



High competitive ability of *Centaurea melitensis* L. (Asteraceae) does not increase in the invaded range

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Abstract Understanding why alien species become dominant in recipient communities requires a biogeographical perspective comparing the ecology of native and introduced populations. The genus *Centaurea* (Asteraceae) is well-known in invasion ecology because several aggressive invaders, including *Centaurea melitensis* L., belong to this genus. We compared the competitive ability of *C. melitensis* individuals from Spain (native range) and Chile (invaded range) when competing against *Helenium aromaticum* (Hook.) L.H. Bailey, a native relative from Chile. We performed germination bioassays and

common garden competition experiments to compare: (1) the germination capacities of *C. melitensis* (Spain and Chile) and *H. aromaticum* (2) the potential allelopathic effect of leaf lixiviates of *C. melitensis* (Spain and Chile) on the seed germination of *H. aromaticum*, (3) the ability of *C. melitensis* from both origins to reduce the growth of *H. aromaticum*. No significant differences in the capacity of seed germination were found among *C. melitensis* from Chile and Spain and the native *H. aromaticum*. However, the seed germination of *H. aromaticum* was inhibited by the presence of *C. melitensis* leaves from Chile and Spain. Also, the biomass of *H. aromaticum* was reduced in the presence of *C. melitensis*, regardless of their origin. Our results demonstrate the competitive superiority of the invasive *C. melitensis* over *H. aromaticum*, but we found no evidence of an evolutionary increase in the competitive ability of the invader populations. Therefore, at least part of the invasive potential of *C. melitensis* seems to be acquired by selective processes in their original range.

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Introduction

In recent decades, many studies have been advocated to understand the ecological mechanisms underlying the success of invasive alien species. While some hypotheses explaining the success of invasive species have pointed to the presence of advantageous intrinsic attributes, such as a rapid growth rate (Grotkopp and Rejmánek 2007), phenotypic plasticity (Niinemets et al. 2003) or allelopathy (Callaway and Aschehoug 2000), other hypotheses have focused on extrinsic characteristics, such as the release from natural enemies (Keane and Crawley 2002), the increase of resource availability (Davis et al. 2000) or the climatic matching between the introduced and the native range (Pauchard et al. 2004). Some studies have suggested that invasion is a complex process where several mechanisms can act in concert (Hierro et al. 2005; Graebner et al. 2012; Fenesi et al. 2015).

Natural selection operates throughout the entire invasion process, from the introduction to the naturalization and the latter spread of invasive plants (Mooney and Cleland 2001). In this context, Blossey and Nötzold (1995) proposed the hypothesis of the “evolution of increased competitive ability” (EICA), which assumes a low pressure of natural enemies in the invaded range and, as a consequence, a positive selection of those individuals that allocate fewer resources to defenses in benefit of growth and reproduction. As an evolutionary corollary of this selective process, alien plants can be better competitors in their new range compared to their native range. Alternatively, Callaway and Ridenour (2004) proposed the hypothesis of “allelopathic advantages against resident species” (AARS). This states that the adaptive increase in the competitive ability of invasive plants could also occur if they are more allelopathic than native plants. Multiple studies have provided evidence in support of either AARS or EICA hypotheses (Lamarque et al. 2011), but, to the best of our knowledge, studies analyzing the invasion mechanisms of an alien plant in the context of both hypotheses are scarce.

Several species of the genus *Centaurea* (Asteraceae) are aggressive invaders (Lejeune and Seastedt 2001). Some of them –such as *C. diffusa* and *C. maculosa*– reduce plant performance of native species by releasing allelopathic compounds from their roots, with an increased allelopathic activity in the invaded

range (Callaway and Aschehoug 2000; Weir et al. 2003; Callaway and Ridenour 2004; He et al. 2009; Vivanco et al. 2004). In contrast, the invasion success of other *Centaurea* species does not seem to be associated with root-mediated allelopathy but with other mechanisms, such as the positive interaction with mycorrhizae (e.g., *C. melitensis*; Callaway et al. 2001, 2003). Studies performed on *C. melitensis*, *C. solstitialis*, and *C. stoebe* suggest that invasive plants assign more resources to growth and reproduction than plants from the native range (Widmer et al. 2007; Henery et al. 2010; Eriksen et al. 2012; Graebner et al. 2012; Moroney et al. 2013), although an increased competitiveness in plants from the invaded range was only demonstrated in the case of *C. solstitialis* (Graebner et al. 2012).

