycle and form	Reproductive output assessed	Origin
	Euphorbia	Open				
Bromus catharticus var. *rupestris*	0.493	0.480	P[a]	AG	Infructescences	N
Hordeum euclaston	0.210	0.116	P[a]	AG	Infructescences	N
Lycopsis arvensis	0.052	0.078	U[b]	AH	Inflorescence and/or infructescences	E
Solanum elaeagnifolium	0.047	0.102	U[a]	PH	Flowers and/or fruits	N
Gamochaeta calviceps	0.044	0.037	P[b]	AH	Inflorescence and/or infructescences	N
Panicum urvilleanum	0.043	0.034	P[a]	PG	Infructescences	N
Cynodon hirsutus	0.039	0.076	P/U[a,b,c]	PG	Infructescences	E
Amelichloa brachychaeta	0.017	0.017	U[a]	PG	–	N
Jarava ichu	0.011	0.004	U[a]	PG	–	N
Conyza bonariensis	0.009	0.011	P[a]	AH	Inflorescence and infructescences	N
Solanum juvenale	0.007	0.027	U[a]	PH	Flowers and fruits	N
Vulpia australis	0.007	0	P[a]	AG	Infructescences	N
Descurainia erodiifolia	0.006	0.007	–	AH	Flowers and/or fruits	N
Chenopodium album	0.006	0.002	P[d]	AH	–	E
Silene anthirrina	0.004	0	–	AH	Flowers and/or fruits	E
Plantago patagonica	0.002	0.002	P[a]	AH	Inflorescences and/or infructescences	N
Piptochaetium napostaense	0.002	0	P[a]	PG	Infructescences	N
Lactuca serriola	0.001	0.002	U[a]	AH	Inflorescences and/or infructescences	E
Centaurea solstitialis	0.001	0	P/U[e]	AH	Inflorescences and/or infructescences	E
Hypochaeris radicata	0.001	0	–	AH	Inflorescences and/or infructescences	E
Oenothera odorata	0.001	0	P[a]	PH	–	N
Baccharis ulicina	0	0.001	U[a]	PSS	Inflorescences and/or infructescences	N
Salsola kali	0	0.001	U[f]	AH	–	E
Unidentified sp.[g]	0	0.002	–	–	–	–

p palatable, *u* unpalatable, – unknown, *A* annual, *P* perennial, *G* grass, *H* herb, *SS* sub-shrub, *E* exotic, *N* native

[a] Cano (1988)

[b] Troiani and Steibel (2008)

[c] *C. hirsutus* produces nitrites and cyanogenic substances under certain conditions of moisture and temperature

[d] Marten and Andersen (1975)

[e] *C. solstitialis* is considered as palatable until the onset of floral stems (Thomsen et al. 1993)

[f] USDA (1937)

[g] Species with only two small individuals (0.015 m and 0.02 m height) in vegetative stage that could not be identified

Mixed Models were conducted with IBM® SPSS® Statistics 20. DCA were performed with the free software PAST 2.17 (Hammer et al. 2001), which uses the same algorithms as DECORANA (Hill and Gauch 1980), with modifications according to Oxanen and Minchin (1997) and Hammer 2012). Finally, means and 95 % confidence intervals of ordination scores were calculated with Systat software® SigmaPlot 11.0.

Results

Community dominants *Bromus catharticus* var. *rupestris* and *H. euclaston* (Table 1) exhibited greater establishment, size, and fecundity in *Euphorbia* than open zones, and these highly palatable species were much more consumed in the open (Table 2; Fig. 1a–d). In contrast, establishment of *Solanum elaeagnifolium*, one of the best defended plants against herbivores in the system (Cano 1988; Troiani and Steibel 2008), was greater in open relative to *Euphorbia* zones, and it experienced low herbivory in both zones. In fact, *S. elaeagnifolium* was the only species for which *Euphorbia* offered no significant protection from herbivores (Fig. 1d). Finally, *Gamochaeta calviceps* also was larger when growing inside than outside *Euphorbia* zones, but showed no statistical differences in number of individuals and fecundity between zones. No herbivory was observed on *Euphorbia*. Feces found in the study area indicated that plant consumption was largely performed by two exotic mammals, red deer (64 % of recorded feces) and European hare (*Lepus europaeus*, 35 %). The rest of the feces were produced by a granivore, the native dove *Patagioenas picazuro*.

