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The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities

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Summary

1. Alien invasive plants possessing attractive flowers can affect the interactions between native plants and their pollinators. The few studies conducted so far have reported positive, negative and neutral effects of the presence of an invasive species on the pollinator visitation rates and seed output of native species. However, the role played by the density of the alien species has been seldom explored.
2. While high densities of the invasive species can negatively effect the pollinator visitation rates and seed output of the native species, due to sequestration of pollinators by the invasive species, at lower densities the invasive can attract pollinators that otherwise would not visit patches of native species, positively affecting their reproduction.
3. Using observations and pollinator exclusions at a site at 2800 m altitude in the central Chilean Andes, we show that the alien herb *Taraxacum officinale* (Asteraceae), possessing showy floral capitula, shares pollinators to a high degree (> 90%) with two co-occurring native Asteraceae: *Hypochaeris thrincioides* and *Perezia carthamoides*. Pollinator exclusion indicated that both natives are highly dependent on insect visitation to produce seeds.
4. Using manipulative supplemental hand-pollination and experiments, where we varied the density of *T. officinale*, we determined that seed output in *H. thrincioides* and *P. carthamoides* is pollen-limited and that its magnitude is not affected by the presence of the exotic. Further, while the presence of one individual of *T. officinale* around focal native individuals showed neutral or facilitative effects on pollinator service or seed output in the two native species, the presence of five individuals of *T. officinale* negatively affected these reproductive variables.
5. *Synthesis*. Our results suggest that the effects of the presence of alien invasive plant species with attractive flowers vary with their density. This demonstrates the need to experimentally test for the potential impacts of introduced species at different densities before prematurely coming to conclusions regarding their assumed negative or positive effects in native ecosystems.

Key-words: competition for pollination, facilitation, high-alpine ecosystems, invasive species, plant reproductive output, pollen limitation, pollinator–plant interactions

Introduction

Biological invasions are recognized as a major environmental problem and pose one of the greatest threats to biodiversity (Drake *et al*. 1989; Mooney & Hobbs 2000; Sala *et al*. 2000). As alien plant species invade natural communities in ever-increasing numbers, it has become imperative to understand the potential impacts of these ecological disruptions on native communities and ecosystems (Blossev 1999; Parker *et al*. 1999; Levine *et al*. 2003). Numerous studies have demonstrated that invasive species are strong competitors that reduce the survival, growth and size of native plants (e.g. Levine *et al*. 2003; Hager 2004; Vilà & Wiener 2004). Beyond vegetative competition, in recent years a growing amount of information has been accumulating on the extent to which alien species that have showy or attractive flowers affect the native flora for pollinator services (Bjerknes *et al*. 2007). So far, the majority of studies have shown that the presence of alien invasive species with attractive flowers draw pollinators away from the native species, resulting in a reduction in the number of visits to the latter (e.g. Grabas & Laverty 1999; Chittka & Schürkens

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2001; Brown *et al*. 2002; Moragues & Traveset 2005; Larson *et al*. 2006; Totland *et al*. 2006). However, only in some cases does a reduction in pollinator visitation result in a concomitant decrease in seed output (e.g. Grabas & Laverty 1999; Chittka & Schürkens 2001; Brown *et al*. 2002).

Rathcke (1983) proposed that competitive and facilitative interactions among plants for pollination service are opposite extremes of a continuum that is a function of population density or relative abundance of the floral resources (see also Feldman *et al*. 2004; Moeller 2004; Ghazoul 2006). Hence, the presence of showy invasives at low densities might increase visitation rate to natives by attracting pollinators that otherwise would not visit monospecific patches of native species as often; some recent studies support this (Moragues & Traveset 2005; Lopezaraiza-Mikel *et al*. 2007), although effects on seed set have been seldom evaluated. Thus, although no clear trends emerge on the effect of alien invasive species on pollinator visitation and seed output of native species, this may be because the role played by the density of the invasive species has not been considered.

Alpine ecosystems could be expected to be particularly sensitive to the presence of invasive species possessing attractive floral displays and thus an appropriate setting for experimentally assessing their impact on the reproductive output of the native flora. Insect pollination is a widespread phenomenon in alpine environments (e.g. Arroyo *et al*. 1982; Medan *et al*. 2002) despite the fact that the diversity, abundance and activity of insect pollinators have been reported to be characteristically low due to the low ambient temperatures, short snow-free growing seasons and strong winds that these environments experience (e.g. Arroyo *et al*. 1985; Totland 1994; Bingham & Orthner 1998). Therefore, it could be predicted that the presence of invasive species with showy floral displays in alpine environments may result in enhanced attractiveness to pollinators to the local patch where these plants are growing, resulting in increased visitation to co-occurring insect-pollinated native plants. However, high densities of these invasive plants could negatively impact the native flora by monopolizing the services of pollinators, resulting in reduced pollinator visitation and ultimately in reduced seed output of the indigenous species.