On the other hand, *Centaurea* species have sesquiterpene lactones stored in the glandular trichomes of their leaves, with potential biological activity (Bruno et al. 2013). As *Centaurea* leaves are disposed in a rosette near the ground, these compounds could be leached and interfere with seed germination of native neighbors (Muir and Majak 1983; Kelsey and Locken 1987). Inter-regional variation in sesquiterpene lactones has been found on leaf surfaces of *C. solstitialis* (Sotes et al. 2015), as have biogeographical differences in the allelopathy potential of their leaf surface extracts (Irimia et al. 2019). Thus far, the existence of biogeographical variation in leaf-mediated allelopathy remains unexplored in other *Centaurea* species.

Invasion mechanisms at early stages of the life cycle (e.g. seed germination) could also be relevant for *Centaurea*. For example, the competitive ability of *C. solstitialis* could, in part, be related to its rapid germination and site monopolization in the Chilean Matorral (Gómez-González et al. 2009), as well as in other Mediterranean-type ecosystems (Hierro et al. 2009). It is also important to consider that, in general, early emergence may be relevant for invasion success in Mediterranean-type ecosystems, where the combination of appropriate temperature and water availability for successful recruitment occurs during very few months (Gómez-González et al. 2009). However, early emergence as an invasion mechanism has been seldom addressed in invasion ecology literature.

Centaurea melitensis L. (Asteraceae) is an annual herb native to the Mediterranean Basin that has been introduced in many areas of the world, and is

particularly invasive in Mediterranean-type climate regions (Moroney and Rundel 2013). In Chile, it is distributed throughout the country but is present at higher densities in the Matorral of the Mediterranean-type climate zone where it is more dominant than in its native range (Matthei 1995; Moroney and Rundel 2013). Moroney et al. (2013) reported increases in growth rates and plasticity in *C. melitensis* populations from Chile compared to populations from Spain. Although these traits are relevant for invasiveness, experiments assessing its competitiveness are still needed to determine the existence of an increased competitive ability in *C. melitensis* populations (Graebner et al. 2012).

The dominance of *C. melitensis* in some areas of the Chilean Matorral occurs in early stages of recruitment. For example, the seedling density of *C. melitensis* (204.3 ± 42.12 seedlings/m²) was three-fold higher than that of all of the pooled native species (53.4 ± 13.47 seedlings/m²), and ca. 12-fold higher than that of *Helenium aromaticum* (16.5 ± 4.38 seedlings/m²), a functionally similar native Asteraceae (Gómez-González et al. 2011a, b). Germination rates of *C. melitensis* have proven to be among the highest in the genus (Riba et al. 2002). However, to our knowledge, there are no studies comparing the germination capacity of *C. melitensis* seeds from native and invaded ranges.

In this study, we assessed whether *C. melitensis* plants from an invaded range (Chile) are more competitive than plants from the native range (Spain). We made a series of competition experiments using the native herb *H. aromaticum* as a target and discussed the results in the context of EICA and AARS hypotheses and early-emergence advantage. Specifically, we evaluated: (1) the germination capacity of *C. melitensis* (Chile & Spain) and *H. aromaticum* seeds; (2) the potential allelopathic effects of *C. melitensis* leaves (Chile & Spain) on the seed germination of *H. aromaticum*; (3) the effect of *C. melitensis* (Chile & Spain) on the growth of *H. aromaticum*. We hypothesized that *C. melitensis* individuals from Chile have a higher germination capacity and stronger competitive effects on *H. aromaticum* than individuals from its native range (Spain).

Methods

Study species

Centaurea melitensis L. (Asteraceae) is an annual plant (up to 85 cm in height) that grows on grasslands and disturbed areas (Moroney and Rundel 2013). *Helenium aromaticum* (Hook.) L.H. Bailey (Asteraceae) is an annual (or biannual) plant native to Chile that is especially abundant in the open sunny microhabitats of the Chilean Matorral, generally in areas that have been disturbed by grazing or fire (Gómez-González et al. 2011b, c; Rodríguez et al. 2018). However, *H. aromaticum* usually appears in lower abundance when co-existing with *C. melitensis* (S. Gómez-González, personal observation). In both species, seed germination begins in early spring after winter rains, and flowering and fruit-set occur during late spring and early-summer. Their phylogenetic relatedness and ecological similarity make these species good models to test invasion hypotheses related to competitive ability (Vilà and Weiner 2004).

