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ARTICLE

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ABSTRACT

Background: The effects of many invasive species on invaded communities are still scarcely known. *Centaurea solstitialis* is an invasive Eurasian herb, widely distributed around the world, but its effects on recipient communities are not well known.

Aims: To evaluate the effect of *C. solstitialis* invasion on richness and cover of native and exotic resident species in naturally established communities.

Methods: We repeated a field experiment in three old-fields of central Chile where *C. solstitialis* was not present. The experiment simulated the invasion of *C. solstitialis* by adding 600 seeds per plots of 1 × 1 m in size and compared the richness and cover of all naturally growing species in plots with and without *C. solstitialis*.

Results: For exotics, initial species richness (average ca.18% and 20% per site), and cover (average ca. 20% and 34% per site) were significantly reduced by *C. solstitialis* in two out of the three sites. The abundances of four out of 17 exotic resident species were negatively affected by *C. solstitialis*. Native species were not affected by *C. solstitialis*.

Conclusions: *C. solstitialis* can outcompete resident species of communities where it invades, but local ecological factors influence its effects producing different impacts among species and localities.

Introduction

The study of biological invasions requires understanding of the factors that drive invasions (e.g. Sax et al. 2005), and the impacts of alien species on resident communities (Levine et al. 2003). Alien species may have both negative and positive effects on the diversity and abundance of other species present in plant communities (Vilà et al. 2011). Negative effects of alien plant species may result from competitive interactions, allelopathic effects, pre-emption of resources, or indirectly from enhancing herbivory (e.g. Levine et al. 2003; Minchinton et al. 2006; Mason and French 2008; Gaertner et al. 2009; Hejda et al. 2009; Rudgers and Orr 2009; Flory and Clay 2010). Positive effects of invaders may result from improved microenvironmental conditions for other species or reduction of herbivores and pathogens (Rodríguez 2006; Fischer et al. 2009; Becerra and Montenegro 2013).

Areas where native vegetation has been degraded or significantly reduced are frequently invaded by exotic plants (Davis et al. 2000; Mitchell et al. 2006). In order to restore native vegetation, exotic species that adversely affect native species should be eradicated or controlled. By contrast, exotics that facilitate native species might be used to accelerate recolonisation and recovery of native vegetation before initiating an eradication programme (D'Antonio and Meyerson 2002; Becerra and Montenegro 2013). Exotic species that have strong negative effects on the invaded community should receive more attention in control and management plans. These species are not necessarily the most abundant within a community (Hulme 2006).

Centaurea solstitialis L. (Asteraceae) is a ruderal herb native to the eastern Mediterranean and the Caucasus region (Maddox et al. 1985). This species has been introduced accidentally around the world (Maddox et al. 1985) and is one of the most abundant exotics in south-western US and central Argentina (Maddox et al. 1985; Hierro et al. 2006). *Centaurea solstitialis* is also present in central Chile, between ca. 32 and 36°S (Matthei 1995); however, its success is highly variable within this region (Andonian et al. 2011). Various studies have evaluated factors affecting the invasion of this exotic herb (Di Tomaso et al. 2003; Reever and Rice

