ORIGINAL PAPER

Biological invasion of a refuge habitat: *Anthriscus caucalis* (Apiaceae) decreases diversity, evenness, and survival of native herbs in the Chilean matorral

Sergio A. Castro · Ernesto Badano · Daniela Guzman · Lohengrin Cavieres

Received: 7 June 2008/Accepted: 21 July 2009/Published online: 20 October 2009 © Springer Science+Business Media B.V. 2009

Abstract In central Chile, the bur beak chervil (*Anthriscus caucalis* M. Bieb.; Apiaceae) is an annual naturalized herb introduced from Europe at least 120 years ago. *Anthriscus* is distributed in vegetation formations such as sclerophyllous shrublands (locally known as "matorral") and spiny savannas of *Acacia caven* (locally known as "espinal"). In matorral formations, *Anthriscus* grows at the edge of native woody fragments. Because these fragments are

S. A. Castro (🖂)

Departamento de Biología, Facultad de Química y Biología, Universidad de Santiago de Chile, Avenida Alameda Libertador Bernardo O'Higgins 3363, Santiago, Chile e-mail: sergio.castro@usach.cl

E. Badano

Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción, Chile

D. Guzman

Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile

L. Cavieres

Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción, Chile

S. A. Castro

Center for Advanced Studies in Ecology and Biodiversity (CASEB), Santiago, Chile

refuges where native herbs recruit, we studied the impact of Anthriscus on the diversity and survival of native forbs established in these sheltering microsites. First, we characterized the spatial distribution of Anthriscus in the matorral, sampling in different micro-habitat types. We differentiated three microhabitat types: under the canopy of a fragment, at the edge of the canopy of a fragment, and in open sites outside the fragments. A total of 40 1×1 m quadrates were randomly distributed in each habitat type. Inside each of them, we recorded the number of seedlings and established plants, including Anthriscus. Then we evaluated experimentally the effect of Anthriscus on diversity and evenness of the local herb assemblages. For this purpose we conducted a field trial using 34 metallic enclosures (0.5 \times 0.5 m) arranged in pairs. In each pair, Anthriscus individuals were removed from one plot, the other paired plot acting as control. We periodically recorded the presence and abundance of the remanent species of herbs inside the plots, and then we characterized the species diversity and evenness over time (Shannon's index, H' and Pielou's index, J'). Finally, in a second experiment we measured experimentally the presence or absence of Anthriscus against the survival of four native herb species (Bowlesia incana, Bromus berteroanus, Pectocarya linearis, and Moscharia pinnatifida). Here we used 20 0.5×0.5 m plots where we randomly transplanted seedlings of native herbs and Arnthiscus. Then, for each species and plot we determined their survival (%) according to the



number of seedlings initially transplanted. The samplings show strong association between the presence of Anthriscus on edge habitat in the matorral. The maximum densities were noted in these microhabitat types whereas in open areas and under-fragment sites Anthriscus shows very low or null densities. At the end of the first trials, the plots with Anthriscus showed a Shannon diversity index $H' = 0.41 \ (\pm 0.11)$ SE), while in plots without *Anthriscus* this value was 1.19 (± 0.1 SE), both as averages. Pielou's evenness index (J') yielded values of 0.23 (± 0.06 SE) and 0.59 $(\pm 0.04 \text{ SE})$ for treatments with and without Anthriscus, respectively. Similarly, the second trials shows that the survival of the four native herbs was drastically decreased in the presence of Anthriscus: by 64% for Bowlesia incana, 43% for Bromus berteroanus, 46% for Moscharia pinnatifida, and 76% for *Pectocaria linearis*. Our study shows that the effects of Anthriscus include an inhibition of the establishment of native plants and a decrease in their survival in edge habitats, therefore affecting the composition and diversity of the local herb layer. Thus, Anthriscus is invading a refuge habitat for native herbs in the Chilean matorral, decreasing the native herb diversity and survival.

Keywords Edge habitat · Refuge · Mediterranean vegetation · Plant invasions · Herb layer

Introduction

Plant invasions can have important effects on the diversity of communities (Myers et al. 2000; Levine et al. 2003; Dukes and Mooney 2004; D'Antonio and Hobbie 2005). Although for most invasions these effects are minimal, some alien species are responsible for dramatic effects, affecting the distribution and abundance of native species (Williamson 1996; Levine et al. 2003). Therefore, some invasive plants may be considered as important drivers of communities and biomes (Vitousek et al. 1996), whose invasibility may depend on the native biodiversity context (Lonsdale 1999).