Seed collection

Seeds of *C. melitensis* were collected from four localities in the Metropolitan Region of Chile: 1) Quebrada de la Plata Natural Reserve (33°29'S-70°52'W); 2) Peñaflor (33°37'S-70°53'W); 3) El Paico (33°41'S-71°3'W); 4) Melipilla (33°42'S-71°16'W), which were pooled to then be used in experiments. We also collected *C. melitensis* seeds from four localities in Spain: 1) Lérida (41°36'N-0°38'E); 2) Cañada de las Higueras (36°50'N-2°16'W); 3) Puerto Real (36°33'N-6°10'W); 4) Dos Hermanas (37°18'N-5°59'W), which were also pooled to later be used in experiments. Seeds of *H. aromaticum* were collected from the Quebrada de la Plata Natural Reserve (33°29'S-70°52'W), located 30 km to the southwest of Santiago, Chile. In Chile, seeds were collected in December 2012 (*C. melitensis*) and January 2013 (*H. aromaticum*). *Centaurea melitensis* seeds from Spain were collected in July 2012. All seeds were preserved in paper bags at room temperature until the germination experiment started in March 2013.

Germination experiments

To assess: (1) the germination capacity of *C. melitensis* (Chile & Spain) and *H. aromaticum* seeds, as well as (2) the potential allelopathic effect of leaves of *C. melitensis* (Chile & Spain) on the seed germination of *H. aromaticum*, we performed the following germination trials: (i) seeds of *C. melitensis* from Chile alone; (ii) seeds of *C. melitensis* from Spain alone; (iii) seeds of *H. aromaticum* alone (used as control); (iv) seeds of *H. aromaticum* in the presence of dry *C. melitensis* leaves from Spain; (v) seeds of *H. aromaticum* in the presence of dry *C. melitensis* leaves from Chile; (vi) seeds of *H. aromaticum* in the presence of fresh *C. melitensis* leaves from Spain; (vii) seeds of *H. aromaticum* in the presence of fresh *C. melitensis* leaves from Chile. In these treatments, we used eight *C. melitensis* intact leaves per sample, which were placed under filter paper. We used fresh and dry leaves of *C. melitensis* to evaluate the allelopathic capacity of live plants as well as that of the leaf litter.

Each germination trial consisted of 25 randomly selected seeds from each pool, these were placed in a *Petri* dish between two layers of wet filter paper. Three replicates of each trial were placed in a growth chamber under controlled conditions of light and temperature (12 h light/20 °C and 12 h dark/10 °C). These conditions aimed to simulate those experienced by the seeds in the field during early spring in Central Chile (Hajek and di Castri 1975). All *Petri* dishes were watered daily with distilled water and seed germination was recorded every two days for two weeks. We considered a seed as germinated when the radicle was visible. We calculated the percentage of the seed germination of each replicate, as well as the coefficient of the velocity of germination: $CV = 100 \cdot \sum N_i / (\sum N_i \cdot T_i)$, where N_i = number of new seeds germinated on day i , T_i = number of days for germination to occur ($i = 1 \dots 14$). This coefficient estimates the days needed for the seeds to germinate and is indicative of the rapidity of germination (Jones and Sanders 1987).

Competition experiments

We performed a common-garden competition experiment under greenhouse conditions. Plants were obtained from the seeds that emerged during the

germination assays with no *C. melitensis* leaves, neither fresh nor dried, as described above. A great number of seedlings were first placed in seedbeds and when they developed their first two leaves they were transplanted to 500 cc pots filled with commercial organic soil (C/N = 40, pH 5.0-8.5) and subjected to periodic watering. We assigned 15 pots to each of the following conditions: (i) *C. melitensis* from Chile grown alone; (ii) *C. melitensis* from Spain grown alone; (iii) *H. aromaticum* grown alone; (iv) *C. melitensis* from Chile and *H. aromaticum* grown together; (v) *C. melitensis* from Spain and *H. aromaticum* grown together; (vi) *C. melitensis* from Chile and Spain grown together. After five months (just before flowering), all of the plants were harvested and dried in an oven for 48 h to calculate their total biomass (aboveground plus belowground biomass). We used the total plant biomass just before flowering as a proxy of plant fitness because bigger plants at that time are expected to produce more flowers and seeds (Younginger et al. 2017). Finally, we calculated the relative interaction index: $RII = (B_w - B_o) / (B_w + B_o)$, where B_o is the biomass of the target plant grown alone and B_w is the biomass of the target plant when grown with another plant. When $RII = (0, 1]$ the result of the interaction is positive (facilitation), when $RII = 0$ the result is neutral, and when $RII = [-1, 0)$ the result is negative (competition) (Armas et al. 2004).