The introduced perennial herb *Taraxacum officinale* Weber (Asteraceae) or common dandelion is a conspicuous component of the flora in some parts of the central Chilean Andes. This cosmopolitan weed has attractive floral capitula, and it is frequently found amongst the native vegetation (Cavieres *et al*. 2005, 2008) attracting a wide variety of insect pollinators. Thus, it is an ideal model species with which to assess the potential impacts of different densities of an attractive alien species on pollinator visitation patterns and seed output of co-occurring species requiring pollinator visitation to produce seeds. In this study we (i) determined the degree of pollinator sharing, in terms of insect species composition and percentage representation of each taxa, between *T. officinale* and two co-occurring and co-flowering native Asteraceae (*Perezia carthamoides* H. et A. and *Hypochaeris thrincioides* (J. Remy) Reiche); (ii) assessed the degree of dependence of these native species on insect pollinator visitation for successful seed production; (iii) determined whether seed output in *P. carthamoides* and *H. thrincioides* is pollen limited and whether the magnitude of pollen limitation is affected by the presence of *T. officinale*; and finally (iv) assessed the impacts of *T. officinale* at two different densities on pollinator visitation and seed output in these two native species.

Methods

STUDY SITE

Research was conducted during two consecutive growing seasons (December 2004 to March 2005, and December 2005 to March 2006) on a 10-ha site at 2800 m altitude in the central Chilean Andes (33°21′S, 70°16′W). The climate is alpine with Mediterranean influence, characterized by a long, snow-free summer period of 5–8 months, with a mean air temperature of 10.9 °C (Cavieres *et al*. 2007). Long-term mean annual precipitation at 2500 m is *c.* 445 mm, falling predominantly as snow during the winter months from June to August (Santibáñez & Uribe 1990). The growing season at 2800 m altitude commonly extends from early-December to mid-May (Arroyo *et al*. 1981). The study site is south-west facing and has moderate to gentle slopes (15–30°). Vegetation is dominated by the cushion plant *Laretia acaulis* Cav. (Apiaceae), interspersed with herbaceous species such as *Haplopappus anthylloides*, *Senecio bustillosianus* and spiny shrubs such as *Chuquiraga oppositifolia*, *Anarthrophyllum cumingii* and *Berberis empetrifolia* (Cavieres *et al*. 2000).

STUDY SPECIES

Taraxacum officinale (Asteraceae), the common dandelion, is a perennial herbaceous species that probably originated in Europe but is now found in most countries of the world (Holm *et al*. 1997). In the study area it produces 20–45 mm (33 ± 2 mm, mean ± 1 SE, $n = 30$) diameter attractive bright yellow floral capitula, terminally positioned on 5–20 cm long, hollow, cylindrical peduncles. Each plant produces between one and three capitula, with each of these producing a composite of 100–250 small bright yellow florets. Although *T. officinale* can reproduce asexually, thus not requiring pollinator vectors to transport its pollen, the possession of large showy capitula has been seen to attract a wide range of insect pollinators (Jones 2004; Alejandro A. Muñoz, personal observations; and this study). This can be explained by the fact that each floret has been reported to produce abundant quantities of pollen and nectar (Solbrig & Simpson 1974). At 2800 m elevation, *T. officinale* flowers along almost the entire duration of the snow-free period (November–April) although peak flowering normally occurs between late-December and mid-January (Alejandro A. Muñoz, personal observations).

The two native Asteraceae species studied, *H. thrincioides* and *P. carthamoides*, are patchily distributed throughout the study site. *Hypochaeris thrincioides* produces a mean of three 25–40 mm (33 ± 1, mean ± 1 SE, $n = 30$) yellow to dark yellow capitula on 5–15 cm peduncles. The peduncles are separated from each other from almost ground level such that the capitula are often 4–5 cm apart within a single individual. Each capitulum produces a mean (± 1 SE) of 65 ± 5 florets. *Perezia carthamoides* produces a mean of three 20–30 mm (27 ± 1, mean ± 1 SE, $n = 30$) pale white capitula on short 2–3 cm peduncles, forming a tightly-grouped single inflorescence almost at ground level. Each capitulum produces 18 ± 2 florets. Both native species flower during January (Hoffmann *et al*. 1998), with peak flowering normally occurring in mid-January at 2800 m elevation (Arroyo *et al*. 1981; Alejandro A. Muñoz, personal observations).

Measurements taken along seven 50-m parallel transects showed a mean of 5 ± 2 (1 SE) and 4 ± 1 individuals of *T. officinale* to co-occur naturally in a 1-m radius around plants of *H. thrincioides* ($n = 34$) and *P. carthamoides* ($n = 32$), respectively. However, not all *T. officinale* plants growing around the native individuals flower synchronously with the native species.

ASSESSMENT OF THE EXTENT OF POLLINATOR SHARING AND COMPARISON OF POLLINATOR VISITATION PATTERNS

During the 2004–05 growing season, pollinator identity, percentage representation (relative visitation frequency), pollinator visitation rates and the duration of pollinator visits were assessed for plants of *T. officinale* and for the two co-occurring native species (*H. thrincioides* and *P. carthamoides*) to determine the degree of pollinator sharing and to compare pollinator visitation patterns. Within the 10-ha study site, a total of 25 individual plants of each of the two native species were randomly selected for observation, as well as 39 individuals of the alien *T. officinale*. All selected plants were at least 2 m away from any other conspecific or heterospecific individuals in bloom, to avoid potentially confounding effects of plant density and interspecific interactions. Observations on visitation patterns were conducted following a similar methodology to that used by Muñoz *et al*. (2005). For each species, three 15-min observation periods per hour per plant were made between 9.00 A.M. and 5.00 P.M. on sunny days between late-December 2004 and mid-January 2005. Pollinator visits were registered by three observers. We defined a 'visit' to a plant as one in which the insect landed on at least one open capitulum. We accumulated a total of 193 15-min observations conducted on a total of 89 individuals of these three plant species.

