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Original article

Cortaderia selloana invasion across a Mediterranean coastal strip

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ABSTRACT

The invasive success of *Cortaderia selloana*, an alien perennial grass introduced from South America, was assessed by comparing plant and population performance in ruderal and non-ruderal habitats across a Mediterranean coastal strip. The main habitat differentiation criterion was the absence or presence of visible signs of recent disturbances. Plant functional group richness (i.e. number of plant groups classified as grasses, herbs, shrubs, vines and trees), total plant cover and percentage of bare ground was calculated in each habitat. In addition, soil samples were randomly taken in order to analyse total soil C, total N, $CaCO_3$, pH and soil texture. *Cortaderia selloana* populations were characterized by calculating total density, proportion of juvenile plants, plant volume, number of panicles and reproductive effort (i.e. number of panicles/plant volume) and fecundity per unit area (number of panicles per ha).

We compared whether population characteristics and plant performance were associated with biotic and abiotic habitat factors. We expected a better performance of *C. selloana* in ruderal habitats than in non-ruderal habitats. As expected, ruderal habitats had larger and denser *C. selloana* populations and recruitment was very high (the proportion of juvenile plants was more than 50%). In consequence, in ruderal habitats, on average, plants were smaller, produced fewer panicles, and had a lower reproductive effort. The high percentage of bare ground, low pH and low functional group richness were the best explanatory variables associated to *C. selloana* invasion success.

1. Introduction

The increasing number of intentional or accidental human introductions of species that is occurring around the world is threatening the conservation of biodiversity through direct and indirect impacts on native species and the modification of ecosystem functions (Vitousek, 1994; Enserink, 1999; Mack and Lonsdale, 2001; Cole and Landres, 2004).

Invasion success not only depends on the characteristics of alien species but also on invasibility, the ecosystem's intrinsic capacity to favour species' survival independently of their introduction rates (Lonsdale, 1999). Invasibility depends both on

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abiotic and biotic factors (Rejmánek et al., 2005). Yet it is not always clear which ecosystem characteristics favour or hinder the invasion of a particular alien species because performance of a species depends on multiple ecological factors (Hobbs and Humphries, 1995). Soil nutrient pulses and suitable climatic conditions are reported to favour ecosystem invasibility (Rejmánek, 1989; Hobbs and Huenneke, 1992; Bastl et al., 1997; Davis et al., 2000). Ecosystem invasibility may increase as there are more resources available to invaders (Davis et al., 2000) and decrease with environmental harness (Davis et al., 1999; Higgins et al., 1999). In addition, disturbances can promote invasions either through a reduction of plant competition, an increase in the availability of specific resources or an increase of the entrance of invader propagules (Hobbs, 1989; Hobbs and Humphries, 1995).

Ruderal habitats, defined as disturbed areas are highly invaded (Lincoln et al., 1998). For example, in the alien flora of the Czech Republic 62.8% of invasions occur in human-made habitats while 11.0% have been recorded in seminatural habitats (Pysek et al., 2003; Chytrý et al., 2005). Similarly, in Spain from 637 naturalised plant species (13% total flora), most of them (44.67%) are found in ruderal and disturbed habitats (Vilà et al., 2001, 2007). Ruderal habitats are characterized by receiving a high propagule pressure and frequent disturbances, which increase their susceptibility to plant invader establishment with respect to unaltered habitats (Tyser and Worley, 1992). Given these differences in the degree of invasion between ruderal and non-ruderal habitats, we focused the present study on finding ecological factors associated to invasions in ruderal habitats.

Ruderal habitats are a common element in the Mediterranean landscape because of widespread modification by humans (Naveh and Vernet, 1991). Most of the alien species that have been intentionally or accidentally introduced are able to successfully invade ruderal habitats (Le Floc'h, 1991). *Cortaderia selloana* (Pampas grass) is an invasive plant species native to South America now invading old fields, riverine and marshland areas worldwide. We assessed *C. selloana* invasion in ruderal and non-ruderal habitats spread along the Catalan Mediterranean coastal strip (NE Spain) by comparing if population characteristics and plant performance were associated to biotic and abiotic ecological factors differing between ruderal and non-ruderal habitats. We expected a better *C. selloana* performance in ruderal habitats than in non-ruderal habitats.