Data analyses

We performed generalized linear models (GLZs) to assess the differences in the percentage of germination of *H. aromaticum* vs. that of *C. melitensis* from Spain and Chile, whereas the differences in the coefficient of the velocity of germination were evaluated by means of non-parametric tests (Kruskal–Wallis). We also used GLZs to evaluate the differences in the percentage of germination of *H. aromaticum* when seeds were alone (control) vs. in presence of leaves of *C. melitensis* (from Spain and Chile). To evaluate the differences in the dry biomass among competition treatments, we performed analyses of variance (ANOVAs) and Tukey tests for post hoc comparisons. To assess the differences in the relative interaction intensity index between pairs of species we performed t-tests. Variables were tested for normality (Shapiro–Wilk test) and homoscedasticity (Levene test) prior to

these analyses. We used the software STATISTICA 6.0 (StatSoft Inc.).

Results

Germination experiment

No significant differences were found in the percentage of seed germination ($F_{2,6} = 0.98$; $P = 0.427$) or in the velocity of germination ($K_2 = 0.35$; $P = 0.83$) in *H. aromaticum* and *C. melitensis* from Chile and Spain (Fig. 1). In all cases, more than 75% of the seeds had germinated by day 6, reaching almost 100% germination in 10 days (Fig. 1).

The final percentage of germination in *H. aromaticum* was significantly reduced (> 80%) ($F_{4,10} = 210.35$; $P < 0.01$) in the presence of dry and fresh leaves of *C. melitensis* from both origins, with no differences among them (Fig. 2).

Competitive interactions

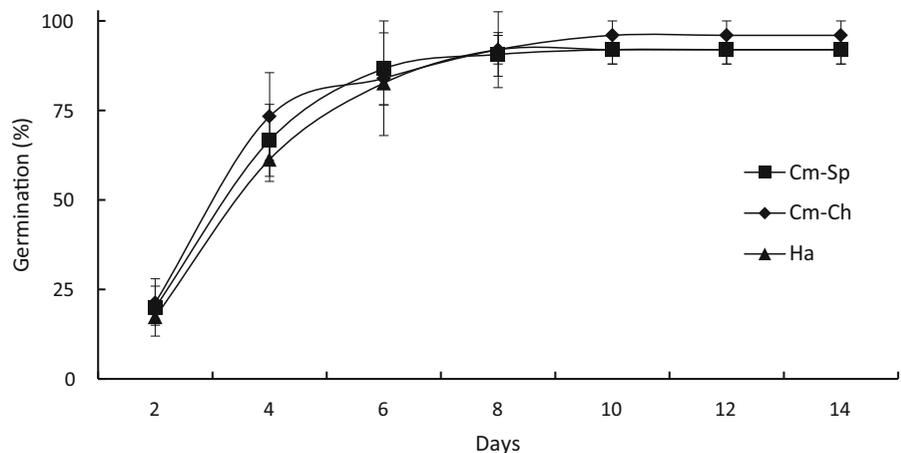
The biomass of *H. aromaticum* was significantly reduced (ca. 60%) in the presence of *C. melitensis* from both Spain (Fig. 3a) and Chile (Fig. 3c). As a consequence, the RII for *H. aromaticum* was significantly lower than those of *C. melitensis* from Spain (Fig. 3b) and Chile (Fig. 3d). There were no significant differences in the biomass of *C. melitensis* from Chile and Spain when grown alone or under intraspecific competition (Fig. 3d). Therefore, there were no differences in their RII indexes (Fig. 3d).

Discussion

No differences were found between the seed germination of *C. melitensis* from Chile and Spain and that of the native *H. aromaticum* when they did not interact. However, the seed germination and plant biomass of *H. aromaticum* were significantly reduced in the presence of *C. melitensis* from both Chile and Spain. Indeed, the RII was similar for both *C. melitensis* origins under inter- and intra-specific competition. Therefore, our results do not support the evolution of an increased competitive ability (EICA hypothesis) or an increased allelopathic activity (AARS hypothesis) of *C. melitensis* plants from the invaded range of Chile. However, further experiments are needed to provide conclusive evidence of our findings.