The degree of pollinator sharing between *T. officinale* and the two native species was estimated via Pianka's (1973) niche overlap index, which takes into account the identity of the various pollinator taxa as well as their relative visitation frequency. Values of this index range between 0% and 100%, indicating from null to complete overlap, respectively.

EVALUATION OF THE DEPENDENCY OF NATIVE SPECIES UPON INSECT VISITATION FOR SEED OUTPUT

We determined whether *H. thrincioides* and *P. carthamoides* depend upon insect pollinator vectors to produce seeds using a manipulative pollinator exclusion experiment conducted between January and March 2005. A total of 30 individual plants of both native species were randomly selected in early-January. As above, selected plants were also > 2 m away from any other conspecific or heterospecific individuals in bloom. During the floral bud stage, 15 of the 30 plants of each species were randomly assigned to a pollinator exclusion treatment. Pollinators were excluded from the floral capitula of these individuals during flowering by placing white semi-transparent cloth mesh bags over floral buds. The remaining 15 plants served as controls to which all pollinators had access. For *H. thrincioides*, floral display of control (mean ± 1 SE = 2.7 ± 0.3 capitula/plant) vs. pollinator exclusion plants (mean ± 1 SE = 2.5 ± 0.3 capitula/plant) did not differ (Student $t = 0.422$, d.f. = 28, $P = 0.676$). Likewise, for *P. carthamoides*, floral display of control (mean ± 1 SE = 2.3 ± 0.3 capitula/plant) vs. pollinator exclusion plants (mean ± 1 SE = 1.9 ± 0.2 capitula/plant) did not differ (Mann–Whitney $U = 91.00$, $z = 0.937$, $P = 0.349$). In late-January, as the capitula began to wither, they were covered with small 8 × 6 cm semitransparent 1-mm aperture white mesh bags to avoid loss of the wind-dispersed achenes (one-seeded fruits). During March, all bags were retrieved from the field and all seeds and aborted ovules were counted. Seed output was expressed as percentage seed set (%SS), measured as the percentage of ovules of open florets per plant that set seeds. We analysed differences in seed output in control vs. pollinator exclusion plants using Mann–Whitney *U* tests as the assumptions of normality of data for parametric tests were not met, even when appropriately transformed.

ASSESSMENT OF THE DEGREE OF POLLEN LIMITATION WITH AND WITHOUT THE PRESENCE OF *TARAXACUM OFFICINALE*

In a second growing season (December 2005 to March 2006) we employed a supplemental hand-pollination experiment to assess if the amounts of pollen reaching the stigma constrained seed production in *H. thrincioides* and *P. carthamoides*. In addition, the degree to which the co-occurrence of plants of *T. officinale* influences the presence and magnitude of pollen limitation in the two native species was also tested. For this, we conducted a 2 × 2 factorial experiment with pollen source (natural or supplemental hand-pollination) and presence/absence of *T. officinale* as the two factors. In late-December 2005 in a 6-ha sector of the study site, we randomly selected individual plants of *H. thrincioides* ($n = 24$) and *P. carthamoides* ($n = 20$), all having three or four floral buds. As above, selected plants were minimally 2 m from any other conspecific or heterospecific individuals. All individuals were randomly subjected to one of four treatments: natural pollination in the absence (Treatment 1) or presence of an individual of *T. officinale* (Treatment 2) and supplemental hand-pollination in the absence (Treatment 3) or presence of *T. officinale* (Treatment 4). Thus, there were six replicate plants of *H. thrincioides* under each treatment and five of *P. carthamoides.* Floral display (number of open capitula) did not differ among the plants under the four different treatments (one-way ANOVA, $F_{3,20} = 1.482$, $P = 0.250$ in *H. thrincioides*, and $F_{3,16} = 0.128$, $P = 0.942$ in *P. carthamoides*).

To accomplish manual supplemental pollen addition we collected florets with orange (*H. thrincioides*) or white (*P. carthamoides*) pollen-laden anthers from 10 individuals per species growing at least 5 m away from target plants. We carefully brushed the collected florets across the receptive stigmas of florets of all capitula on the supplemental pollination plants. We hand-pollinated plants on three separate days during peak flowering of each individual during mid-January 2006.

To assess the influence of the presence of single individuals of *T. officinale* on pollen limitation in the two native species as well as to evaluate their impacts at two densities around native target plants (see the 'Impact' experiment described below), we used *T. officinale* individuals grown from seeds between August and December 2005 in a greenhouse at Universidad de Concepción. Seedlings were planted into nitrogen-enriched soil in 8-cm diameter and 15-cm high black plastic bags and watered regularly. A total of 250 plants having floral buds were taken to the study site during early-January. Flowering *T. officinale* individuals were placed into holes dug at *c.* 20–30 cm distance from the target native plants.