Although the distributions of ordination scores resulting from plant counts in *Euphorbia* and open zones displayed some overlap (Fig. 2a), communities associated with these zones differentiated in relation to axis 2 of the DCA (Fig. 2b). Also, DCA conducted with total plant counts for each species showed that different species tended to occur in different zones (Fig. 2c). In fact, six species, that is, 25 % of the total number of species recorded in the study area (Table 1), occurred only in zones occupied by *Euphorbia*, while other three species occurred only in open zones. Species palatability seemed to be important in this association, as all species with reported palatability growing only in the *Euphorbia* zone were palatable, while all identified species occurring only in the open were unpalatable (Table 1; Fig. 2c). Similarly, ordination scores of most palatable species tended to be closer to *Euphorbia*, while those of most unpalatable species tended to be closer to open zones. Lastly, both community richness and diversity were slightly, but significantly higher in *Euphorbia* than open zones [richness: 2.695 ± 0.218 (mean ± SD) vs. 2.291 ± 0.399, respectively, $F_{zone\ 1,360} = 6.057$, $p = 0.014$; diversity: 0.753 ± 0.107 vs. 0.606 ± 0.175, $F_{zone\ 1,\ 325.419} = 8.637$, $p = 0.004$].

Discussion

Studies of positive interactions among plants have been conducted in many communities (Fuentes et al. 1986; Vieira et al. 1994; Bertness and Leonard 1997; Callaway et al. 2002; Gómez-Aparicio et al. 2005; Graff et al. 2007; Lortie and Turkington 2008; Fajardo and McIntire 2011; Cavieres and Almeida 2012), but excepting for marsh environments (Bertness 1991; Bertness and Shumway 1993; Huckle et al. 2000; Alberti et al. 2008), they are surprisingly rare in communities establishing at the onset of secondary successions. In our work, dominant and highly palatable ruderal species displayed increased establishment, size, and reproductive output, and decreased consumption when growing within zones occupied by an herb rich in latex, *Euphorbia*, than when in open zones free of the herb. Similarly, a less abundant, but also palatable, species showed increments in size, and lower consumption in *Euphorbia* relative to open zones. The exception to this pattern was a species physically (abundant spines) and chemically (alkaloids) well defended against herbivores, *S. elaeagnifolium* (Cano 1988), for which establishment was greater in the open and, as expected, herbivory was low in both sampling zones. In addition, palatable plants tended to be associated to *Euphorbia*, while unpalatable plants tended to be associated to open spaces. Importantly, the plant community occurring in *Euphorbia* zones differed in composition, richness, and diversity from that in the open, with a richer and more diverse community growing in zones covered by the herb. These results strongly suggest that *Euphorbia* exerts community-level facilitation by protecting other ruderals from herbivory in recently disturbed sites in the semi-arid forest of central Argentina. The study thus indicates that positive interactions can also play an important role in organizing plant communities initiating secondary successions in terrestrial systems.

Although data from this research offer evidence in support of our hypothesis, the descriptive approach of the study precludes ruling out the possibility that

Table 2 Statistical results for species common enough to conduct comparisons in plant number, size, reproductive output, and consumption between zones occupied by *Euphorbia* and adjacent open zones

Species	Number of individuals	Size	Reproductive output	Herbivory
Bromus catharticus var. *rupestris*	$F_{zone\ 1,\ 318} = 28.753$; $p < 0.001$	$F_{zone\ 1,\ 259.741} = 369.170$; $p < 0.001$	$F_{zone\ 1,\ 238.494} = 33.511$; $p < 0.001$	$F_{zone\ 1,\ 265} = 354.028$; $p < 0.001$
Hordeum euclaston	$F_{zone\ 1,\ 220} = 59.141$; $p < 0.001$	$F_{zone\ 1,\ 132.103} = 146.079$; $p < 0.001$	$F_{zone\ 1,\ 145.423} = 11.368$; $p = 0.001$	$F_{zone\ 1,\ 147} = 51.238$; $p < 0.001$
Solanum elaeagnifolium	$F_{zone\ 1,\ 128} = 7.670$; $p = 0.006$	–	–	$F_{zone\ 1,\ 84} = 0.280$; $p = 0.598$
Gamochaeta calviceps	$F_{zone\ 1,\ 100} = 1.671$; $p = 0.199$	$F_{zone\ 1,\ 43.097} = 40.460$; $p < 0.001$	$F_{zone\ 1,\ 57.088} = 3.386$; $p = 0.071$	$F_{zone\ 1,\ 58} = 13.257$; $p = 0.001$