2. Materials and methods

2.1. *Field survey*

From mid August to mid September 2004, at the stage of plant flowering, we conducted a survey of 27 introduced populations of *C. selloana* in a Mediterranean coastal strip in Catalonia (NE Spain). Coordinates and altitude above sea level of each population were measured with a GPS. Mean annual temperature ranged from 15 to 17 °C and mean annual rainfall varied from 400 to 700 mm. The habitat was classified ''a priori'' as ruderal or non-ruderal. The main habitat differentiation criterion was the visual identification of signs of anthropogenic disturbance in ruderal habitats. Ruderal habitats had trampled areas and waste deposits while non-ruderal habitats were mainly old fields, grasslands, woodlands and marshes without signs of recent disturbances (Table 1).

Populations were less than 35 km from the seashore and they were at least 1 km apart; the same distance chosen in a previous study that used herbarium records to determine the expansion history of *C. selloana* in California (Lambrinos, 2001). A population was identified as a group of 5 or more plants present in an area where *C. selloana* could really spread in any direction. Populations situated in road sides or agricultural field margins were not included in our survey because they could only spread linearly.

Vegetation characteristics of each invaded site were estimated by the point-intercept method conducted in one 50-m line transect in the centre of each population. We identified all functional groups (i.e. grasses, herbs, shrubs, vines and trees) found every 50 cm. Plant functional group richness (i.e. number of functional groups), total plant cover and percentage of bare ground was calculated in each site. In each site we randomly took 5 soil samples of the first 20 cm mineral soil with a 6 cm diameter drill. Soil samples of each site were pooled after air-drying on flat trays in the laboratory and we

Table 1 – *Cortaderia selloana* populations surveyed in a Mediterranean coastal strip of Catalonia (NE Spain)

Code	Location	UTM coordinates		Altitude (m.a.s.l.)	Habitat
		X	Y		
1	Roses	510750	4679323	0	Non-ruderal
2	Rubina	512231	4679854	1	Non-ruderal
3	Dos Rius	507650	4671121	0	Non-ruderal
4	Empuriabrava	509682	4676255	0	Non-ruderal
5	Malgrat de Mar	477828	4611642	32	Ruderal
6	Blanes	482492	4614647	20	Ruderal
7	Blanes-Lloret	482928	4614957	20	Ruderal
8	Lloret	484952	4615929	23	Ruderal
9	Lloret-Tossa	489996	4617685	103	Ruderal
10	Sta. Maria de Lloret	492372	4618622	131	Ruderal
11	Tossa	484781	4620686	163	Ruderal
12	Mollet	434621	4599996	85	Ruderal
13	Parets	436127	4601152	73	Non-ruderal
14	Matadepera	419200	4605353	405	Non-ruderal
15	Terrassa (Sta. Margarita)	419189	4599821	239	Ruderal
16	Terrassa (Les Fonts)	420590	4599318	242	Ruderal
17	Sant Boi	420436	4577016	23	Ruderal
18	Regarons	419718	4570752	3	Non-ruderal
19	Castelldefels	419587	4569946	0	Non-ruderal
20	Filipines	420647	4570227	3	Non-ruderal
21	Mallola de Dalt	418715	4569935	0	Non-ruderal
22	Gavà Mar	417996	4569770	0	Non-ruderal
23	Viladecans	418189	4570365	0	Non-ruderal
24	Toro Bravo	421225	4570632	5	Non-ruderal
25	UAB	424524	4594041	171	Ruderal
26	Calafell	379153	4560457	350	Non-ruderal
27	Vinaròs	287582	4485612	6	Non-ruderal

analysed total soil C, total N, $CaCO_3$, pH and texture. Total C and N was conducted with an elemental analyser of CE Instruments (NA2100 model). Organic carbon was calculated by subtracting the C of calcium carbonate ($CaCO_3$) from the total C. Calcium carbonate was analysed following the pressure calcimeter method (Porta-Casanellas, 1986). pH was measured with a glass pH-meter in a soil suspension with water 1:2.5 (w:v). Texture was analysed following the pipet method (Gee and Bauder, 1986). Percentage of macro-elements (i.e. particle size >2-mm) was also determined by dividing the macro-element weight of the soil sample by the total weight of the sample.