Differences in seed output of *H. thrincioides* and *P. carthamoides* under the four treatments were analysed following the same protocol described before for the experiment testing for the degree of dependency upon pollinator visitation to produce seeds. Differences in %SS were analysed using two-way ANOVAs with pollen source and presence/absence of *T. officinale* as the factors, after testing for normality and homogeneity of variances using the Shapiro–Wilks and Bartlett tests, respectively. Data were transformed appropriately when the normality condition was not met. *A posteriori* multiple comparisons were conducted using the Tukey HSD test. All statistical analyses were done using the software R v.2.3 (R Development Core Team 2005).

EVALUATION OF THE IMPACT OF THE PRESENCE OF *TARAXACUM OFFICINALE* AT TWO DIFFERENT DENSITIES ON POLLINATOR VISITATION AND SEED OUTPUT

Finally, we used a further manipulative experiment to assess the potential impact of the presence of *T. officinale* plants at two different densities on pollinator visitation rates, duration of pollinator visits, and seed output in *H. thrincioides* and *P. carthamoides.* As in the previous experiment, in late-December 2005, we randomly selected another 18 individuals of *H. thrincioides* and 15 of *P. carthamoides*, all possessing three or four floral buds and growing at least 2 m away from other plants. All individuals were randomly assigned to one of three treatments: without *T. officinale* (Treatment 1), with the presence of one *T. officinale* individual (Treatment 2) and with five *T. officinale* plants around the corresponding native target plants (Treatment 3). These two densities corresponded to those naturally occurring around the two native species at the study site. Thus, there were six replicate *H. thrincioides* individuals under each treatment and five of *P. carthamoides.* Floral display (number of open capitula) did not differ among the plants under the three different treatments (Kruskall–Wallis, $H = 2.147$, $P = 0.342$ in *H. thrincioides*, and $H = 0.499$, $P = 0.779$ in *P. carthamoides*). Following the same procedure described in the pollen limitation experiment, one, five or no *T. officinale* plants were placed into holes dug *c.* 20–30 cm around the target native plants.

Observations on pollinator visitation were carried out as described under the section on pollinator sharing above. Three 15-min observation periods per hour per plant were made between 10.00 A.M. and 4.00 P.M. (corresponding the period of maximum pollinator activity) on 15 sunny days during January 2006. Each individual was observed on three to five different occasions at different times of the day within three to four consecutive days. We accumulated a total of 74 and 66 15-min observations on *H. thrincioides* and *P. carthamoides*, respectively. Pollinator visitation rates and duration of pollinator visits were calculated as mean values for each individual plant for 15-min observation periods. To assess if the presence of one or five *T. officinale* individuals affected pollinator visitation rates, duration of pollinator visits and seed output (%SS) of *H. thrincioides* and *P. carthamoides*, the Relative Neighbour Effect index (RNE) was calculated for each species at each density of *T. officinale*.

$$\mathrm{RNE} = \frac{(Bo - Bw)}{\mathrm{Max}(Bw, Bo)}$$

RNE is an adequate index for the analysis of plant interactions because of their statistical properties (Weigelt & Jolliffe 2003). By multiplying by –1, positive values of RNE indicate facilitative interactions, while negative values indicate competitive interactions. In our case *Bw* corresponded to the value of one of the studied variables (e.g. pollinator visitation rates) when *T. officinale* was present (one or five individuals) while *Bo* was the value of that variable when *T. officinale* was not present. For each native species we randomly paired without replacement each of the individuals without neighbouring *T. officinale* with one of those where one *T. officinale* individual was present, and calculated the RNE for each pair. This same procedure was employed to assess the effects on native individuals when five *T. officinale* individuals were present. Significant differences from zero values of RNE (i.e. no interaction or null hypothesis) were assessed with one sample *t*-test.

Results

DEGREE OF POLLINATOR SHARING BETWEEN *TARAXACUM OFFICINALE* AND THE NATIVE SPECIES

Taraxacum officinale was visited by a wide range of different pollinator taxa including Hymenoptera, Diptera and Lepidoptera. The most frequent pollinators were the small andrenid bee *Lipanthus* sp., representing 51.2% of all visits, and the syrphid fly *Scaeva melanostoma*, tachinid flies and the leaf-cutting bee *Megachile semirufa* (Table 1). Likewise, *H. thrincioides* was also visited by a large variety of different pollinator taxa, with the most frequent taxa also being *Lipanthus* sp. (39.5% of all visits), followed by *S. melanostoma*, *M. semirufa* and the bee *Caenolictus* sp. (Table 1). *Lipanthus* sp. was by far the most common visitor to plants of *P. carthamoides* (89.3%), while only a few other taxa were seen at these plants, some of which also visited *T. officinale* (Table 1). Consequently, the degree of pollinator sharing between *T. officinale* and each of the two native plants, expressed using Pianka's niche overlap index, was very high, 94% and 91% with *H. thrincioides* and *P. carthamoides*, respectively.