additional mechanisms are at work. For example, *Euphorbia* could also exert direct positive effects on other plants by improving physical conditions (Callaway 2007). The studied ruderal community occurs on coarse soils, and shading from *Euphorbia* may locally reduce water deficits and accelerate mineralization rates (e.g. Maestre et al. 2003; Gómez-Aparicio et al. 2005). Also, seed trapping by *Euphorbia* could contribute to differences in plant number between zones with and without the species (Day and Wright 1989). Similar growth forms between the benefactor and beneficiaries rise, on the other hand, the possibility that net direct effects of *Euphorbia* on other ruderals may not only be positive (He et al. 2013). In fact, in the absence of herbivores, direct resource competition may become the prevailing interaction between *Euphorbia* and the other ruderals (Holmgren et al. 1997). This change in the sign of the net effects of the interaction may explain the greater number of individuals outside than inside *Euphorbia* zones in *S. elaeagnifolium*, a species that presumably does not need further protection from herbivores. Also, shifts in facilitative and competitive net effects mediated by herbivores have been shown to alter successional trajectories and rates (Alberti et al. 2008), and similar processes could operate in the studied community. Additional experimental work is warranted to fully assess these direct and indirect interactions (e.g., Chaneton et al. 2010) and how they affect successional dynamics in our system. The herbaceous nature of the community offers an exceptional opportunity for conducting required manipulations.

Protection from herbivory is the most studied type of indirect facilitation among plants (Callaway 2007); however, only a few studies have previously assessed the effects of this indirect interaction at the community level. Moreover, compared to studies at individual and population levels, community-level assessments are uncommon in research on facilitation in general (Cavieres and Badano 2009). Nonetheless, inquiries at this level are important because they allow evaluating how facilitation affects ecological metrics relevant for conservation agendas, such as species richness and diversity (Groom et al. 2006). Similar to our findings, Callaway et al. (2000, 2005) reported changes in composition between communities growing under the protection of unpalatable plants, *Cirsium obvalatum* and *Veratrum lobelianum*, versus those in open microsites, as well as increments in richness and diversity in communities associated to *C. obvalatum* in overgrazed grasslands in the Caucasus. In turn, Rebollo et al. (2002) detected increments in diversity in communities protected by *Opuntia polycantha* relative to unprotected communities in the North American shortgrass steppe. Differences in species diversity responded to changes in species dominance, not number, in that system. As already proposed, variations in grazing pressure, plant community composition, and/or grazing evolutionary history may explain differences in the effect of facilitation via protection from herbivory on plant richness among systems (Milchunas et al. 1988; Rebollo et al. 2002; Callaway et al. 2005).

In a recent evaluation of direct facilitative effects on plant richness, Cavieres and Badano (2009) emphasized that rather than differences in richness between zones with and without a benefactor, what matters is to determine whether the number of species in the community is increased because of the presence of the benefactor. That is, even when richness is lower in zones with than without a benefactor, the overall richness of the community can be increased if the composition of the communities growing in these zones differs. In our study, six out of 24 species