Plant invasions in Mediterranean ecosystems have special importance due to their intrinsic diversity and value as biodiversity hotpots. Mediterranean biomes contain near 20% of the vascular taxonomic diversity (Cowling et al. 1996; Myers et al. 2000), and support large and expanding human settlements (di Castri 1981; Rundel 1998; Aronson et al. 1998). Comparative patterns and processes implicated in the invasion of those ecosystems have been attended only recently attended (Arroyo et al. 2006; Holmgren 2002; Sax 2002; Pauchard et al. 2004; Jiménez et al. 2007). A recognized -but scarcely studied- pattern is that alien and native plants tend to occupy different habitats. For example, in mediterranean California it has been documented that serpentine grasslands, characterized by low Ca⁺²:Mg⁺² ratio and low macronutrient levels (N and P), contain a large diversity of native herbs, whereas in non-serpentine soils alien herbs are more common (Murphy and Ehrlich 1989; Harrison 1997, 1999; Gelbard and Harrison 2003; Gram et al. 2004).

In mediterranean Chile, early observations of the ecology of alien plants were made by Gulmon (1977) and Keeley and Johnson (1977), who independently documented that native and alien herbs were differentially distributed. They noted that naturalized herbs were mainly established in open microhabitats while native ones were more diverse underneath the canopy or at the edge of woody matorral fragments. Since then, local researchers have shown that the microhabitat of the canopy edge constitutes a refuge for native plants, because in open areas they are displaced by the combined effect of competition with naturalized herbs (Fuentes et al. 1986), grazing by alien herbivorous mammals (Jaksic and Fuentes 1980; Fuentes et al. 1984), and human disturbance (Holmgren 2002).

The bur beak chervil Anthriscus caucalis M. Bieb., Apiaceae (hereafter called simply Anthriscus) is an annual naturalized herb introduced from Europe in the second half of the nineteenth century. Its original distribution included the Mediterranean Basin and the Caucasus region (Tutin et al. 1968), and it has been introduced into North America, New Zealand, and South America (Randall 2002). In Chile, Reiche (1899) documented its presence (as the synonym A. vulgaris Pers., non Bernh.) in 'some localities' around the city of Santiago, indicating that this species was first observed in 1888 and that it was accidentally introduced to the country. Currently, Anthriscus is distributed throughout central Chile,



occupying cooler microsites in vegetation formations such as the sclerophyllous matorral and *Acacia caven* espinal (Montenegro et al. 1991). Additionally, it is present in abandoned sites in urban areas and in agricultural lands, where it is considered a weed (Matthei 1995). In the matorral, *Anthriscus* grows at the edge of woody canopy and its presence is associated with low native plant diversity (Figueroa et al. 2004).

Because Anthriscus recruits and becomes a dominant plant in a refuge habitat for native herbs, we studied the putative effects of this species on the diversity and survival of native forbs established in that habitat. We first characterized the spatial distribution of Anthriscus in the matorral, and by means of two field experiments, assessed the effect of Anthriscus on the diversity and evenness of the herb layer (including both native and naturalized herbs), and on the survival of four native herbs.

Materials and methods

Study area

In mediterranean Chile, the evergreen shrub vegetation is called matorral (Rundel 1981), an ecological analogue of the Californian chaparral (di Castri 1981). The actual composition and physiognomy of the matorral are determined by human effects on the originally continuous vegetation (Rundel 1981), which over the centuries have produced a mosaic of secondary fragments or patches of native species of woody flora with variable composition, size and shape (Fuentes et al. 1984). These woody patches are surrounded by a rather continuous matrix of herbaceous vegetation, composed of variable combinations of native and naturalized species (Figueroa et al. 2004), the latter chiefly originated in Eurasia and brought via Europe (Montenegro et al. 1991).

We conducted our study at the Estación de Investigaciones Ecológicas Mediterráneas (EDIEM; 33°23′S, 70°31′W) located ca. 20 km east of Santiago on the Andean foothills. This protected area occupies 835 ha, with elevations ranging from 1050 to 1915 m. The climate is mediterranean (di Castri and Hajek 1976) with an annual mean rainfall of 370 mm, mainly concentrated during the austral winter months (June to August). The mean temperature is

highest from December to March (corresponding to the austral summer) and lowest from June to August (the austral winter). Details of the climate, weather, and habitat conditions at our study site are found in www.bio.puc.cl/sca/.