We counted all *C. selloana* plants and measured the area of occupation with a GPS to estimate *C. selloana* density. When a population had more than 500 plants or when the invaded area was too large (>4000 m^2) or highly impenetrable, *C. selloana* density was estimated by counting all plants inside two randomly chosen 20 × 20 m plots. We also randomly sampled 30 plants and measured their height, two perpendicular plant diameters and the number of panicles. Moreover, the number of panicles of 20 randomly chosen plants were additionally recorded. If the population had less than 30 plants, all plants were sampled. We estimated plant volume (V) as the shape of a semi-sphere whose formula is $V = 2/3\pi R^2 H$, where "R" is the mean plant radius which was estimated with the two perpendicular diameters and "H" is plant height (Domènech et al., 2005).

Therefore, variables could be classified into population characteristics, plant characteristics, and abiotic and biotic site variables. Population characteristics included plant density, the proportion of juvenile plants, measured as the ratio between juvenile plants (i.e. had not produced panicles yet) and the total number of plants and the fecundity per unit area, measured as the number of panicles per hectare. Plant characteristics included plant volume, number of panicles per plant and reproductive effort (i.e. number of panicles/plant volume). Abiotic site variables referred to altitude and soil characteristics (i.e. total soil N, total organic C, pH, percentage of macroelements and percentages of sand, silt and clay). Finally, habitat type, total cover (without including *C. selloana*), percentage of bare ground and richness of plant functional groups were classed as biotic site variables.

2.2. Statistical analysis

In order to characterize both ruderal and non-ruderal habitats, unpaired *t*-tests were used to compare differences in abiotic and biotic variables. Total N was transformed as $1/(X)^{1/2}$ and total cover was log $(1 + X)$ transformed to meet the assumptions of parametric statistical analysis.

An unpaired *t*-test was used to compare total plant density and proportion of juveniles between ruderal and non-ruderal habitats. Differences in fecundity per unit area were analysed with a Mann–Whitney test. Differences between habitats in volume of reproductive plants, number of panicles per plant and reproductive effort were analysed with a nested ANOVA with habitat as a fixed factor and population nested within habitat as a random factor. Total plant density was log $(X + 1)$ transformed to homogenize variances.

In order to explore the association of *C. selloana* with habitat characteristics, we conducted a Principal Components Analysis (PCA) in which we included *C. selloana* population variables and the biotic and abiotic habitat factors in order to detect correlations and to determine how *C. selloana* populations grouped. Previously, correlations between variables were tested by conducting a contingency table. When 2 variables were strongly correlated (i.e. correlation coefficient >0.8) we only included one of them in the PCA. We also analysed the association between *C. selloana* density and proportion of juveniles as dependent variables, and biotic and abiotic habitat factors as independent variables with a stepwise regression analysis. As mentioned before, plant density, total N and total cover were transformed in order to meet the assumptions of homogeneity of variances.

3. Results

Ruderal habitats were characterized by having significantly less total soil N, less soil organic C and a higher percentage of macro-elements than non-ruderal habitats (Table 2). Altitude, pH and percentages of sand, silt and clay did not vary significantly between ruderal and non-ruderal habitats.

Significant differences in total cover and percentage of bare ground were also found between habitats. Ruderal habitats had a lower total cover and a higher percentage of bare ground than non-ruderal habitats (Table 2). However, richness of plant functional groups did not vary significantly between habitats.