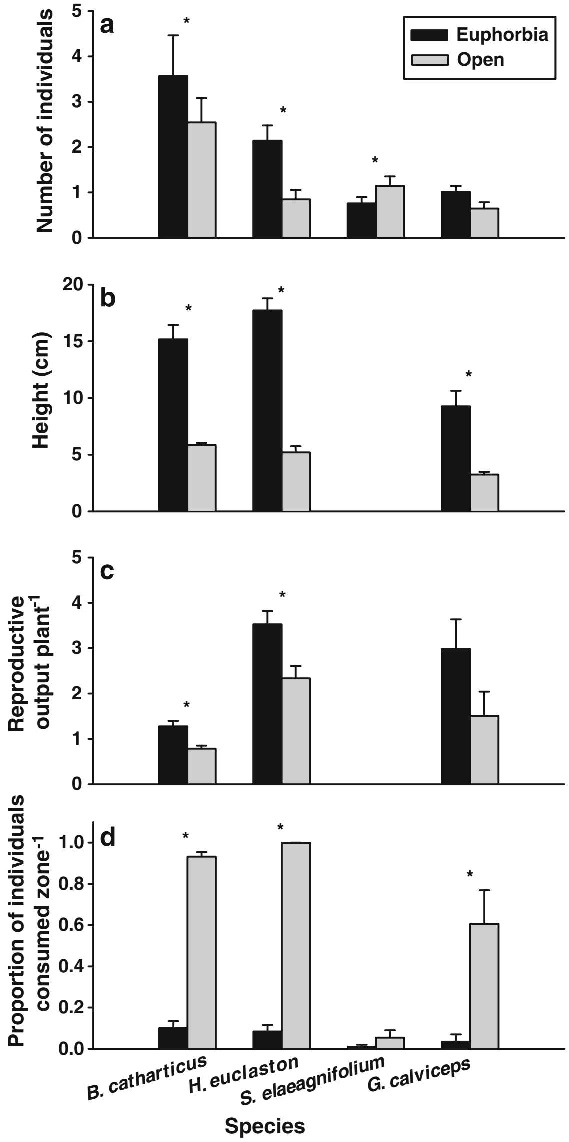

Fig. 1 Number of individuals (**a**), size (**b**), reproductive output (**c**), and herbivory (**d**) for four ruderal species with enough data to conduct statistical comparisons between *Euphorbia* and adjacent open zones. *Asterisks* indicate significant differences ($p < 0.05$) between zones. Bars are means+1 SE ($n = 6$ *Euphorbia* populations)

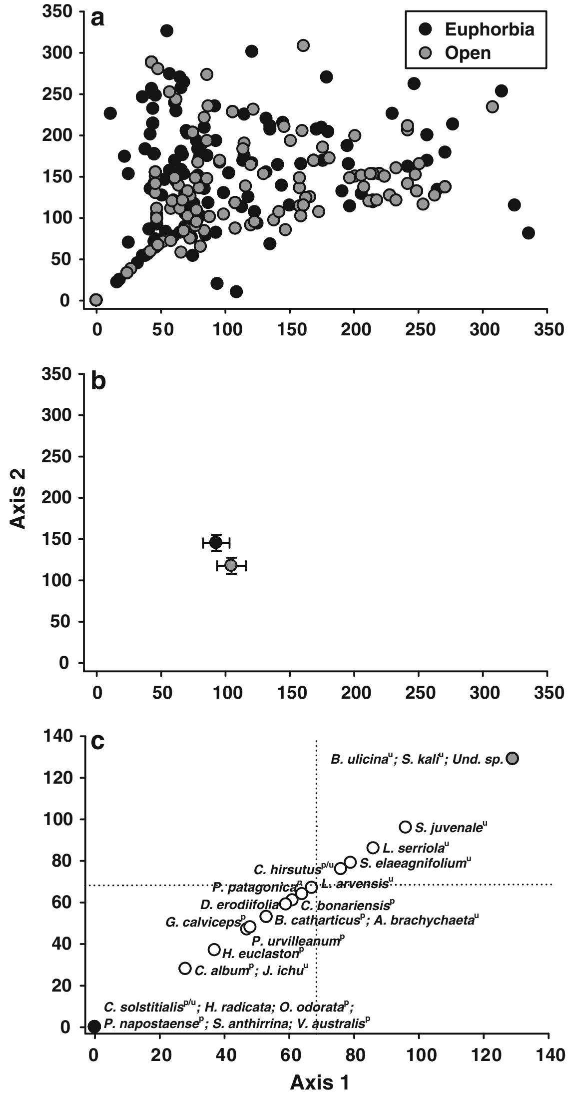

Fig. 2 Distributions of ordination scores for all plant counts recorded in *Euphorbia* and open zones ($n = 181$ *per* zone, **a**). Means and 95 % confidence intervals of these ordination scores (**b**). Distribution of ordination scores (*white symbols*) using total plant counts per species along with scores of sampling zones; symbols of species occurring only in either *Euphorbia* or open zones are under symbols of sampling zones (**c**)

occurred exclusively in the zones protected by *Euphorbia*; consequently, 25 % of the richness in the community resulted from the presence of *Euphorbia*.