The study site is covered by sclerophyllous vegetation (Jaksic 2001), which physiognomically may be described as a mosaic of evergreen shrubland patches. Trees and shrubs of *Lithrea caustica* are dominant in these fragments, with cover ranging from 12% to 42% depending on slope orientation. Other shrubs such as *Kageneckia oblonga* (Rosaceae), *Colliguaja odorifera* (Euphorbiaceae), *Baccharis rosmarinifolia* (Asteraceae), *Quillaja saponaria* (Rosaceae), *Podanthus mitique* (Asteraceae), *Acacia caven* (Fabaceae), and *Azara dentata* (Flacourtaceae) are also present in the fragments. These patches are surrounded by a herb layer with mixed native and alien herbs, which is distributed mainly between matorral fragments.

Spatial distribution of Anthriscus

During 2004 and 2005 we studied the spatial distribution of Anthriscus in different habitat types in our study site. We differentiated basically three microhabitat types: under the canopy of a fragment, at the edge of the canopy of a fragment, and in open sites outside fragments. These three sites were recognized because previous reports indicate that they are micro-climatically differentiated (temperature, humidity, solar insulation; del Pozo et al. 1989; Rozzi et al. 1989). The under-fragment sites (called hereafter under habitat) were areas located inside woody fragments of continuous canopy cover, >3 m from the fragment's edge. Open sites (hereafter open habitat) were >3 m outside neighboring fragments, in the herb layer. Finally, the fragment's edge sites (hereafter edge habitat) were areas below the shrub canopy projection, up to 2 m toward the fragment's core.

A total of 40.1×1 m quadrates separated by at least 50 m from each other were randomly distributed in each habitat type, with a total of 120 quadrates. In each of them, we recorded the number of seedlings and established plants, including *Anthriscus*. To this end, each quadrate was subdivided into 100 10×10 cm cells. Thus, we determined the relative cover (%) for each species by counting the number of



cells occupied. The sampling took place between July and October of both 2004 and 2005, during late winter and early spring, the season with highest diversity of emerged herbs, and encompassing the entire phenology of *Anthriscus*.

Effect of *Anthriscus* on herb diversity

To determine the putative effects of *Anthriscus* on the diversity of the herb layer, a field trial was conducted in 2006. We used 34 metallic enclosures $(0.5 \times 0.5 \text{ m})$ arranged in pairs 10–20 cm apert. Each pair of plots was distanced 20 m or more from others, all of them located in edge habitat. In each pair, *Anthriscus* individuals were removed from one plot, the other plot acting as control.

From August to November 2006 (spanning 9 weeks) we periodically recorded the presence and abundance of species of herbs inside the plots. Then each plot was characterized by its species diversity and evenness through time. Species diversity was calculated by Shannon's index, computed as $H' = \Sigma$ $(p_i \times \text{Ln}(p_i))$, where p_i corresponds to the relative abundance of each species in the plot. To compare plots differing in their diversity, we standardized the diversity indices obtained over time with respect to the initial one, using the following algorithm $\Delta H' = (H_f - H_i)/H_i$, where $\Delta H'$ is the change in diversity, H_f is the diversity recorded in each plot at different times, and H_i is the diversity recorded at the onset of the experiment. Additionally, the evenness was calculated by Pielou's index, computed as $J' = H'/H_{\text{max}}$, where H' is Shannon's index, H_{max} equals Ln(S), and S is the maximum number of species counted in the plots.

Effect of Anthriscus on native herb survival

To determine the putative effects of *Anthriscus* on the survival of native herbs, a set of trials was carried out during 2005. We used 80.5×0.5 m plots located in edge habitat. Into each plot we randomly transplanted ten seedlings of each of the following native plant species: *Bowlesia incana*, *Bromus berteroanus*, *Pectocarya linearis*, and *Moscharia pinnatifida*. These species were chosen because they were the most abundant native plants growing in edge habitat. Then, 10 seedlings of *Anthriscus* were randomly inoculated in half of the plots (i.e., 40 plots). Thus,

we had two experimental treatments: plots transplanted with native herbs growing with or without Anthriscus, both replicated 10 times. Inside the plots, the transplanted plants were determined randomly using 5×5 cm cells. Each of the 100 cells was numbered and sorted for each transplant.

All the transplanted plants were marked individually using small plastic stakes for temporal localization and monitoring, and all independently emerged seedlings were removed manually. All plots were enclosed with metal fencing and were monitored periodically, counting the number of plants that survived since the initial transplantation. From July to October 2005 (spanning 14 weeks) we determined if the marked herbs were present and erect; withered herbs were considered as not having survived. For each species and plot their survival (%) according to the number of seedlings initially transplanted.