DEPENDENCY OF NATIVE PLANT SPECIES UPON POLLINATION VECTORS

Results of the pollinator exclusion experiment revealed that both native species tested produced almost no seeds when pollinator vectors were excluded during flowering, with mean %SS being only 1.3% and 0.3% in *H. thrincioides* and *P. carthamoides*, respectively. %SS in control plants of both species (54.8% and 31.0% in *H. thrincioides* and *P. carthamoides*, respectively) was significantly higher than in pollinator exclusion plants (Mann–Whitney *U* test, $U = 0.00$, $z = 4.825$, $P < 0.001$ for *H. thrincioides* and $U = 24.00$, $z = 4.059$, $P < 0.001$ for *P. carthamoides*).

POLLEN LIMITATION AND INFLUENCE OF *TARAXACUM OFFICINALE*

Supplemental hand-pollination resulted in a significant *c.* 35% and 87% enhancement in seed output (%SS) of *H. thrincioides* ($F_{1,20} = 8.73$, $P < 0.01$) and *P. carthamoides* ($F_{1,16} = 11.09$, $P < 0.01$), respectively (Fig. 1). The presence of one individual of *T. officinale*, however, did not alter seed output of either control or supplemental hand-pollinated plants of either native species ($F_{1,20} = 0.09$, NS and $F_{1,16} = 0.10$, NS for *H. thrincioides* and *P. carthamoides*, respectively; Fig. 1).

Table 1. List of insect pollinator taxa, number of individuals of each taxon observed (*N*), and percentage (%) of the total number of visits that each pollinator taxon made to individuals of the invasive plant species *Taraxacum officinale* and to two co-occurring native species, *Hypochaeris thrincioides* and *Perezia carthamoides*, at a site at 2800 m elevation within the Valle Nevado Ski complex, Andes of central Chile between late-December 2004 and January 2005

	Taraxacum officinale		*Hypochaeris thrincioides*		*Perezia carthamoides*	
	N	%	*N*	%	*N*	%
Hymenoptera						
Megachile semirufa (Megachilidae)	8	10.3	6	12.5		
Megachile sp. 1			1	2.1		
Centris nigerrima (Anthophoridae)			1	2.1		
Caenolictus sp. (Halictidae)			5	10.4		
Heterosarus sp. (Andrenidae)			1	2.1	6	4.0
Lipanthus sp. (Andrenidae)	40	51.2	19	39.5	133	89.3
Diptera						
Scaeva melanostoma (Syrphidae)	12	15.4	7	14.6	2	1.3
Tachinidae	11	14.1	4	8.3	4	2.7
Villa sp. (Bombyllidae)					4	2.7
Bombyllidae sp. 1	1	1.3				
Bombyllidae sp. 2	1	1.3				
Unidentified			1	2.1		
Lepidoptera						
Lycanidae			1	2.1		
Yramea spp. (Nymphalidae)	5	6.4				
Unidentified			1	2.1		
Unidentified taxa			1	2.1		
Total	78	100%	48	100%	149	100%
Number of plant individuals observed	39		25		25	
Number of 15-min observations	83		56		54	

IMPACT OF *TARAXACUM OFFICINALE* ON POLLINATOR VISITATION AND SEED OUTPUT

The most frequent pollinator taxa that visited control plants of *H. thrincioides* under this experiment conducted during the 2005–06 growing season, were small andrenid bees and leaf cutting bees *Megachile* spp. (each making 31% of the total number of visits) followed by the syrphid fly *S. melanostoma* (20.7%) (Fig. 2). While the presence of five *T. officinale* did not markedly alter the composition and relative visitation frequency of the insect assemblage that pollinated the *H. thrincioides* plants under study ($\chi^2 = 1.52$, d.f. = 4, NS), the presence of one *T. officinale* did significantly alter this ($\chi^2 = 9.88$, d.f. = 4, $P < 0.05$). This was mainly seen as a decrease in Andreanidae and Bombyllidae, and an increase in visitation by 'others' (Fig. 2). In contrast, *T. officinale* at the two different densities applied markedly altered the relative visitation frequency of the insect assemblage that pollinated the *P. carthamoides* plants under study ($\chi^2 = 573.3$, d.f. = 4, $P < 0.01$; $\chi^2 = 1343.8$, d.f. = 4, $P < 0.01$, for one and five *T. officinale* surrounding plants, respectively). When one *T. officinale* plant surrounded *P. carthamoides*, Bombyllidae visits decreased from 25.4% in control plants to 4.2%, whereas *S. melanostoma* increased from 1.8% to 33.3% (Fig. 2). In contrast, while andrenid bees were by far the most frequent visitors (69.1%) to control plants of *P. carthamoides*, their relative representation dropped to only 15% when these native plants were surrounded by five plants of *T. officinale* (Fig. 2) and the percentage representation of *S. melanostoma* increased from 1.8% in control plants to 50% in plants under the five *T. officinale* plants treatment (Fig. 2).

RNE index indicated that while the addition of one flowering plant of *T. officinale* around single native individuals of *H. thrincioides* did not significantly change pollinator visitation rates, both duration of pollinator visits and seed output were significantly increased (i.e. facilitated) (Fig. 3). While the increase in pollinator visits was *c.* 25%, seed output increased by *c.* 15%. In contrast, the presence of five flowering plants of *T. officinale* around single native individuals of *H. thrincioides* did not change the duration of pollinator visits, but significantly decreased pollinator visitation rates and seed output (Fig. 3). In this case, decreases in pollinator visitation rates and seed output were 26% and 10%, respectively. In *P. carthamoides*, while the presence of one flowering plant of *T. officinale* did not change any of the parameters evaluated, the presence of five *T. officinale* individuals significantly decreased pollinator visitation rates and seed output, yet not duration of pollinator visits (Fig. 4). While pollinator visitation rates decreased by 25%, seed output was reduced by 34%.