C. selloana populations in ruderal habitats had a significantly higher plant density and proportion of juvenile individuals than populations in non-ruderal habitats. Consequently, reproductive *C. selloana* plants in non-ruderal habitats were on average 1.5 times larger than plants in ruderal habitats (Table 3). We postulate that *C. selloana* plants in ruderal habitats are smaller because they are younger. In ruderal habitats there is ongoing recruitment and therefore, non-reproductive plants

Table 2 – Biotic and abiotic habitat characteristics of ruderal and non-ruderal habitats invaded by *C. selloana* (mean ± SE). *Unpaired *t*-test

	Ruderal	Non-ruderal	t_{25}*	*P*
Altitude (m)	106.09 ± 26.69	58.19 ± 31.95	1.07	0.29
Total N (%)	0.08 ± 0.01	0.14 ± 0.02	2.87	0.008
Soil organic C (%)	0.73 ± 0.22	2.74 ± 0.24	5.79	0.0001
Macro elements (%)[a]	39.1 ± 3.6	16.1 ± 4.8	3.52	0.002
pH	8.08 ± 0.12	8.23 ± 0.05	0.71	0.48
Sand (%)	62.21 ± 6.33	68.87 ± 4.14	0.92	0.37
Silt (%)	14.12 ± 3.75	11.92 ± 2.62	0.50	0.62
Clay (%)	21.46 ± 2.02	16.83 ± 1.64	1.79	0.09
Total cover (%)	51.7 ± 5.0	112.8 ± 12.5	3.89	0.0007
Bare ground (%)	44.5 ± 4.1	10.5 ± 2.5	7.53	<0.0001
Richness of plant functional groups[b]	3.0 ± 0.2	3.5 ± 0.3	1.43	0.17

a Particle size >2-mm.
b Number of functional groups.

Table 3 – C. *selloana* population and plant characteristics in ruderal and non-ruderal habitats (mean ± SE). *Mann–Whitney test

	Total density (plants/ha)	Proportion of juvenile plants	Number of panicles	Volume of reproductive plants (m^3)	Reproductive effort[a]	Fecundity per unit area[b]
Ruderal	1429.8 ± 540.7	0.54 ± 0.09	11.0 ± 3.0	6.9 ± 0.4	1.6 ± 0.5	2608.8 ± 1020.2
Non-ruderal	253.1 ± 63.4	0.24 ± 0.07	32.6 ± 5.5	10.4 ± 0.8	4.3 ± 1.0	11302.9 ± 4033.5
(t_{25}, *P*)	(2.40, 0.02)	(2.64, 0.01)				
(Z^*, *P*)						(1.27, 0.20)
($F_{25,\ 581}$, *P*)			(9.07, 0.001)		(15.40, 0.001)	
($F_{24,\ 353}$, *P*)				(4.68, <0.0001)		

a Number of panicles/plant volume.
b Number of panicles per hectare.

are more abundant than reproductive plants. In addition, *C. selloana* reproductive effort is low in ruderal habitats, probably because plants are still investing in vegetative growth and have not arrived to full reproductive capacity. Although plant volume distribution of *C. selloana* had a reversed-J shape in both habitats, it was more skewed in non-ruderal than in ruderal habitats (Fig. 1). Given the small plant size of reproductive *C. selloana* plants in ruderal habitats, panicle production was approximately 3 times and reproductive effort 2.7 times higher in non-ruderal habitats than in ruderal habitats (Table 3). However, no significant differences between ruderal and non-ruderal populations were found in the fecundity per unit area.