2005; Hierro et al. 2006, 2009, 2011, 2016; Qin et al. 2007; Lortie et al. 2009; Munshaw and Lortie 2010; Miguel et al. 2017). For Hierro et al. (2006), Hierro et al. (2009, 2016) have found that recruitment of *C. solstitialis* was enhanced by higher humidity and that disturbances increased the success of this species. Hierro et al. (2016) have also shown that the presence of *C. solstitialis* negatively affected the post-disturbance recovery rate of resident species. Lortie et al. (2009) have found that the density of *C. solstitialis* monocultures was positively related to survival and negatively related to germination of this species. Hierro et al. (2011) have found that the removal of resident vegetation enhanced *C. solstitialis* performance. However, the impacts of *C. solstitialis* on plant communities present in regions that it has invaded are still not well known. Qin et al. (2007) have shown in the laboratory that *C. solstitialis* competitively suppressed five species native to California. Gómez-González et al. (2009) have shown that in a greenhouse setting, this exotic species has the potential to outcompete two native species of central Chile. Hulvey and Zavaleta (2012), in a mesocosm experiment (made in a field where all species were artificially established), found that the increase of *C. solstitialis* biomass reduced the individual size of a native resident herb species, and Zavaleta and Hulvey (2007), in the same mesocosm system, have found that *C. solstitialis* reduced species richness and biomass of forbs but not those of other functional groups. Thus, the impacts of this worldwide invasive herb at a community level have been little studied and impacts on diversity of resident species have not been experimentally evaluated on naturally regenerated communities. The extent to which these impacts may vary among resident species and localities has also not been evaluated. We report the effect of the exotic herb *Centaurea solstitialis* on resident plant species of natural communities of a Mediterranean-type ecosystem in central Chile, and the extent to which this effect varies within this region. We simulated the invasion of *C. solstitialis* beginning at the seed stage, through sowing of this species in natural communities.

Materials and methods

The study species

Centaurea solstitialis is a facultative winter annual species (sometimes biennial or short-lived perennial with a tap root). It produces rosette leaves that lie close to the ground, and erect stems 0.15–2 m in height. *Centaurea solstitialis* has a large taproot that grows to 1 m deep or more (Sheley et al. 1993). The yellow flower heads produce two types of achenes (seeds), most of them (75–90%) with a short pappus but some achenes lacking a pappus (mainly at the periphery of the flower head). Large plants can produce nearly 75,000 seeds with 87.6% to 95.2% viability (Benefield et al. 2001). In *C. solstitialis* populations, seed density in the soil can range from 3,000 to 10,000 seeds m^{-2} (Di Tomaso et al. 1999), and seedbank longevity can be as long as 10 years (Callihan et al. 1993).

Study area

The study was carried out in the Mediterranean-type region of central Chile. Like all regions with Mediterranean-type climate, central Chile has been intensively disturbed by humans, and currently has large areas of open vegetation such as disturbed native forests, open shrublands, savannas and grasslands. These are frequently dominated by ruderal species, many of which are exotic annual herbs (Arroyo et al. 1995; Sax 2002; Figueroa et al. 2004).

We used three sites near the city of Santiago, situated between 5 and 20 km apart: San Carlos (33º23′54” S, 70º29′06” W; 1081 m a.s.l.) and San Ramón (33º25′51” S, 70º30′49” W; 919 m a.s.l.) located at a pre-Andean zone, and Rinconada (33º29”06” S, 70º52′30” W; 480 m a.s.l.) located in the central valley. Rainfall during the experiment was particularly low, reaching 203 mm at 500 m a.s.l. (Santiago-MOP station) and 259 mm at 700 m a.s.l. (Cerro Calán station) of annual precipitation during 2007 (348 and 441 mm are the historical average for 500 and 700 m a.s.l, respectively). We estimate that Rinconada probably received ca. 203 mm during the experimental year, and the other two sites probably more than 259 mm, as precipitation and soil moisture increases with elevation in this region (Becerra et al. 2016).

The San Carlos and San Ramón sites were located in open areas dominated by grasslands, surrounded by remnant fragments of native sclerophyllous forests. The Rinconada site was also grassland, but in this case within a savanna dominated by the tree *Acacia caven* and some few native shrubs. This indicates that the area of Rinconada probably had a longer history of anthropic disturbances (logging, fires, livestock), and/or that the other two sites have been able to recover better than Rinconada (Armesto and Pickett 1985). The experimental areas of all three sites were old fields with herbaceous vegetation

dominated by exotic herb species, mainly annuals (Figueroa et al. 2004). These sites are exposed to herbivory by European rabbits and sporadically by cattle and horses. However, there have been no recent fires or soil disturbance and the grassland has developed uninterruptedly in each site. The three sites all lacked *C. solstitialis*, but were located ca. 1 km from naturalised populations of *C. solstitialis*, which allowed us to minimise potential seed dispersal of this species. Thus, the sites represented elevations and habitats where *C. solstitialis* may potentially colonise.