It has been proposed that early emergence and rapid adaptive changes in germination strategies could favor the invasion of some *Centaurea* species in detriment of native plants with slow germination rates (Gómez-González et al. 2009; Hierro et al. 2009). However, no differences in the germination rates of *C. melitensis* from both ranges and *H. aromaticum* seeds were found. Alternatively, the dominance of *C. melitensis* seedlings found in the field (around 200 seedlings/m²) could, in part, be explained by propagule pressure and disturbance (Moroney and Rundel 2013). Compared to Mediterranean plants, Chilean native herbs have lower tolerances to anthropogenic disturbances such as wild-fires or overgrazing (Arroyo et al. 2000; Gómez-González et al. 2011a). It has been reported that vegetation gaps generated by disturbances favor

Fig. 1 Cumulative germination of *H. aromaticum* (Ha) and *C. melitensis* from Chile (Cm-Ch) and Spain (Cm-Sp). Dots represent the mean values and error lines are standard deviations ($n = 3$)



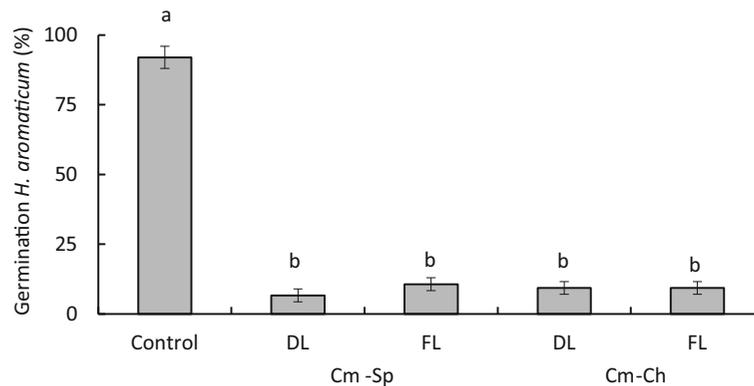


Fig. 2 Effect of *C. melitensis* leaves on *H. aromaticum* seed germination. Bars are mean values and error lines are standard deviations (n = 3). DL: dry leaves, FL: fresh leaves, Cm-Sp: *C.*

melitensis from Spain, Cm-Ch: *C. melitensis* from Chile. Different letters indicate significant differences among treatments ($P < 0.05$; Glz)

the growth and reproduction of *C. melitensis* (Gerlach and Rice 2003). Therefore, frequent disturbances could increase the proportion of *C. melitensis* seeds stored in the soil seed bank over successive generations. However, Moroney and Rundel (2013) showed that disturbance also favors the establishment of *C. melitensis* in Spain, therefore, disturbance alone would not explain its invasion success in Chile.

Our results show that *C. melitensis* reduced the seed germination and plant biomass of *H. aromaticum*, indicating that this alien species has a higher competitive ability than its native relative. In a study carried out in California, the high competitive ability of *C. melitensis* was also shown in relation to other plant invaders (Moroney et al. 2011). However, as already mentioned, we found no evidence for an evolutionary increase in the competitive ability or the allelopathic activity of the studied populations. The RII of *C. melitensis* was similarly independent of their origin and higher than that of *H. aromaticum*. This supports other studies that have not verified the EICA hypothesis in invasive plants (see Atwood and Meyerson 2011 and references therein) and suggests that the high competitive ability of *C. melitensis* is acquired by selective processes that occurred previously in its native range. However, Moroney et al. (2013) documented increases in plasticity and fitness-related traits in *C. melitensis* populations from Chile compared to populations from Spain. It has to be noted that population sampling in our study was limited (only four populations from each country) and it probably does not reflect *C. melitensis* distribution in the native and the invaded range. Thus, further assessments using

a wide range of target species (and other invaded regions) should be performed to assess the consequences of the biogeographical variation of *C. melitensis* traits on its invasion success.