Statistical analyses

We analyzed the spatial distribution of Anthriscus using one-way ANOVA (Sokal and Rohlf 1995). We used habitat as the independent factor with three treatments: under, edge, and open habitats. Anthriscus cover (%) was the dependent variable, previously normalized by arcsine transformation (Sokal and Rohlf 1995). Changes in diversity and evenness were analyzed with one-way ANOVA for repeated measures. The independent factor was Anthriscus presence (with or without), replicated 17 times. The dependent variables (with repeated measures, 9 times) were values of H', $\Delta H'$ and Js. Finally, we estimated the survival curves for each native species with and without Anthriscus using the Kaplan-Meier's method (Kaplan and Meier 1958). Later, to assess the effects of exotic species, survival curves were compared with the two-sample Cox-Mantel test (Lee et al. 1975).

Results

Spatial distribution of Anthriscus

Inside the plots we found 15 species of herbs, eight native and seven naturalized species. Seedlings and established plants of herb species were very scarce in the under-habitat, reaching a mean cover of 0.5% per



Table 1 Herb composition	and abundance (mea	an cover \pm standard	deviation) of herb	s in three	microhabitats of	the Chilean
matorral						

Species	Family	Biogeographical origin	Under habitat	Edge habitat	Open habitat
Amsinkia calycina	Boraginaceae	Native	-	0.09 ± 0.1	5.67 ± 6.8
Anthriscus caucalis	Apiaceae	Naturalized	0.23 ± 0.7	81.4 ± 9.0	_
Bowlesia incana	Apiaceae	Native	0.11 ± 0.9	5.12 ± 4.3	0.14 ± 0.7
Bromus berteroanus	Poaceae	Native	_	2.43 ± 4.3	7.54 ± 8.1
Capsella bursa-pastoris	Brassicaceae	Naturalized	_	0.02 ± 0.1	2.67 ± 3.8
Centaurea melitensis	Asteraceae	Naturalized	_	0.3 ± 2.9	27.4 ± 18.1
Cotula australis	Asteraceae	Native	_	_	0.17 ± 0.1
Erodium cicutarium	Geraniaceae	Naturalized	_	0.3 ± 0.9	3.23 ± 3.3
Erodium moschatum	Geraniaceae	Naturalized	_	_	1.02 ± 1.1
Gamochaeta stachydifolia	Asteraceae	Native	_	_	1.72 ± 1.6
Moscharia pinnatifida	Asteraceae	Native	_	0.07 ± 0.1	2.11 ± 3.4
Pasithea coerula	Liliaceae	Native	_	4.07 ± 28.1	12.07 ± 33.1
Pectocaria linearis	Boraginaceae	Native	_	2.26 ± 3.6	0.9 ± 1.56
Trifolium glomeratum	Fabaceae	Naturalized	_	_	1.25 ± 1.6
Vulpia bromoides	Poaceae	Naturalized	_	1.72 ± 3.6	7.23 ± 7.5
Spp. unidentified			0.02 ± 0.1	_	-

m² (Table 1). In contrast, the other two habitats showed higher richness of herb species, reaching mean covers of 98% and 73% per m² for edge and open habitats, respectively (Table 1).

Anthriscus exhibited a spatial distribution and dominance clearly associated with the edge habitat (ANOVA, F = 12.4; df = 2; P < 0.05), was very scarce in the under-habitat, and was absent in the open areas (Table 1). In fact, in the edge habitat Anthriscus was the dominant species, reaching a mean cover of 81%, followed only by B. incana and B. berteroanus whose respective covers were 5 and 3% (Table 1). The open habitat was more diverse, with Centaurea melitensis and Pasithea coerulea reaching covers of 27 and 12%, respectively (Fig. 1).