We compared soil moisture among sites in December 2007 (six months after the first rain) through the gravimetric method. We collected soil samples (10 cm depth) from 10 randomly selected points within the experimental area in each site, during the same day. The observed soil water content was 1.30% ± 0.11 (mean ± 1 SE) for Rinconada, 1.73% ± 0.16 for San Ramón, and 1.52% ± 0.27 for San Carlos. Soil water content significantly differed between sites (ANOVA, F = 11.57, $P < 0.001$). San Ramón and San Carlos were not significantly different, but both were significantly moister than Rinconada (Tukey tests, $P < 0.05$).

Experimental design

At each of the three sites, an open herbaceous experimental area of 30 m x 30 m was fenced to prevent damage from domestic animals and rabbits. Within each exclosure, forty 1 m x 1 m experimental plots were established, separated by 1 m. In 20 randomly selected plots we sowed 600 seeds each of *C. solstitialis* in the central 0.5×0.5 part of the plots to control for edge effect. To do this, we buried the seeds under a thin layer of soil collected from the surrounding 1×1 m plot. Seeds were sown before germination of all resident species; as all species in the area were annuals, no live vegetation was present at the time of sowing. The remaining 20 experimental plots were maintained without the addition of *C. solstitialis* seeds. The total number of plots in this experiment was 120 (2 treatments x 20 replicates x 3 sites). The seed density used for this experiment was representative of real values of seed banks observed for *C. solstitialis* in the field (Hierro et al. 2006).

Seeds were sown in April 2007, before the arrival of the first rains. To avoid seeds being washed away, 0.5 m x 0.5 m x 0.15 m plastic frames were placed around the seeded area. We also installed identical frames in the unseeded plots in order to maintain similar micro-environmental conditions between treatment and control. Frames were removed shortly after the first seeds germinated. Each plot was visited at six, eight and ten months after sowing (in October 2007, December 2007 and February 2008).

At each visit, resident species composition and the percent cover of each species was estimated. Also, in order to describe the abundance reached by *C. solstitialis* in plots with seed addition, the number of individuals and percent cover of *C. solstitialis* present on each plot was recorded. The cover of each species was assessed by the point-intercept method using a 0.5 m x 0.5 m grid with 100 points.

Centaurea solstitialis was well established six months after the beginning of the experiment and the peak of its flowering phase was eight months after sowing (December 2007). The peak of cover and establishment of most resident species was six months after sowing (October 2007). This was probably the period with maximal plant–plant interactions. Therefore, we used data recorded during the sixth month after the beginning of the experiment.

Data analyses

We evaluated the effect of *C. solstitialis* on resident species through Generalised Linear Models (GLM, ANOVA), using the software *Statistica* 8. We considered the seed addition (presence of *C. solstitialis*) as factor (independent variable) and the performance of other species as dependent variables. Dependent variables were species richness, total cover of native and exotic species (analysed separately for the two groups), and cover of individual species. Species richness was the total number of species in each plot. Total cover per plot was the sum of cover of all species in each plot (recorded separately for exotics and natives). Exotic resident species richness or cover did not include *C. solstitialis*. In order to describe and compare species composition of the sites, we additionally assessed the Jaccard index among them.

For statistical analyses of species richness, we used a Poisson distribution of data and a logarithmic link function. For total cover, we used a Gaussian distribution of data and an identity link function. For cover of individual species, we used a Gaussian distribution of data and an identity link function.

Results

The mean (±S.E.) density of *C. solstitialis* individuals in the sown plots (0.25 m^2) was 68.3 ± 5.7 for San Ramón, 59.2 ± 7.1 for San Carlos, and 55.6 ± 4.9 for

Rinconada, representing 11.4%, 9.8% and 9.3% of the 600 seeds initially added per plot. The mean (±S.E.) cover of *C. solstitialis* was 20.3% ± 2.5, 26.9% ± 3.8, and 20.1% ± 1.9 (mean ± 1S.E.) in San Ramón, San Carlos and Rinconada. Density and cover were not significantly different among sites (ANOVA, F = 1.18, *P* = 0.31 and F = 1.89, *P* = 0.16, respectively).