Two human effects set the stage where the explored indirect positive interaction occurs. First, the ruderal community colonizes sites that had been altered by an anthropogenic disturbance, plowing, applied to limit the propagation of fire. Second, feces found in the study area indicate that facilitative effects of *Euphorbia* on other ruderals are largely mediated by two exotic herbivores, the European hare and red deer, introduced in Argentina in late 1800 and early 1900, respectively (Navas 1987; Bonino 2006). Actually, the site of introduction of the red deer was Parque Luro in times when the reserve was a private ranch. This positive indirect interaction, however, might not be that novel to the system. Natural disturbance, such as animal borrowing, fire, and grazing could have provided sites for colonization, and native ruderals, such as *Euphorbia* and several others recorded in the studied community, are common and diverse in the Caldenal (Rúgolo et al. 2005; Troiani and Steibel 2008). Also, now locally absent native herbivores, including guanacos (*Lama guanicoe*), venados de las pampas (*Ozotocerus bezoarticus*), vizcachas (*Lagostomus maximus*), and maras (*Dolichotis patagonum*), in addition to those belonging to the rich array of families extinct in the Pleistocene (Patterson and Pascual 1972; Bucher 1987) could have promoted similar protective effects by *Euphorbia*. Moreover, suggestive of a typical neotropical anachronism (Janzen and Martin 1981), physical and chemical defenses are common in native herbs in the Caldenal (Cabrera and Willink 1973). Thus, this interaction could have influenced plant communities over evolutionary time in this system.

While asserting the novelty of this interaction can be difficult, our study shows that currently *Euphorbia* protects several species from overgrazing, and that this indirect interaction exerts effects at the community level of organization, altering species composition and increasing richness and diversity in ruderal communities in central Argentina. These findings make imperative the integration of positive interactions among plants into conservation plans.

Acknowledgments We are in debt to students in the 2009 Biogeography course, FCEyN, UNLPam, and personnel of the Parque Luro Provincial Reserve for field assistance and logistical support. Plant species in this study were generously identified by A. Prina. We also thank R. Callaway and two anonymous reviewers for insightful comments on earlier versions of this manuscript. Funds for this research were provided by FCEyN, UNLPam (Project No. 219), and Agencia Nacional de Promoción Científica y Tecnológica-UNLPam (PRH PICT 0287).

References

Agrawal A, Konno K (2009) Latex: a model for understanding mechanisms, ecology, and evolution of plant defense against herbivory. Annu Rev Ecol Evol Syst 40:311–331

Alberti J, Escapa M, Iribarne O et al (2008) Crab herbivory regulates plant facilitative and competitive processes in Argentinean marshes. Ecology 89:155–164

Bach CE (1994) Effects of a specialist herbivore (*Altica subplicata*) on *Salix cordata* and sand dune succession. Ecol Monogr 64:423–445

Bazzaz FA (1979) The physiological ecology of plant succession. Annu Rev Ecol Evol Syst 10:351–371

Bertness M (1991) Interspecific interactions among high marsh perennials in a New England salt marsh. Ecology 72:125–137

Bertness M, Callaway RM (1994) Positive interactions in communities. Trends Ecol Evol 9:191–193

Bertness M, Leonard GH (1997) The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78:1976–1989

Bertness M, Shumway SW (1993) Competition and facilitation in marsh plants. Am Nat 142:718–724

Bolker BM, Brooks ME, Clark CJ et al (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Bonino NA (2006) Estado actual del conocimiento sobre la liebre europea y el conejo europeo introducidos en la Argentina. INTA, Bariloche (in Spanish)

Bruno JF, Stachowicz JJ, Bertness M (2003) Inclusion of facilitation into ecological theory. Trends Ecol Evol 18:119–125