Discussion

It has been suggested that alien plants with a taxonomic affinity to natives can be rapidly incorporated into plant-pollinator networks because their similar floral morphology to natives enables them to share their pollinators (Memmott & Waser

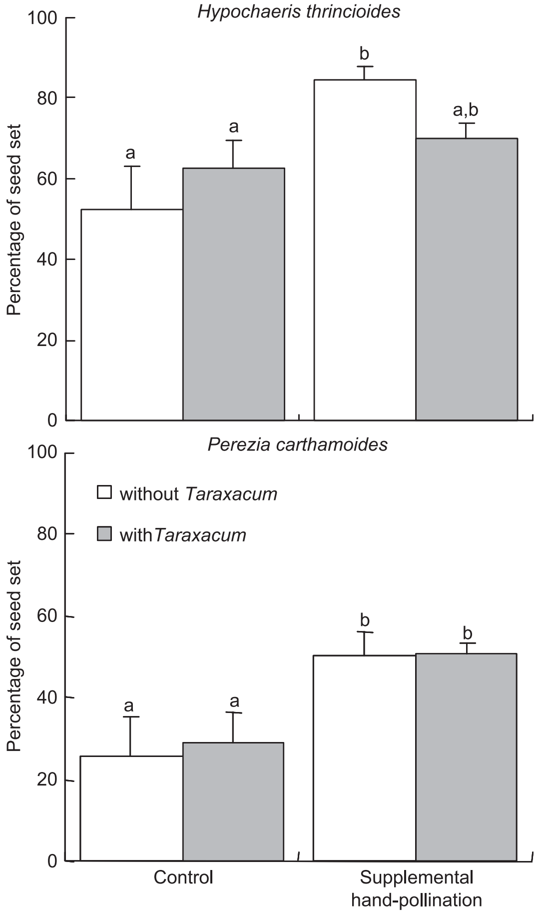

Fig. 1. Percentage seed set (%SS) of control (natural pollination) and supplemental hand-pollinated plants of two native species: *H. thrincioides* and *P. carthamoides*, in the presence or absence of one individual of the alien herb *T. officinale* during the 2005–06 growing season at the 2800 m elevation site. Number of replicates per treatment was six and five individuals of *H. thrincioides* and *P. carthamoides*, respectively. Bars are means + 1 SE. Treatments sharing the same letter within each panel do not differ significantly ($P > 0.05$).

2002). This seems to be the case with *T. officinale* in the Andes of central Chile, where we have shown that this showy invasive plant species shares, to a very large extent, insect pollinators with two sympatric native Asteraceae: *Hypochaeris thrincioides* and *P. carthamoides*. In a parallel study, we also found that *T. officinale* also shares a very high number of insect pollinators with three other Asteraceae species of the Andes of central Chile (*H. clarionoides* (J. Remy) Reiche, *Haplopappus anthylloides* Meyen & Walp and *Senecio bustillosianus* Remy) (Muñoz, Chacón & Cavieres, unpublished results), supporting the idea that invasives with similar floral morphologies with natives are more easily incorporated into the pollinators' web (but see Morales & Aizen 2006).

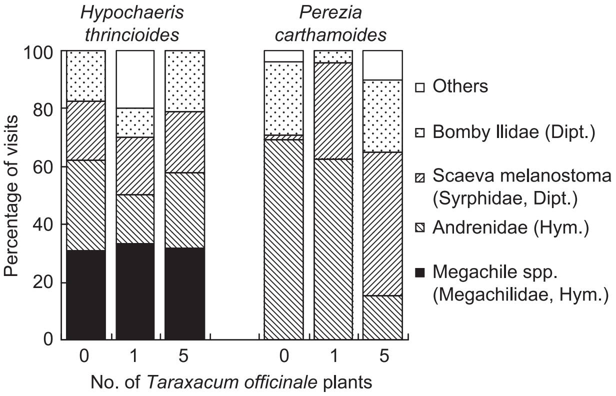

Fig. 2. Percentage of the total number of pollinator visits that each of the most frequent insect taxa made to individuals of *H. thrincioides* and *P. carthamoides* under three different treatments: without *T. officinale* (0), in the presence of one *T. officinale* individual (1) and surrounded by five *T. officinale* plants (5) during the 2005–06 growing season. 'Others' category includes infrequent visitors such as Lepidoptera species (see Table 1).

Pollination-generalist alien species are more likely to alter pollinator interactions of more native plant species than a specialist that attracts fewer pollinator species (Richardson *et al.* 2000; Memmott & Waser 2002; Lopezaraiza-Mikel *et al.* 2007). According to our results *T. officinale* individuals were visited by a wide range of pollinators (Table 1), where most of them are recognized as frequent visitors of several native plant species along the Chilean Andes (e.g. Arroyo *et al.* 1982, 1985; Arroyo & Squeo 1990; Muñoz *et al.* 2005), indicating that *T. officinale* met all the attributes needed to alter the pollination service in native species of this alpine ecosystem.