Effect of Anthriscus on herb diversity

Plots with *Anthriscus* showed a mean diversity of H = 0.76 (± 0.09 SE) at the beginning of the experiments, and of H = 0.41 (± 0.11 SE) at the end of the trials (Fig. 2; open squares). Plots without *Anthriscus* showed values ranging between H = 0.66 (± 0.27 SE) and H = 1.19 (± 0.1 SE) at the beginning and end of the experiments, respectively (Fig. 2; solid squares). These treatments were significantly different in their diversity indices (Fig. 2; ANOVA,

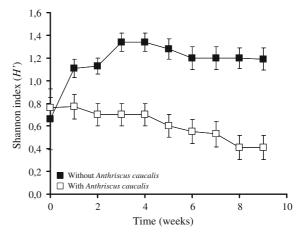


Fig. 1 Herb diversity (Shannon's index, H'; mean \pm SE) recorded in 0.5×0.5 m plots in the matorral of central Chile. The *curves* correspond to two different treatments: with and without *Anthriscus*

F=11.3; df=1; P<0.05), plots without Anthriscus having higher diversity than those with Anthriscus. Standardizing the changes of H values over time $(\Delta H')$, the previous pattern remained constant (Fig. 3). Plots with Anthriscus finished with $\Delta H'=-0.35$ (± 0.11 SE) as mean value, while those without Anthriscus finished with $\Delta H'=0.08$ (± 0.09 SE). Again, these changes in $\Delta H'$ were statistically significant (ANOVA, F=17.5; df=1; P<0.05).



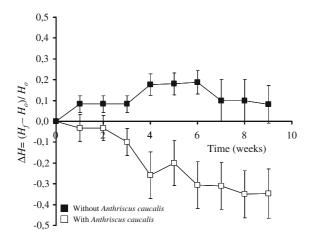


Fig. 2 Standardized Shannon's index ($\Delta H'$; mean \pm SE) recorded in 0.5 \times 0.5 m plots in the material of central Chile. The *curves* correspond to two different treatments: with and without *Anthriscus*

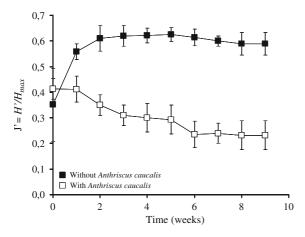


Fig. 3 Herb evenness (J'; mean \pm SE) recorded in 0.5×0.5 m plots in the matorral of central Chile. The *curves* correspond to two different treatments: with and without *Anthriscus*

The evenness index (J') showed similar trends as the previous ones (Fig. 4). Plots with *Anthriscus* had a negative change in evenness throughout the experiments, contrasting with plots without. In the first case, evenness decreased from $J' = 0.41 \ (\pm 0.04 \ \text{SE})$ to 0.23 ($\pm 0.06 \ \text{SE}$) while in the second case it increased from $J' = 0.35 \ (\pm 0.14 \ \text{SE})$ to 0.59 ($\pm 0.04 \ \text{SE}$). In combination, these results indicate that the presence and dominance of *Anthriscus* cover in edge habitat affects negatively the richness, diversity, and evenness of the local herb assemblages.

Effects of Anthriscus on native herbs survival

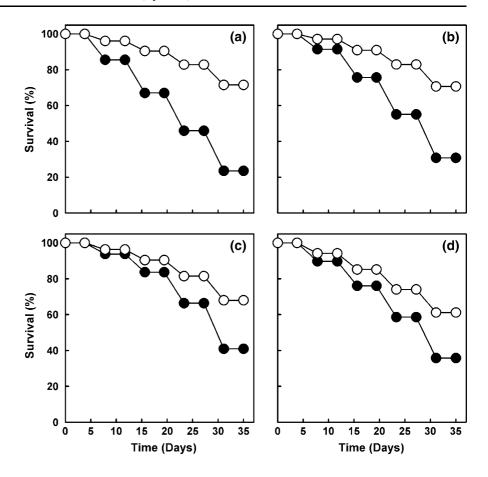
The experiments showed that Anthriscus was important in determining the survival of native herbs B. incana, B. berteroanus, M. pinnatifida and P. linearis. Overall, these four species responded by decreasing their survival when growing together with Anthriscus. Comparing the final survival figures for plots without and with Anthriscus, these values were 74% and 10% for *B. incana* ($\Delta = 64\%$), 62% and 19% for B. berteroanus ($\Delta = 43\%$), 63% and 18% for M. pinnatifida ($\Delta = 46\%$), and 77% versus 7% for P. linearis ($\Delta = 70\%$), respectively, so survival declined more steeply when these species were grown with Anthriscus (Fig. 4), and significant differences were indicated in all cases (Cox-Mantel test P < 0.001). The strongest effect of Anthriscus was detected on P. linearis (Fig. 4a). This species showed a final survival of 23% in plots in which the exotic species had been inoculated. Conversely, in the absence of Anthriscus, the final survival of P. linearis was higher than that of any other native species (72%). A similar pattern was observed for B. incana (Fig. 4b), which showed final survival rates of 29% and 71% when it was grown with and without Anthriscus, respectively. At the end of the experiment, survival of B. berteroanus (Fig. 4c) and M. pinnatifida (Fig. 4d) were 41 and 36%, respectively, but their survival rates were higher than 60% when they were grown without Anthriscus.