Pooling the three sites, we detected a total of 21 species, of which four were natives. Most exotic species were native to Europe (Table 1). Most observed species were annuals, with two species being biennials (Table 1). The similarity of species composition (Jaccard index) between San Ramón and Rinconada was 56.3%, San Ramón and San Carlos 21.1%, and San Carlos and Rinconada 36.8%. Three species were present in all three sites: *Erodium cicutarium* and *Hordeum murinum* (exotic) and the native *Bromus berteroanus* (Table 1). San Ramón had 10 exotic species and one native species, and was dominated by *Vulpia bromoides*; San Carlos presented nine exotics and three native species, and was dominated by *Erodium cicutarium*; Rinconada had 10 exotic species and four natives, and was dominated by *Avena barbata* (Table 1).

For exotic species, *C. solstitialis* significantly reduced species richness at the San Ramón and Rinconada sites (Figure 1), and reduced exotic cover at San Ramón and San Carlos (Table 2, Figure 1). For native species, *C. solstitialis* did not significantly affect cover or species richness in any of the three sites (Table 2, Figure 1). As San Ramón, only one native species was present (*Bromus berteroanus*) the results for native cover at this site are equivalent to results for this species, while results of species richness correspond to the probability of presence of this species in plots with and without *C. solstitialis*.

In general, individual species reached lower cover values in the presence of *C. solstitialis*. The cover of four species at San Ramón, and one species at Rinconada and San Carlos each were significantly reduced by the experimental invasion of *C. solstitialis* (Table 3). The cover *Centaurea melitensis* was significantly affected by *C. solstitialis* in both sites where the former was present (Table 3). No species was significantly enhanced by the presence of *C. solstitialis* (Table 3).

Discussion

Seed addition of *Centaurea solstitialis* at the three sites resulted in a relatively low rate of establishment of plants (ca. 10%) and cover values (ca. 22%). Density resulted in values of ca 244 individuals m^{-2}, which is considered a high-density value in other studies (e.g. Di Tomaso et al. 2003), although values up to 1900 individuals m^{-2} have been reported (Di Tomaso et al. 2003). In our case, although density of individuals may be considered relatively high, cover values suggest that *C. solstitialis* did not become dominant in plots where it was sown in any of the three sites. The open environment (grassland) where this experiment was carried out is a favourable habitat for *C. solstitialis* (Di Tomaso et al. 2003; Hierro et al. 2006). However, the abundance of this species can be enhanced by additional disturbances (clipping, recent fires, ploughing) (Hierro et al.

Table 1. The composition and frequency of resident species observed at three study sites – San Carlos (33°23′54″ S, 70°29′06″ W; 1081 m a.s.l.), San Ramón (33°25′51″ S, 70°30′49″ W; 919 m a.s.l.) and Rinconada (33°29′06″ S, 70°52′30″ W; 480 m a.s.l.), Chile. Frequency values are percentage of 40 plots in which each species was observed.