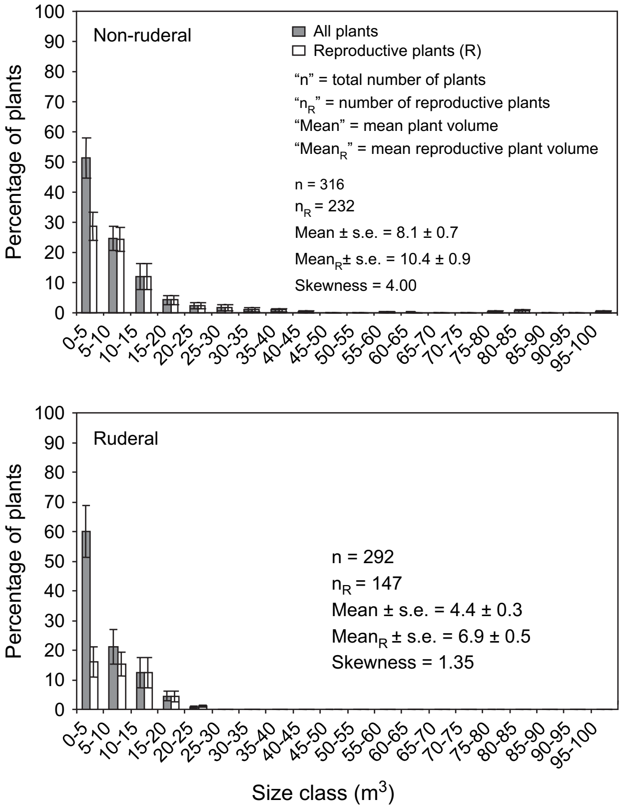

Fig. 1 – Plant size distribution (mean ± SE) of C. *selloana* invasion in non-ruderal and ruderal habitats.

The contingency table between ecological factors revealed that there was a strong, negative correlation between the percentage of sand and either the percentage of silt (correlation coefficient = 0.97) or the percentage of clay (correlation coefficient = 0.91). Therefore, only the percentage of sand was used as a variable in the PCA.

The PCA explained 52.87% of the variance in plant density. In the first component (PCA_1), which explained 34.46% of the variance, *C. selloana* populations clustered in response to

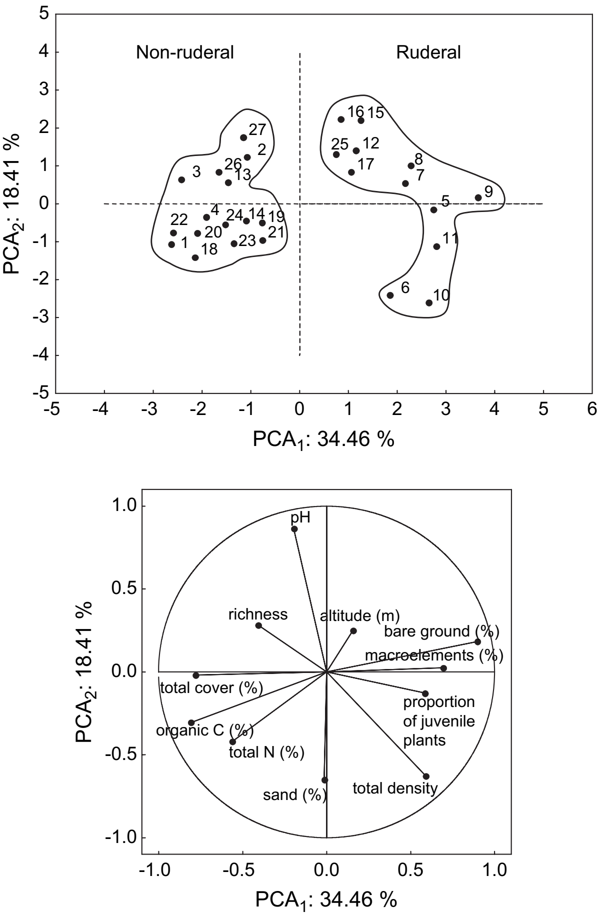

Fig. 2 – Projections of C. *selloana* populations and biotic, abiotic and population invasion variables in the factor-plane extracted with a PCA. Numbers indicate the population sampled according to Table 1.