Discussion

Our results show that *Anthriscus* exhibits a strong spatial zonation, distributing mainly in the edgehabitat of the Chilean matorral. More than 98% of the established plants of *Anthriscus* were recorded in this habitat type, whereas a marginal proportion (< 2%) was observed inside the woody fragments (the underhabitat) and none were recorded in the open-habitat. In the edge-habitat *Anthriscus* reached a mean cover of 81%, becoming the dominant species in both abundance (individuals \times m⁻²) and cover. Futhermore, *Anthriscus* affected negatively the diversity of the herb assemblage and the survival of four native herb species: *B. incana*, *B. berteroanus*, *M. pinnatifida* and *P. linearis*. Complementarily, inside the experimental plots where *Anthriscus* was excluded



Fig. 4 Kaplan–Meier estimated survival curves for a *P. linearis*, **b** *B. incana*, **c** *B. berteroanus*, and **d** *M. pinnatifida*. The *curves* correspond to two different treatments: with (*solid dot*) and without (*open dot*) *Anthriscus*



we recorded a higher diversity and evenness of herbs (H' = 1.2; J' = 0.53) than in those plots where it was not excluded (H' = 0.4; J' = 0.23).

Considering the spatial distribution of Anthriscus in the edge-habitat, several attributes of that species can be associated with its success in this patch type. First, the seeds of Anthriscus exhibit morphophysiological latency that is interrupted by low temperatures (<5°C), and its optimal temperature for germination is also low, around 8-4°C (Baskin and Baskin 1998). During the austral autumn-winter the monthly minimum temperatures drop below 10°C in our study site (Jaksic 2001), so the germination and emergence of seedlings of Anthriscus occurs earlier than those of other herbs. Interestingly, examining the data documented by Figueroa and Jaksic (2004), who compiled the optimal temperatures for seed germination of 99 species in central Chile, no species showed such a low optimal temperature as Anthriscus. Also, a previous study on the matorral seed bank showed that *Anthriscus* is a super-abundant component of the easily germinating seed bank (Figueroa et al. 2004), outnumbering most native and naturalized species. Moreover, the emerged seedlings usually show a high survival rate in the edge habitat (Guzmán, unpublished data), decreasing towards open areas and inside fragments.

Since the early contributions of Gulmon (1977) and Keeley and Johnson (1973), herb zonation in the Chilean matorral has scarcely been studied. Those authors reported that native and naturalized species show spatial zonation because the former are more common under the woody canopy (i.e. edge-habitat) while the latter are more frequent in open areas. Subsequently, Jaksic and Fuentes (1980) and Fuentes et al. (1983) documented that zonation of some perennial herbs was caused by grazing of introduced European rabbits (*Oryctolagus cuniculus*). Later, Holmgren et al. (2000) and Holmgren (2002) documented that in experimental plots, native grasses



were more sensitive than alien grasses to grazing by rabbits, giving support to grazing as a determinant of herb zonation, but also mentioning human disturbance as an agent. Finally, Figueroa et al. (2004) questioned the generality of that zonation pattern pointing out that six exotic annual herbs can establish underneath woody canopy (edge-habitat) in opposition to the expected spatial segregation. Although plant zonation by biogeographical origin (native versus alien species) in the Chilean matorral may need more study (Figueroa et al. 2004), it was partially detected in our study area. At least two (P. linearis and B. incana) of 18 native forbs showed higher recruitment and establishment in edge-habitat, while six alien forbs were established mainly in open areas.

Levine et al. (2003) and Theoharies and Dukes (2007) recognized that the most prevalent mechanism implicated in the impact of alien plants on native ones is inter-specific competition, and seemingly the case of *Anthriscus* is no exception. This species shows a strong growth rate that usually results in a multi-layer cover of 100%, which strongly limits light availability to other species. For this reasons we proposed that the lower light availability determined by the interference mediated by *Anthriscus* constitute the principal mechanism that excludes the native herbs in the edge habitat of the matorral.