There are invasive *Centaurea* species that produce significant negative effects on the growth of native neighbors by releasing root exudates with strong allelopathic activity (Callaway and Aschehoug 2000; Weir et al. 2003; Vivanco et al. 2004; He et al. 2009). In our study, we could not discern whether the biomass reduction of *H. aromaticum* was due to root exudates. However, some studies performed in California suggest that *C. melitensis* roots do not produce allelopathic compounds. Instead, *C. melitensis* seems to benefit from its relationship with arbuscular mycorrhizal fungi in the presence of some native species, establishing a sort of fungi-mediated parasitism (e.g. *Nassella pulchra*; Callaway et al. 2003). This could even over-compensate for the damage caused by herbivores, providing this alien species with a high competitive ability under grazing conditions (Callaway et al. 2001). However, it remains to be explored whether these kind of complex interactions occur in other species and ecosystems, such as the Chilean Matorral.

Invasive plants escape from the specialist enemies of their native range, but they still have to face the generalist organisms in the new range (Memmott et al. 2000). Therefore, selection could favor those phenotypes with greater resource allocation to defense against generalists (Joshi and Vrieling 2005). These kinds of defenses are secondary metabolites that are highly toxic at low concentrations (Müller-Schärer

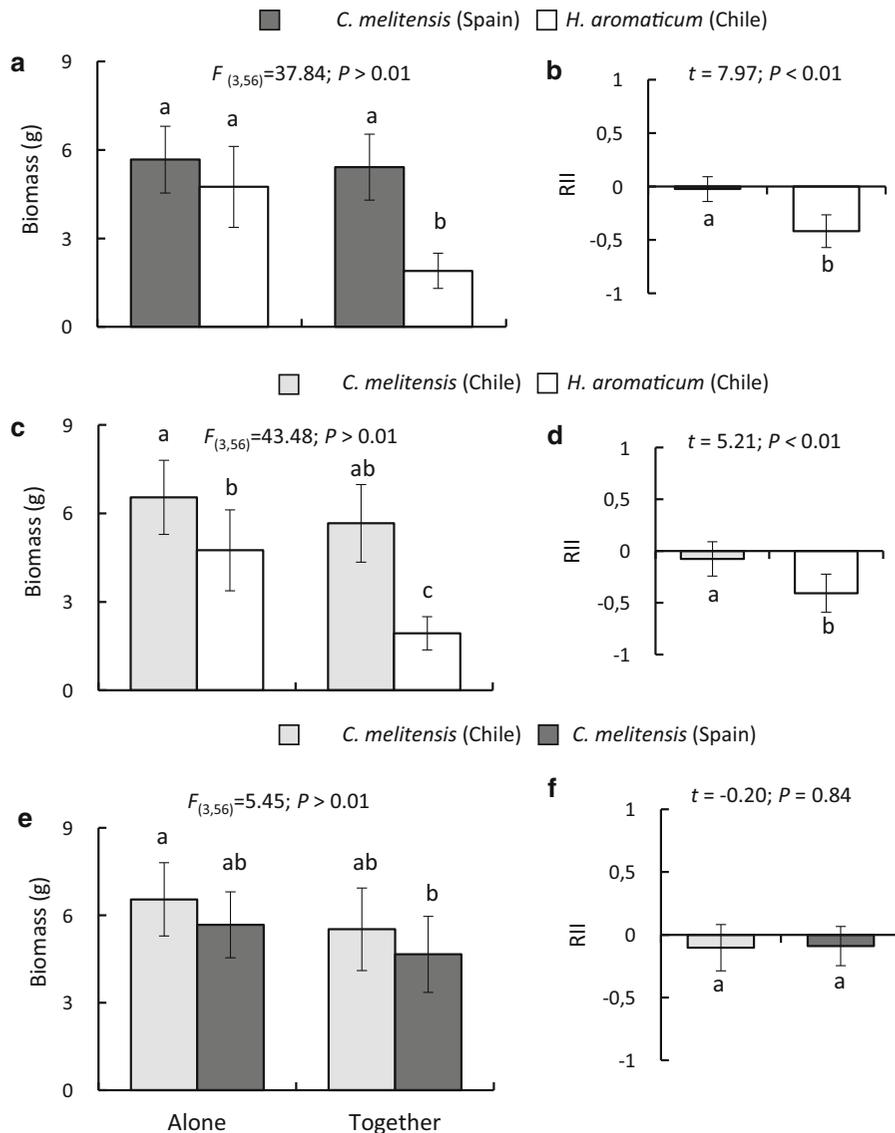


Fig. 3 Competitive interactions between *H. aromaticum* and *C. melitensis* from Spain and Chile. On the left side (panels **a**, **c** and **e**), the mean plant biomass of *H. aromaticum* (white bars), *C. melitensis* from Chile (gray bars) and from Spain (black bars) are shown when they grew alone or in competition with another plant (together). On the right side (panels **b**, **d** and **f**), the mean