Table 4 – Stepwise regression between demographic parameters of *C. selloana* and biotic and abiotic significant habitat factors

Dependent variable	Predictors	Coefficient	*F*-value	% var.[a]	d.f.	
					Regression	Residual
Plant density	Intercept	9.86	11.24			
	Percentage of bare ground	0.01	6.33	34.4		
	pH	−0.81	4.94	46.3		
	Richness of plant functional groups	−0.37	9.37	55.8		
					3	23
Proportion of juvenile plants	Intercept	0.18	4.09			
	Percentage of bare ground	0.01	8.17	21.6		
					1	25

a % var. = % cumulative variation explained.

habitat type (Fig. 2). Plant density was positively correlated to the percentage of bare ground and it was negatively correlated with pH and richness of plant functional groups ($F_{3,\ 23} = 9.68$, $P = 0.0003$) (Table 4, Fig. 3). These 3 factors explained 55.8% of the variation. The remaining 8 variables did not contribute significantly to explaining the variation in total plant density. Percentage of bare ground explained 21.6% of the proportion of juvenile plants ($F_{1,\ 25} = 8.17$, $P = 0.008$) (Table 4, Fig. 3).

4. Discussion

Alien species abundance has been reported to be high in ruderal habitats because they have been greatly modified by human activities (Vilà et al., 2001; Sobrino et al., 2002). In particular, disturbances, which often occur in ruderal habitats, can provide open windows for alien species to colonize and spread into new habitats through the creation of patches of open ground or a reduction in levels of competition (Hobbs, 1989; Hobbs and Huenneke, 1992; Hobbs, 2000).

As expected, our study along the Mediterranean coastal strip has revealed that although *C. selloana* invasion takes place in both ruderal and non-ruderal habitats, the most successfully invaded habitats are ruderal. The proportion of small plants is similar between both habitats but in non-ruderal habitats there is a greater variation of sizes, some plants reaching 100 m^3. This difference is probably because non-ruderal habitats have been invaded for a longer period of time.