Taraxacum officinale individuals experimentally placed at different densities around focal individuals of the two native species altered the pollinator service and reproductive output of these native species in this alpine ecosystem. Nevertheless, the direction (positive or negative) of the response was dependent on the density of the invasive species. While the presence of one flowering *T. officinale* individual around individuals of *P. carthamoides* did not change any of the reproductive parameters evaluated (i.e. neutral effects), in *H. thrincioides* duration of pollinator visits and seed output were increased, indicating facilitative effects on these reproductive variables. Alpine habitats are well known for their harsh environmental conditions that limit plant reproduction, and any amelioration of these conditions can have tremendous impacts on the population dynamics of native populations (Körner 2003). Accordingly, the 15% increase in seed set observed for *H. thrincioides* is likely to have an impact on the population dynamics of this native species, especially when we consider that successful recruitment in an alpine habitat is highly seed limited (Klanderud & Totland 2007).

Similar positive effects due to the presence of an invasive species were reported by Moragues & Traveset (2005) who found a potential facilitative effect of invasive *Carpobrotus* spp. through enhanced pollinator visitation in two of the native species they studied (*Cistus salviifolius* and *Anthyllis cytisoides*) in rocky coastal habitats of the Spanish Balearic Islands. Recently, Lopezaraiza-Mikel *et al.* (2007) showed that in a community context the presence of the invasive

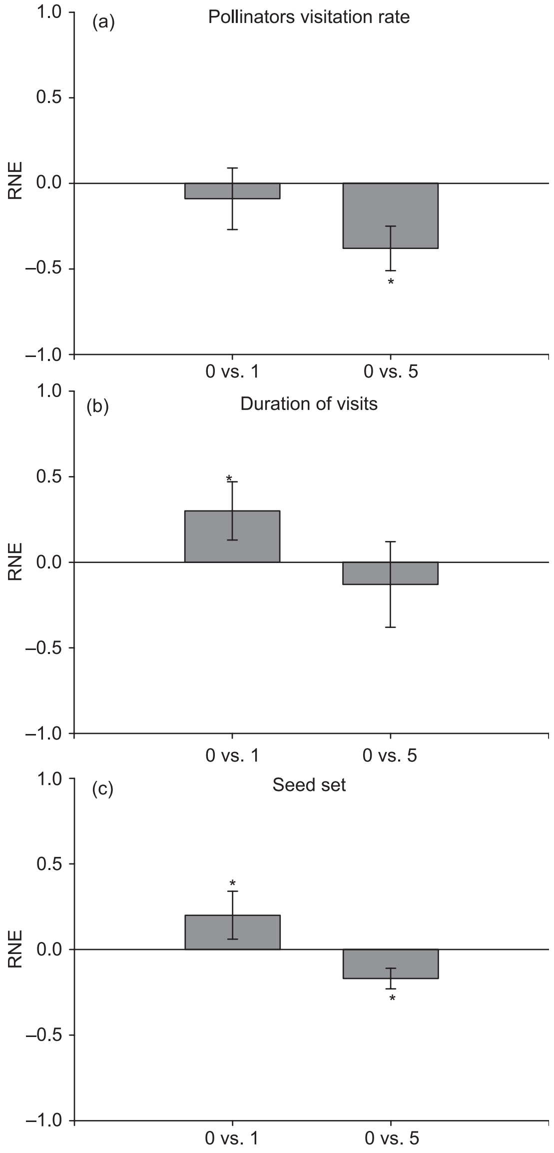

Fig. 3. Effects of the presence of one *T. officinale* individual (0 vs. 1), and five *T. officinale* plants (0 vs. 5) on the pollinators visitation rate (a), duration of pollinators visit (b) and seed set (c) of *Hypochaeris thrincioides* during the 2005–06 growing season. Error bars are ± 2 SE. Asterisk indicates significant differences from zero ($P < 0.05$).