Species	Life form	Origin	San Ramón	Rinconada	San Carlos
Aira caryophyllea	Annual	Exotic (Eurasia, North Africa)			7.5
Amsinckia calycina	Annual	Native (Central Chile)		62.5	47.5
Avena barbata	Annual	Exotic (Europe)	52.5	97.5	
Bromus berteroanus	Annual	Native (Central Chile)	65	42.5	57.5
Capsella bursa-pastoris	Annual	Exotic (East Europe)			2.5
Carduus pycnocephalus	Annual	Exotic (Mediterranean Basin)	17.5	7.5	
Centaurea melitensis	Annual	Exotic (Mediterranean Basin)	80	70	
Cirsium vulgare	Biennial	Exotic (Mediterranean Basin)	7.5		
Clarkia tenella	Annual	Native (Central Chile)		12.5	47.5
Erodium cicutarium	Annual	Exotic (Europe)	82.5	47.5	97.5
Escholzia califonica	Biennial	Exotic (California, North America)			2.5
Galium aparine	Annual	Exotic (Eurasia)		50	2.5
Helenium aromaticum	Annual	Native (Central Chile)		5	
Hordeum murinum	Annual	Exotic (Europe, Mediterranean Basin)	12.5	27.5	2.5
Madia sativa	Annual	Exotic (North America)			87.5
Matricaria chamomilla	Annual	Exotic (Southern and Eastern Europe)		5	
Medicago lupulina	Annual	Exotic (Eurasia)	10	72.5	
Melilotus albus	Annual	Exotic (Eurasia)	5		
Rapistrum rugosum	Annual	Exotic (Mediterranean Basin)	82.5	70	
Rostraria cristata	Annual	Exotic (Eurasia)			15
Vulpia bromoides	Annual	Exotic (Eurasia, North Africa)	90	35	60
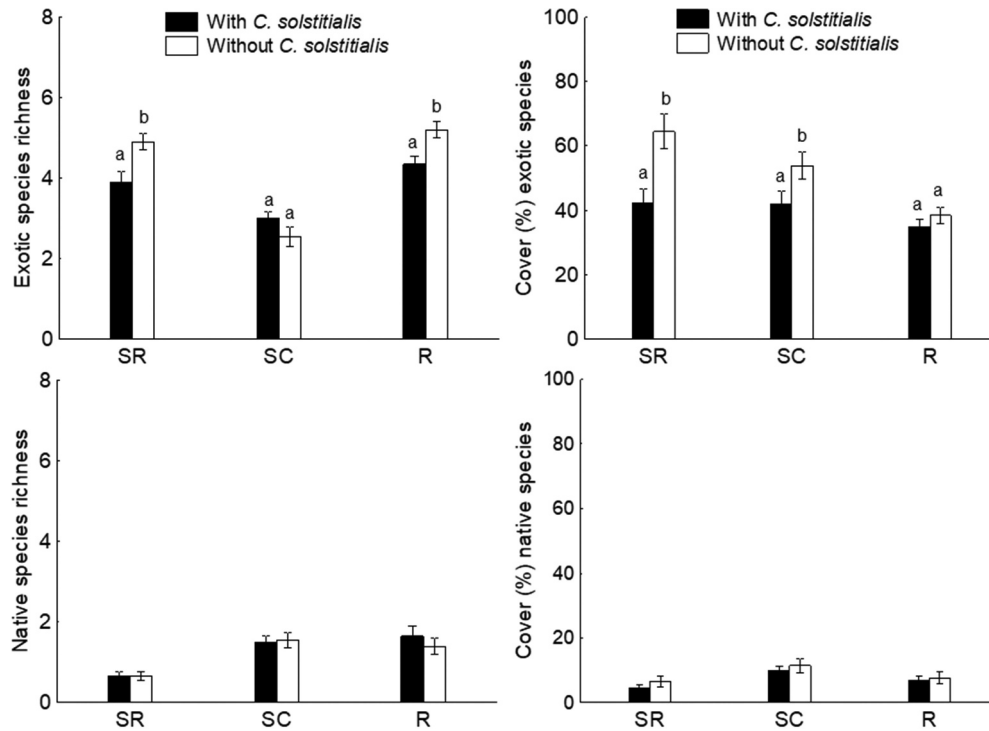
Figure 1. Resident species richness and cover with and without *C. solstitialis* in each of three sites, San Carlos (SC, 33º23′54″ S, 70º29′06″ W; 1081 m a.s.l.), San Ramón (SR, 33º25′51″ S, 70º30′49″ W; 919 m a.s.l.) and Rinconada (R, 33º29″06″ S, 70º52′30″ W; 480 m a.s.l.), Chile. Results for native and exotic species are shown separately. Lowercase letters indicate significant differences (GLM tests, *P* < 0.05) between *C. solstitialis* treatments for each site separately.