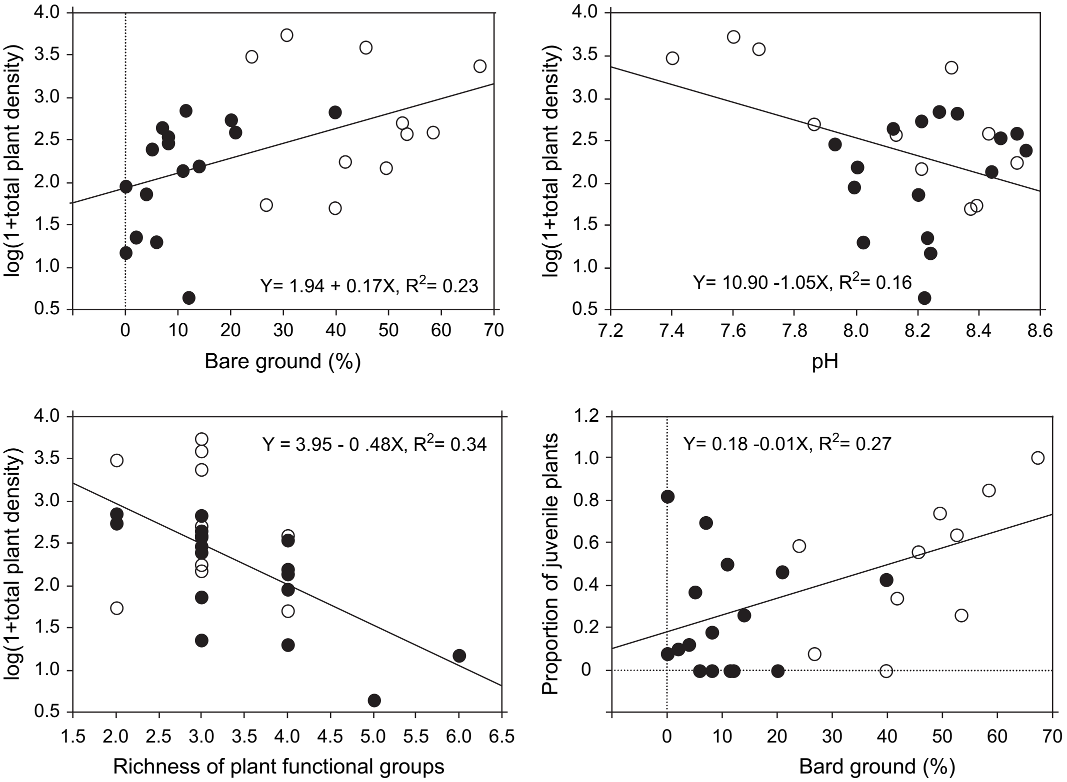

Fig. 3 – Linear regression of the significant relationships found in the stepwise regression between *C. selloana* demographic variables and ecological factors in non-ruderal (filled circles) and ruderal (open circles) habitats.

In addition, populations in ruderal habitats are larger and have greater proportions of juvenile plants than populations in non-ruderal habitats. Consequently, *C. selloana* plants in ruderal habitats are younger and there is ongoing recruitment. In addition, *C. selloana* reproductive effort is low in ruderal habitats because plants are still investing in vegetative growth and have not arrived to full reproductive capacity. Data obtained from North American herbarium records has revealed that *C. selloana* has frequently occupied non-ruderal habitats in southern California over the past 50 years (Lambrinos, 2001). However, *C. selloana* has also been reported to easily invade waste areas, open and disturbed areas (Harradine, 1991). Ruderal habitats had a substantial percentage of bare ground, which has been suggested to be a good predictor of ecosystem invasibility since most invader recruitment occurs after soil disturbance (Cronk and Fuller, 1995). In fact, we found in experiments that *C. selloana* seedling survival and establishment is enhanced by soil disturbances (Domènech and Vilà, 2006).

Total plant density was negatively associated to plant functional group richness indicating that the invader attained a high dominance in structurally simplified communities. There are many correlational studies showing that more species-diverse communities contain more exotic species (Levine and D'Antonio, 1999). Most of these studies have focussed on the relationship between native and alien species richness (Stohlgren et al., 2006; Vilà et al., 2007). In contrast, we focus on the relationship between the abundance of a particular invader and an estimation of vegetation complexity. This controversy of the native-invader relationship could be explained by the hypothesis posed by Maskell et al. (2006) who suggest that the positive native-alien species relationship can be truncated as succession progresses when a suppressive invader such as *C. selloana*, becomes dominant in the community.

As other alien species, *C. selloana* tolerates a wide range of environmental conditions (Bossard et al., 2000). However, we found that low pH values favoured *C. selloana* establishment. It has also been suggested that *C. selloana* seedling establishment requires sandy soils (Bossard et al., 2000), yet we found that the percentage of sand did not influence the presence of this species. Moreover, *C. selloana* seedling establishment is not necessarily correlated with high nutrient levels. We found that ruderal habitats, which are successfully invaded by *C. selloana*, have a lower total soil N concentration than that of non-ruderal habitats. We believe that differences in soil N content are more a consequence than a cause of *C. selloana* presence. In a previous study it was found that soils surrounding *C. selloana* invading Mediterranean coastal grasslands have a lower N content than soil of non-invaded sites probably due to the low N content in *C. selloana* leaves compared to other coexisting native annual grasses (Domènech et al., 2006). Dead leaves remain attached to the mother plant for a long time and this can reduce N inputs to the soil. The high *C. selloana* density in ruderal habitats could be responsible for the scaling-up of this neighbourhood effect, decreasing total soil N content with respect to non-ruderal habitats which are far less invaded.

Overall, *C. selloana* performance was considerably better in ruderal habitats than in non-ruderal habitats. Specifically, the existence of high percentages of bare ground, low pH values and low richness of plant functional groups increased the recruitment of seedlings suggesting that as long as disturbances occur *C. selloana* expansion is guaranteed.

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