Stohlgren et al. (2001) emphasized the importance for biological conservation of hotspots and rare habitats as refuges for native flora. Although the edge habitats in central Chile are not strictly a hotspot, some proposals of Stholgren et al. (2001) may apply. The edge habitat constitutes an important refuge for the recruitment of shrub and tree species, which contributes strongly to the regeneration of the woody vegetation in central Chile (Fuentes, et al. 1984, 1986; Armesto et al. 1995). Thus, Anthriscus may be limiting the natural regeneration of the matorral herb layer by inhibiting plant establishment in edge habitat. Interestingly, seedlings of woody plants were not found in our plots. Also, the importance of the edge habitat as a refuge increases as human disturbance increases; anthropic disturbance usually is concentrated in open areas, thus reducing the survival success of native species in those areas.

Anthriscus is considered a weedy species in agricultural fields (Matthei 1995), but not an invasive

species in natural or semi-natural areas. Our study shows that the effects of *Anthriscus* include an inhibition of the establishment of native plants and a decrease in their survival in edge habitats, thus affecting the composition and diversity of the local herb layer. Thus, *Anthriscus* is invading a refuge habitat for native herbs.

Acknowledgments This study was partially funded by the A. W. Mellon Foundation and the Center for Advanced Studies in Ecology and Biogeography (CASEB). Sergio Castro is also grateful to FONDECYT 3060015 and 11085013.

References

- Armesto JJ, Vidiella PE, Jiménez HE (1995) Evaluating causes and mechanisms of succession in the mediterranean regions in Chile and California. In: Arroyo MTK, Zedler PH, Fox MD (eds) Ecology and biogeography of mediterranean ecosystems in Chile, California, and Australia. Springer-Verlag, New York, pp 418–433
- Aronson J, del Pozo A, Ovalle C, Avendaño J, Lavín A, Etienne M (1998) Land use changes and conflicts in central Chile. In: Rundel PW, Montenegro G, Jaksic FM (eds) Landscape degradation and biodiversity in mediterraneantype ecosystems. Springer-Verlag, Berlin, pp 155–168
- Arroyo MTK, Marquet P, Marticorena C, Simonetti JA, Cavieres LA, Squeo FA, Rozzi R, Massardo F (2006) El hotspot chileno de biodiversidad, una prioridad mundial para la conservación. In: Saball P, Arroyo MTK, Castilla JC, Estades C, Ladrón de Guevara JM, Larraín S, Moreno C, Rivas F, Rovira J, Sánchez A, Sierralta L (eds) Biodiversidad de Chile: patrimonio y desafios. Comisión Nacional del Medio Ambiente, Santiago, pp 94–99
- Baskin CC, Baskin JM (1998) Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego
- Cowling RM, Rundel PW, Lamont BB, Arroyo MK, Arianoutsou M (1996) Plant diversity in mediterranean-climate regions. Trends Ecol Evol 11:362–366
- D'Antonio CM, Hobbie S (2005) Plant species effects on ecosystem processes: insights from invasive species. In: Sax D, Stackowich J, Gaines S (eds) Insights from invasive species. Sinauer, Sunderland, pp 65–84
- del Pozo A, Fuentes E, Hajek ER, Molina J (1989) Microclima y manchones de vegetación. Rev Chil Hist Nat 62:85–94
- di Castri F (1981) Mediterranean-type shrublands of the world. In: di Castri F, Goodall DW, Specht RL (eds) Mediterranean-type shrublands. Elsevier, New York, pp 1–52
- di Castri F, Hajek ER (1976) Bioclimatología de Chile. Ediciones Universidad Católica de Chile, Santiago
- Dukes JS, Mooney HA (2004) Disruption of ecosystem processes in western North America by invasive species. Revista Chilena de Historia Natural 77:411–437
- Figueroa JA, Jaksic FM (2004) Latencia y banco de semillas en plantas de la región mediterránea de Chile central. Rev Chil Hist Nat 77:201–215