values of the relative interaction index (RII) of every interaction are shown. Error lines are the standard deviations ($n = 15$). Different letters indicate significant differences between conditions ($P < 0.05$; Tukey test post-ANOVA for biomass and t test for RII)

et al. 2004) and, interestingly, can also act as allelopathic compounds. Similar to other invasive *Centaurea* species (e.g. *C. maculosa*; Kelsey and Locken 1987, and *C. solstitialis*; Sotes et al. 2015), *C. melitensis* has sesquiterpene lactones stored in the glandular trichomes of their leaves (Bruno et al. 2013). Sesquiterpene lactones act as a defense against herbivores, but they can also inhibit the seed

germination of other species (Kelsey and Locken 1987; Bruno et al. 2013). Although, in our study, we did not identify the chemical compounds responsible for the inhibition of the seed germination of *H. aromaticum*, our results suggest that leaf defenses could favor the invasion of *C. melitensis* through the additional role they play in interference competition (allelopathy). However, we can not discard that the

effects observed in the controlled conditions of our experiments could be amplified or underestimated in relation to nature. In any case, since we found similar effects of *C. melitensis* leaves from both regions, we can suggest that there is no adaptive increase in the allelopathic potential of this species in the invaded range. In order to explain the greater dominance of *C. melitensis* in recipient communities, future studies should assess whether their effects are stronger on neighbors in the invaded range compared to those in the original range (Callaway and Aschehoug 2000).

The Chilean Matorral is an ecosystem that is highly vulnerable to the invasion of annual plant species originating from the Mediterranean Basin (Arroyo et al. 2000). Some studies have hypothesized that the higher competitive ability of alien plants might explain the low abundance of native herbs in the Chilean Matorral (Figueroa et al. 2004; Holmgren et al. 2000), although few experimental assessments have been done in this regard (Gómez-González et al. 2009; Castro et al. 2010). Our results support the former hypothesis provided that *C. melitensis* could out-compete the native *H. aromaticum*, even though *H. aromaticum* is an abundant ruderal native species that successfully colonizes disturbed habitats (Gómez-González et al. 2011b, c). The millenary presence of human populations in the Mediterranean Basin has probably created a selective pressure on the invasive plants (mostly annuals) that are now strongly adapted to anthropogenic disturbances (Martín-Forés et al. 2015). On the contrary, ruderal annuals are infrequent in the native flora of central Chile (Arroyo et al. 2000; Holmgren et al. 2000) and, therefore, invasive annual species from the Mediterranean Basin could not have had to face a strong biotic filter during the invasion process, particularly in disturbed habitats (Martín-Forés et al. 2015). Nonetheless, more studies are needed to assess the potential negative effects of *C. melitensis* on other native species from the Chilean Matorral.

Conclusion

Centaurea melitensis has a higher competitive ability than its Chilean relative *H. aromaticum*. This competitive superiority was found to be similar in *C. melitensis* plants originating from native and invaded ranges, suggesting that no evolutionary change in its

traits has occurred to increase its resource competition. Our results support the hypothesis that the high invasive potential of this species was acquired during previous adaptation processes in its native range. Considering that *H. aromaticum* is a common native ruderal species colonizing disturbed matorral sites, our results suggest that plant diversity in the Chilean Matorral could be seriously affected by the invasion of *C. melitensis*. The competitive impacts of *C. melitensis* on native species can occur by means of reducing plant growth, but also by inhibiting seed germination due to the potential allelopathic effects of the leaf leixivates of *C. melitensis*. This reveals the potential role of defensive leaf trichomes on plant invasion throughout their allelopathic effects on seed germination of native species, a mechanism that has been little addressed in invasion ecology literature.

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Author's contribution All of the authors contributed to the conception and design of this study. Preparation of materials, experiments, data collection and analyses were performed by Gastón J. Sotes. Gastón J. Sotes and Susana Gómez-González wrote the draft and Lohengrin A. Cavieres contributed substantially with important comments and editions. All of the authors read and approved the final manuscript.

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Availability of data and materials The datasets generated during the current study will be available in the FIGSHARE repository, <https://figshare.com/s/affe156b5afb0ce37bc4>.

Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflicts of interest.

Ethics approval This study was carried out with permission from the Agricultural and Livestock Services of Chile (SAG).

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