Table 2. The impact on species richness and cover of exotic and native species in experimental plots sown with *C. solstitialis*, at three study sites – San Carlos (33º23′54″ S, 70º29′06″ W; 1081 m a.s.l.), San Ramón (33º25′51″ S, 70º30′49″ W; 919 m a.s.l.) and Rinconada (33º29″06″ S, 70º52′30″ W; 480 m a.s.l.), Chile. Values are Statistical results (GLM, ANOVA) for the effects of *Centaurea solstitialis* (with vs. without) on richness and cover of native and exotic resident species in each study site separately. Significant effects are indicated in bold typeface.

Dependent	San Ramón		Rinconada		San Carlos	
variable	Chi^2	*P*	Chi^2	*P*	Chi^2	*P*
Exotic richness	6.921	**0.008**	8.222	**0.004**	1.927	0.165
Exotic cover	9.386	**0.002**	1.209	0.271	4.145	**0.041**
Native richness	0.001	0.999	0.456	0.499	0.008	0.927
Native cover	0.879	0.348	0.091	0.761	0.426	0.513

2006), which did not affect our study sites (we excluded livestock and rabbits during the experiment). Furthermore, precipitation during the experimental year 2007 (especially the spring) was unusually low (170 mm). *C. solstitialis* germinates during autumn but seems to increase its recruitment and survival in wet winters and springs (Hierro et al. 2009). Other studies have shown a positive correlation between the success of invasion by *C. solstitialis* and soil water availability during late spring and summer (Dukes 2001; Dlugosch et al. 2015). Thus, the absence of recent disturbance and low precipitation may have constrained the cover reached by this species in our

study, and consequently its impacts on the resident plant community. Nevertheless, *C. solstitialis* after six months produced significant negative effects on species richness and total cover of exotic species (other than *C. solstitialis*). Species richness and cover were not always affected similarly. At San Ramón, both species richness and cover were significantly reduced by *C. solstitialis*; at Rinconada only species richness; and at San Carlos, only cover was reduced by *C. solstitialis*. These results should be considered conservative, given the relatively short length of our experiment (eight months). Studies conducted over longer periods in general are expected to show stronger impacts of exotic invasion (Maron and Marler 2008a, 2008b; Gaertner et al. 2009).

Different mechanisms may mediate the negative effects produced by *C. solstitialis* observed in our study. First, although Qin et al. (2007) have suggested that this species would not produce allelopathic compounds, Sotes et al. (2015) have found that the species might produce allelopathic leaf leachates. Secondly, this species may also use important volumes of soil water (Dlugosch et al. 2015) and hence competition for water is likely to have occurred. Di Tomaso et al. (2003) have observed that densities > 90 individuals m^{-2} of *C. solstitialis* rapidly depleted moisture from all depths in the soil profile by preflowering growth stages. High density expanded the

Table 3. (Mean ± S.E.) cover values of species present in each of three sites in the plots sown with *C. solstitialis* (+) and in the control without *C. solstitialis* (−) in San Carlos (33º23′54″ S, 70º29′06″ W; 1081 m a.s.l.), San Ramón (33º25′51″ S, 70º30′49″ W; 919 m a.s.l.) and Rinconada (33º29″06″ S, 70º52′30″ W; 480 m a.s.l.), Chile. Absence of values indicates that the species was not present in the site. Zero value indicates that the species was present in the site but not in the treatment; * indicates significant difference (GLM, *P* < 0.05) between *C. solstitialis* treatments.