- Figueroa JA, Teillier S, Jaksic FM (2004) Composition, size and dynamics of the seed bank in a mediterranean shrubland of Chile. Austral Ecol 29:574–584
- Fuentes ER, Jaksic FM, Simonetti JA (1983) European rabbits versus native rodents in central Chile: effects on shrub seedlings. Oecologia 58:411–414
- Fuentes ER, Otaíza RD, Alliende MC, Hoffmann AJ, Poiani A (1984) Shrub clumps of the Chilean matorral vegetation: structure and possible maintenance mechanisms. Oecologia 62:405–411
- Fuentes ER, Hoffmann AJ, Poiani A, Alliende MC (1986) Vegetation change in large clearing: patterns in the Chilean matorral. Oecologia 68:358–366
- Gelbard JL, Harrison S (2003) Roadless habitats as refuges for native grasslands: interactions with soil, aspect, and grazing. Ecol Appl 13:404–415
- Gram WK, Borer ET, Cottingham KL, Seabloom EW, Boucher VL, Goldwasser L, Micheli F, Kendal BE, Burton RS (2004) Distribution of plants in a California serpentine grassland: are rocky hummocks spatial refuges for native species? Plant Ecol 172:159–171
- Gulmon SL (1977) A comparative study of the grasslands of California and Chile. Flora 166:261–278
- Harrison S (1997) How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. Ecology 78:1898–1906
- Harrison S (1999) Local and regional diversity in a patchy landscape: native, alien, and endemic herbs on serpentine. Ecology 80:70–80
- Holmgren M (2002) Exotic herbivores as drivers of plant invasions and switch to ecosystem alternative states. Biol Inv 4:25–33
- Holmgren M, Avilés R, Sierralta L, Segura AM, Fuentes ER (2000) Why have European herbs so successfully invaded the Chilean matorral? Effects of herbivory, soil nutrients, and fire. J Arid Envir 44:197–211
- Jaksic FM (2001) Spatiotemporal variation patterns of plants and animals in San Carlos de Apoquindo, central Chile. Rev Chil Hist Nat 74:477–502
- Jaksic FM, Fuentes ER (1980) Why are native herbs in the chilean matorral more abundant beneath bushes: microclimate or grazing? J Ecol 68:665–669
- Jiménez A, Pauchard A, Cavieres LA, Marticorena A, Bustamante RO (2007) Do climatically similar regions contain similar alien floras? A comparison between the mediterranean areas of central Chile and California. J Biogeogr 35:614–624
- Kaplan EL, Meier P (1958) Nonparametric estimation from incomplete observations. J Am Stat Assoc 53:457–481
- Keeley SC, Johnson AW (1977) A comparison of the pattern of herb and shrub growth in comparable sites in Chile and California. Am Midl Nat 97:120–132
- Lee ET, Desu MM, Gehan EA (1975) A Monte Carlo study of the power of some two-sample tests. Biometrika 62:425–432
- Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasion. Proc Roy Soc Lond B 270:775–781

- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536
- Matthei O (1995) Manual de las malezas que crecen en Chile. Alfabeta impresores, Santiago
- Montenegro G, Teillier S, Arce P, Poblete V (1991) Introduction of plants into the mediterranean-type climate area of Chile. In: Groves H, di Castri F (eds) Biogeography of mediterranean invasions. Cambridge University Press, New York, pp 103–114
- Murphy DD, Ehrlich PR (1989) Conservation biology of California's remnant grasslands. In: Huenneke LF, Mooney H (eds) Grassland structure and function: California annual grassland. Kluwer Academic Publishers, Dordrecht, pp 201–211
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858
- Pauchard A, Cavieres LA, Bustamante RO (2004) Comparing alien plant invasions among regions with similar climates: where to from here? Divers Distrib 10:371–375
- Randall RP (2002) A global compendium of weeds. RG, FJ Richardson, Merredith, Victoria
- Reiche K (1899) Estudios críticos sobre la flora de Chile. Anales de la Universidad de Chile 104:767–847
- Rozzi R, Molina JD, Miranda P (1989) Microclima y períodos de floración en laderas de exposición ecuatorial y polar en los Andes de Chile central. Revista Chilena de Historia Natural 62:74–85
- Rundel PW (1981) The matorral zone of central Chile. In: di Castri F, Goodall FD (eds) Mediterranean type shrublands. Elsevier, New York, pp 175–201
- Rundel PW (1998) Landscape disturbance in mediterraneantype ecosystems: a review. In: Rundel PW, Montenegro G, Jaksic FM (eds) Landscape degradation and biodiversity in mediterranean-type ecosystems. Springer-Verlag, Berlin, pp 3–22
- Sax DF (2002) Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. Divers Distrib 8:193–210
- Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. WH Freeman and Co. New York, New York
- Stohlgren TJ, Otsuki Y, Villa CA, Lee M, Belnap J (2001)
 Patterns of plant invasions: a case example in native species hotspots and rare habitats. Biol Invasions 3: 37–50
- Theoharies KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytol 176:256–273
- Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DA (1968) Flora Europaea, vol 2: Rosaceae to Umbelliferae. Cambridge University Press, Cambridge
- Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. Am Sci 84:468–478
- Williamson M (1996) Biological invasions. Chapman and Hall, London