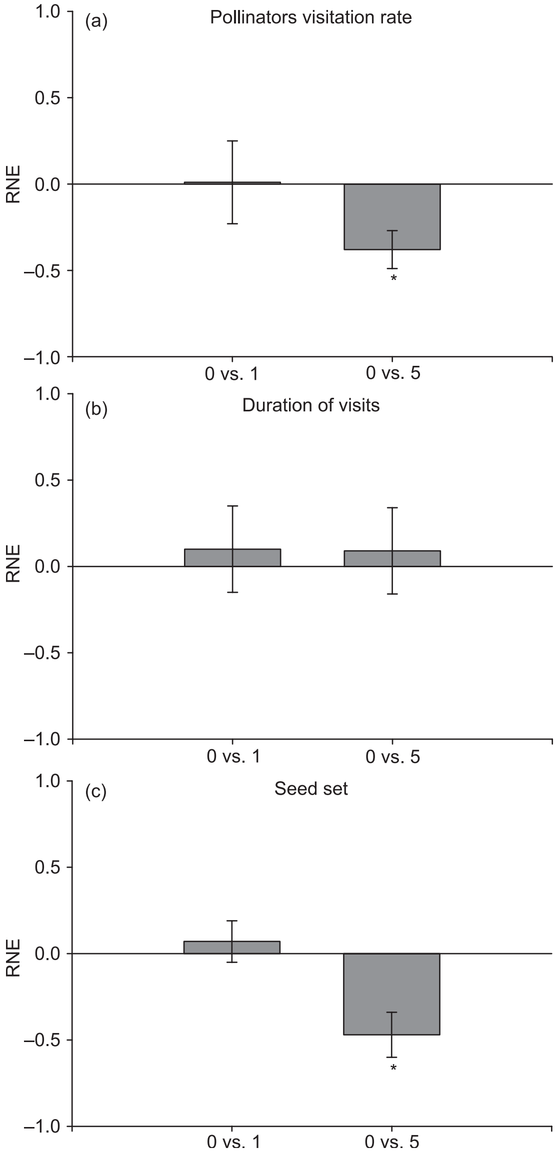

Fig. 4. Effects of the presence of one *T. officinale* individual (0 vs. 1), and five *T. officinale* plants (0 vs. 5) on the pollinators visitation rate (a), duration of pollinators visit (b) and seed set (c) of *P. carthamoides* during the 2005–06 growing season. Error bars are ± 2 SE. Asterisk indicates significant differences from zero ($P < 0.05$).

Impatiens glandulifera has a facilitative effect on the pollinator visitation to native species, although effects on seed output were not evaluated.

In contrast, the presence of five flowering *T. officinale* individuals around individuals of the two native species studied produced negative effects on pollinator visitation rates and seed output, indicating that the positive or neutral effects of the invasive at lower densities changed to negative as the density of the invasive species increased. The negative effects found here at higher densities of *T. officinale* agree with those of Brown *et al*. (2002), who reported a 14%–54% reduction in pollinator visitation to the native species *Lythrum alatum* due to the experimental addition of potted plants of the showy native congener *L. salicaria* in wetland habitats of Ohio, USA. These competitive effects translated into a *c.* 22% to 34% reduction in seed output in the native species. Competition was also suggested in the invasive Asian *I. glandulifera*, which reduced the number of pollinators and seed set of the native *Stachys palustris* by *c.* 50% and 25%, respectively, through an experimental addition experiment and comparison of pure and mixed patches in riverbank habitats of central Europe (Chittka & Schürkens 2001).

However, the majority of the studies that evaluate the presence of invasive species on pollinator visitation and/or seed output of native species have reported null effects (Aigner 2004; Jones 2004; see reviews of Traveset & Richardson 2006 and Bjerknes *et al*. 2007). As predicted by previous theoretical studies (e.g. Ratchke 1983; Feldman *et al*. 2004), our results suggest that null effects are part of a continuum of positive and negative responses that depends on the abundance of the invasive species. Thus, current neutral responses can become negative if the density of the alien invasive increases. In addition, different reproductive parameters (i.e. visitation rates, seed output) differ in their functional response to plant density (Feldman *et al*. 2004) indicating that evaluations of the impact of the presence of alien invasive species should include different reproductive parameters, where seed set is vital to assess the long-term ecological impacts on native populations and communities. For instance, while the presence of one flowering individual of the exotic dandelion *T. officinale* did not affect pollinator visitation rates to *H. thrincioides*, duration of pollinator visits and seed output were increased. This may be related to the significant changes in the pollinator assemblage observed in this native species when one individual of the invasive was present (Fig. 2). Whilst the 'others' category of pollinators increased, Andreanidae and Bombyllidae decreased their visits compared to when no invasive individuals were present.

An alternative explanation for these null impacts on the reproductive output of the native species tested could be that seed output in some of them may not be pollen-limited or may be limited by other resources such as soil nutrients or low genetic diversity (Ghazoul 2004; Totland *et al*. 2006). Another explanation might be that other 'unusual' pollinators compensate the loss of the 'usual' pollinators. For instance, Ghazoul (2004) reported a decrease in butterfly visitations on the native *Dipterocarpus obstusifolius* after the invasion of *Chromolaena odorata*, but birds replaced them and seed set was unaffected.

In conclusion, the exotic species *T. officinale* shares pollinators to a large degree with the two native co-occurring Asteraceae species, *H. thrincioides* and *P. carthamoides*. These native species require pollinator visitation for successful seed production, and their seed output is pollen limited. Our results suggest that the presence of *T. officinale* is altering pollinator visitation and seed output in *H. thrincioides* and *P. carthamoides*, with the direction of the impact varying with the density of the invasive species: while at lower densities effects were positive or neutral, at higher densities they were negative. This demonstrates the need to experimentally test for the potential impacts of introduced species at different densities before prematurely presuming that they have negative or positive effects in native ecosystems. In addition, our results have some important management implications, at least for one of the studied species (*H. thrincioides*) in our system, where the total elimination of the alien invasive have more negative results than its presence at low densities. Thus, considering the widely differing findings reported in the literature of exotic species effects on pollinator service and reproductive output in native species (negative, null, and positive), future work should test the role played by the density of the invasive species before prematurely coming to conclusions regarding their assumed negative effects in native ecosystems. In some instances the presence of alien invasives at very low densities could have positive effects. Nonetheless, the dependency of these alien impacts on both temporal and spatial observation scales is another issue that must be addressed in future studies (Bjerknes *et al*. 2007).

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