Bucher EH (1987) Herbivory in arid and semi-arid regions of Argetina. Rev Chil Hist Nat 60:265–273

Cabrera A, Willink A (1973) Biogeografia de America Latina. Serie Biologia No: 13. OEA, Washington, DC (in Spanish)

Callaway RM (2007) Positive interactions and interdependence in plant communities. Springer, Dordrecht

Callaway RM, Kikvidze Z, Kikodze D (2000) Facilitation by unpalatable weed may conserve plant diversity in overgrazed meadows in the Caucasus Mountains. Oikos 89:275–282

Callaway RM, Brooker RW, Choler P et al (2002) Positive interactions among alpine plants increase with stress. Nature 417:844–848

Callaway RM, Kikodze D, Chiboshvili M et al (2005) Unpalatable plants protect neighbors from grazing and increase plant community diversity. Ecology 86:1856–1862

Cano E (1988) Pastizales naturales de La Pampa. Descripción de las especies más importantes. Convenio AACREA—Provincia de La Pampa, Santa Rosa (in Spanish)

Carson WP, Root RB (1999) Top-down effects of insect herbivores during early succession: influence on biomass and plant dominance. Oecologia 121:260–272

Cavieres L, Almeida A (2012) Facilitative interactions do not wane with warming at high elevations in the Andes. Oecologia 170:575–584

Cavieres L, Badano E (2009) Do facilitative interactions increase species richness at the entire community level? J Ecol 97:1181–1191

Chaneton EJ, Mazia CN, Kitzberger T (2010) Facilitation vs. apparent competition: insect herbivory alters tree seedling recruitment under nurse shrubs in a steppe-woodland ecotone. J Ecol 98:488–497

Chiuffo M (2009) Efecto de las picadas y caminos en la invasión de especies herbáceas en la Reserva Provincial Parque Luro. Undergraduate Thesis. Universidad Nacional de La Pampa, Santa Rosa (in Spanish)

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. Am Nat 111:1119–1144

Day TA, Wright RG (1989) Positive plant spatial association with *Eriogonum ovalifolium* in primary succession on cinder cones: seed-trapping nurse plants. Vegetatio 80:37–45

Fajardo A, McIntire EJB (2011) Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. J Ecol 99:642–650

Fuentes ER, Hoffmann AJ, Poiani A, Alliende MC (1986) Vegetation change in large clearings: patterns in the Chilean Matorral. Oecologia 68:358–366

Gómez-Aparicio L (2009) The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. J Ecol 97:1202–1214

Gómez-Aparicio L, Gómez JM, Zamora R (2005) Microhabitats shift rank in suitability for seedling establishment depending on habitat type and climate. J Ecol 93: 1194–1202 (in Spanish)

González-Roglich M, Villarreal D, Castro M (2012) Evaluación de la efectividad de la Reserva Parque Luro como herramienta de conservación del Caldenal pampeano: cambios en la cobertura vegetal a nivel de paisaje entre 1960 y 2004. Ecología Austral 22:11–21

Graff P, Aguiar M, Chaneton EJ (2007) Shift in positive and negative plant interactions along a grazing intensity gradient. Ecology 88:188–199

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194

Groom MJ, Meffe GK, Carroll CR (2006) Principles of conservation biology. Sinauer Associates, Sunderland

Hammer Ø (2012) PAST, PAleontological Statistics, Version 2.17. Reference manual

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontol Electron 4(1):9

Harris LG, Ebeling AW, Laur DR et al (1984) Community recovery after storm damage: a case of facilitation in primary succession. Science 224:1336–1338

He Q, Bertness M, Altieri AH (2013) Global shifts towards positive species interactions with increasing environmental stress. Ecol Lett. doi:10.1111/ele.12080

Hill MO, Gauch HG Jr (1980) Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47–58

Holmgren M, Scheffer M (2010) Strong facilitation in mild environments: the stress gradient hypothesis revisited. J Ecol 98:1269–1275

Holmgren M, Scheffer M, Huston MA (1997) The interplay of facilitation and competition in plant communities. Ecology 78:1966–1975

Holmgren M, Gómez-Aparicio L, Quero JL, Valladares F (2012) Non-linear effects of drought under shade: reconciling physiological and ecological models in plant communities. Oecologia 169:293–305