Species	San Ramón +	San Ramón −	Rinconada +	Rinconada −	San Carlos +	San Carlos −
Aira caryophyllea					0.0 ± 0.0	1.0 ± 0.6
Amsinckia calycina			2.4 ± 0.6	2.4 ± 0.6	3.1 ± 0.9	6.5 ± 2.1
Avena barbata	1.5 ± 0.6	3.8 ± 0.8*	15.0 ± 2.3	11.5 ± 2.4		
Bromus berteroanus	4.6 ± 1.1	6.4 ± 1.7	3.3 ± 1.1	3.0 ± 1.1	5.1 ±1.3	2.5 ± 0.7
Capsella bursa-pastoris					0.1 ± 0.1	0.0 ± 0.0
Carduus pycnocephalus	0.1 ± 0.1	3.8 ± 1.8*	0.0 ± 0.0	0.3 ± 0.3		
Centaurea melitensis	3.4 ± 0.7	7.6 ± 1.0*	3.1 ± 0.9	6.7 ± 1.0*		
Cirsium vulgare	0.1 ± 0.1	0.4 ± 0.3				
Clarkia tenella			0.4 ± 0.3	0.4 ± 0.3	1.7 ± 0.6	2.5 ± 0.5
Erodium cicutarium	6.7 ± 1.2	11.0 ± 2.2*	2.5 ± 0.7	3.1 ± 1.0	19.9 ± 3.1	33.9 ± 4.9*
Escholzia californica					0.0 ± 0.0	1.5 ± 1.5
Galium aparine			3.8 ± 1.4	3.6 ± 1.1	0.1 ± 0.1	0.0 ± 0.0
Helenium aromaticum			0.1 ± 0.1	0.3 ± 0.3		
Hordeum murinum	0.7 ± 0.4	1.0 ± 1.0	1.9 ± 1.0	0.6 ± 0.3	0.0 ± 0.0	0.1 ± 0.1
Madia sativa					9.6 ± 1.3	9.9 ± 1.8
Matricaria chamomilla			0.0 ± 0.0	0.3 ± 0.3		
Medicago lupulina	0.1 ± 0.1	0.4 ± 0.3	4.3 ± 1.3	4.9 ± 1.2		
Melilotus albus	0.0 ± 0.0	0.8 ± 0.5				
Rapistrum rugosum	11.6 ± 2.6	15.8 ± 2.4	2.6 ± 0.9	4.8 ± 1.0		
Rostraria cristata					0.3 ± 0.2	0.1 ± 0.1
Vulpia bromoides	18.3 ± 3.4	20.1 ± 3.5	2.0 ± 1.3	2.8 ± 1.1	12.0 ± 2.7	7.3 ± 2.5

moisture reduction zone and lead to increased shallow moisture depletion, and in high-density plots, soil moisture did not recharge, compared with bare-ground plots, after subnormal winter and spring precipitation (Di Tomaso et al. 2003). Zavaleta and Hulvey (2007) also found that *C. solstitialis* strongly reduces soil moisture. Thus, particularly during dry years in our study area, such as 2007, when water may be the most critical limiting resource, probably *C. solstitialis* rapidly outcompeted both shallow-rooted and deep-rooted annual species, which were the dominant life form in our study sites. Consistent with this possibility, Enloe et al. (2004) have observed that a *C. solstitialis*-dominated community maintained a significantly drier soil profile than an annual grass community. In addition, Gómez-González et al. (2009) have suggested that pre-emption of resources through more rapid germination of *C. solstitialis* than other species, may contribute to suppressing the growth of neighbours.

Some studies have shown that invasion of exotic species typically reduces performance (abundance or species richness) of native species present in recipient communities, but not of other exotics (Levine et al. 2003; Hejda et al. 2009; Gaertner et al. 2009; Flory and Clay 2010), and that native resident species produce stronger negative effects on invasion of exotics than on other native species (Sun et al. 2015). This may reflect co-adaptation of species that coexist in the same microenvironment (Sax et al. 2005). Some support for this hypothesis was documented by Xiao et al.

(2016) for *C. solstitialis*. In contrast, we found no support for this hypothesis in our study, neither at community nor at individual species levels. Nevertheless, a lack of significant effect of *C. solstitialis* on native species in our study does not allow us to generalise that native species of this region are unaffected by this exotic herb. First, we found very few native species in these sites, and secondly Gómez-González et al. (2009) have shown in a greenhouse experiment that this exotic species has the potential to outcompete two native shrub species from central Chile (*Baccharis linearis* and *B. paniculata*), both of them typical pioneer species of open shrublands and grasslands of this region (Armesto and Pickett 1985).