Huckle JM, Potter JA, Marrs RH (2000) Influence of environmental factors on the growth and interactions between salt marsh plants: effects of salinity, sediment and waterlogging. J Ecol 88:492–505

Huston M, Smith T (1987) Plant succession: life history and competition. Am Nat 130:168–198

Janzen DH, Martin PS (1981) Neotropical anachronisms: the fruits the Gomphoteres ate. Science 215:19–27

Lortie CL, Turkington R (2008) Species-specific positive effects in an annual plant community. Oikos 117:1511–1521

Lortie CL, Brooker RW, Choler P et al (2004) Rethinking plant community theory. Oikos 107:433–438

Maestre FT, Bautista S, Cortina J (2003) Positive, negative, and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. Ecology 84:3186–3197

Maestre FT, Callaway RM, Valladares F, Lortie CJ (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. J Ecol 97:199–205

Marten GC, Andersen RN (1975) Forage nutritive value and palatability of 12 common annual weeds. Crop Sci 15:821–827

Medina AA, Dussart EG, Estelrich HD et al (2000) Reconstrucción de la historia del fuego en un bosque de *Prosopis caldenia* (Burk.) de Arizona, sur de la provincia de San Luis. Multequina 9:91–98

Michalet R, Broker RW, Cavieres LA, Kikvidze Z, Lortie CJ, Pugnaire FI, Valiente-Banuet A, Callaway RM (2006) Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? Ecol Lett 9:767–773

Milchunas DG, Sala OE, Lauenroth WK (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. Am Nat 132:87–106

Navas JR (1987) Los vertebrados exóticos introducidos en la Argentina. Museo Argentino de Ciencias Naturales, Buenos Aires (in Spanish)

Oxanen J, Minchin PR (1997) Instability of ordination results under changes in input data order: explanations and remedies. J Veg Sci 8:447–454

Patterson B, Pascual R (1972) The fossil mammal fauna of South America. In: Keast A, Erk F, Glass B (eds) Evolution, mammals, and the southern continents. State University of New York Press, New York, pp 247–309

Rebollo S, Milchunas DG, Noy-Meir I et al (2002) The role of a spiny plant refuge in structuring grazed short grass steppe plant communities. Oikos 98:53–64

Rees M, Condit R, Crawley M et al (2001) Long-term studies of vegetation dynamics. Science 293:650–655

Rúgolo de Agrasar ZE, Steibel PE, Troiani HO (2005) Manual ilustrado de las gramíneas de la provincia de La Pampa. Editorial de la Universidad Nacional de La Pampa. Santa Rosa-Editorial de la Universidad Nacional de Río Cuarto, Río Cuarto (in Spanish)

Salomone F (2005) Desarrollo de un índice de abundancia relativa para ciervo colorado (*Cervus elaphus*) en la reserva provincial Parque Luro, La Pampa. Informe final. Consejo Federal de Inversiones Provincia de La Pampa. (in Spanish)

Seabloom EW, Harpole WS, Reichman OJ et al (2003) Invasion, competitive, dominance, and resource use by exotic and native California grassland species. Proc Natl Acad Sci USA 100:13384–13389

Shannon CE (1948) A mathematical theory of communication. Bell System Tech J 27(379–423):623–656

Thomsen CD, Williams WA, Vayssies MP et al (1993) Controlled grazing on annual grassland decreases yellow starthistle. Calif Agric 47:36–40

Thorpe AS, Aschehoug E, Atwater DZ, Callaway RM (2011) Interactions among plants and evolution. J Ecol 99:729–740

Tilman D (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecol Monogr 57:189–214

Troiani H, Steibel P (2008) Reconocimiento de malezas: Región subhúmeda y semiárida pampeana. Universidad Nacional de La Pampa, Colegio de Ingenieros Agrónomos de La Pampa, Santa Rosa

U.S. Department of Agriculture, Forest Service (1937) Range plant handbook. Washington, DC

Vieira ICG, Uhl C, Nepstad D (1994) The role of the shrub *Cordia multispicata* Cham. as a "succession facilitator" in an abandoned pasture, Paragominas. Amazônia. Vegetatio 115:91–99