The impacts of invasive species frequently vary between biogeographic regions (Vilà et al. 2011) as well as among sites within a biogeographic region (Mason and French 2008; Hejda et al. 2009). Similarly, the effects of *C. solstitialis* at the community level differed among sites, suggesting that biotic and/or abiotic local conditions can modulate the impacts of *C. solstitialis*. Several factors may be related to these differences. A first factor may be the species similarity among sites, since, at least at a community level, sites with more similar species composition should respond more similarly to invasion by an exotic species (e.g. Mason and French 2008). Consistent with this possibility, San Ramón and Rinconada showed very similar effects of *C. solstitialis* on exotic species richness and were also the most similar sites in species composition.

A second factor that can modulate the impact of invaders on resident species (and thus potentially produce different results among sites) is the species diversity of resident communities. It has been proposed that richer resident communities would be more resistant to invasion and also less impacted by exotic species (e.g. Maron and Marler 2008b). Consistent with this hypothesis, we observed that Rinconada, with the highest species richness in plots without *C. solstitialis*, was also the only site where *C. solstitialis* had no significant impact on the total cover of resident exotic species. However, species richness at Rinconada was negatively impacted by *C. solstitialis*, and the site with the lowest resident species richness (San Carlos), was not impacted by this exotic herb. Thus, it is not clear if resident species richness is a relevant factor affecting the different impacts of *C. solstitialis* among sites.

A third factor potentially producing different results among sites could be resource availability, especially, soil water content. It has been documented that increasing resource supply often enhances the competitive dominance of exotics (Thomsen et al. 2006). It has also been proposed that when the stress factor is a resource shortage (e.g. that of water), interactions may change from negative under low stress, to positive under medium levels of stress, and then to negative again under high stress conditions (Maestre et al. 2009). Precipitation during the experimental year was extremely low and hence the three sites may be considered to be under high stress. The only significant effects of *C. solstitilis* were negatives at all the three sites, which is consistent with Maestre et al. (2009). However, Rinconada showed the driest condition among the three sites and hence we should have observed more negative effects of *C. solstitialis* in this site (Maestre et al. 2009). Instead, the frequency of significant negative effects of *C. solstitialis* (at a community or individual species level) was similar than in the other sites. Hence, although soil water availability could be related to our results, differences in precipitation and soil moisture among sites were not an important factor modulating differences observed among sites.

Other factors that may have contributed to different results among sites are herbivory and soil pathogens. It has been documented that when *C. solstitialis* is more affected by herbivores, it intensifies its negative effects on neighbours (Callaway et al. 2006). It has also been observed that differences in soil pathogens among geographic regions contributed to differential invasion success of *C. solstitialis* (Andonian et al. 2011). Although our experimental sites excluded mammals, insect herbivory and soil pathogens may have differed among sites. However, these possibilities require further research.

Our results may be generalised only for grasslands and open shrublands, which are the habitats where *C. solstitialis* is able to grow (Hierro et al. 2006). *C. solstitialis* does not invade dense shrublands and forests in central Chile nor in other regions of the world (Maddox et al. 1985; Hierro et al. 2006; Andonian et al. 2012). The communities in which *C. solstitialis* occurs in central Chile are mostly composed of other exotic herbs with few native herbs or shrubs since native species are very infrequent in grasslands and open shrublands of this region (Arroyo et al. 1995; Matthei 1995).

Conclusions

We found that the widely invasive herb *C. solstitialis* is capable of reducing diversity and abundance of species present in recipient communities and thus modifying ecosystems that it invades. However, some species are apparently more resistant to the negative impacts of *C. solstitialis* than others, and it is not clear if the biogeographic origin of resident species is critical in these differences. In addition, although some negative effect of *C. solstitialis* was observed at all sites, the impacts of this exotic species were not identical everywhere, suggesting that local biotic and/or abiotic conditions influence the effect of this invasive species within this biogeographic region. Additional research on ecological factors and mechanisms triggering different impacts of *C. solstitialis* among species and localities is needed.

Disclosure statement

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Notes on contributors

Pablo I. Becerra is interested in invasion ecology as well as conservation and restoration ecology of forest ecosystems.

*Lohengrin Caviere*s is interested in invasion ecology and biodiversity conservation.

Ramiro Bustamante is interested in understanding the ecology and evolution of invasive species.

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