

Demographic effects of large, introduced herbivores on a long-lived endemic plant

Stefania Pisanu · Emmanuele Farris ·
Rossella Filigheddu · Maria Begoña García

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Abstract The introduction of alien ungulates is a major threat for the survival of endangered plants, especially in island ecosystems. However, very few studies have investigated the potential damage of large herbivores on plant diversity in Mediterranean protected areas. In this study, we describe the population structure and the long-term dynamics of the main populations of the Sardinian narrow endemic *Centaurea horrida* Bad. (Asteraceae), by means of permanent plots where individual plants were tagged and monitored through 6 years (2004–2009). We monitored this endangered plant at three sites: two were protected areas where introduced and feral ungulates are present, and the other one was a non-protected site without introduced

ungulates. We found that adults and saplings were more abundant at the non-protected site. Through matrix models, we also highlighted that the non-protected population showed the highest population growth rate. Finally, by means of an exclusion experiment for ungulates at one protected site, we demonstrated that herbivores had a negative effect on the survival of seedlings and adult plants, and reduced the stochastic population growth rate. An LTRE analysis showed that differences in the survival, especially of adult individuals, had the highest responsibility in explaining the higher population growth rate when herbivores are excluded. Our study constitutes a clear example on how the protection of alien large herbivores can have opposite effects on the conservation of an endangered plant. Some management options are proposed, and the urgent need of manipulative experiments on species-specific interactions between protected plants and alien herbivore species is invoked.

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S. Pisanu (✉) · E. Farris · R. Filigheddu
Dipartimento di Scienze della Natura e del Territorio,
Università degli Studi di Sassari, Via Piandanna 4, 07100
Sassari, Italy
e-mail: pisanus@uniss.it

E. Farris
e-mail: emfa@uniss.it

R. Filigheddu
e-mail: filighed@uniss.it

M. B. García
Instituto Pirenaico de Ecología (CSIC), Apdo 13034,
50080 Zaragoza, Spain
e-mail: mariab@ipe.csic.es

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Introduction

Herbivory is one of the most dominant biotic interactions in nature. Plants form the basal resource of virtually all food webs, and herbivores consume 10–15 % of the plant biomass produced annually in

both natural and managed ecosystems (Cyr and Pace 1993). Herbivory effects on plant performance have been widely recognized, both at the individual and population level (Ehrlén 2002; Hawkes and Sullivan 2001; Maron and Crone 2006; Jenkins et al. 2007). Interactions among plants and herbivores are increasingly men-mediated in many biogeographical areas by means of both shepherding activities (Farris and Filigheddu 2008) and/or ungulates introduction (Dolman and Waber 2008). Actually, introduced ungulates and feral domestic animals may constitute one of the major threats to plant biodiversity (Spear and Chown 2009), in particular in insular ecosystems (Courchamp et al. 2003). Island ecosystems (Whittaker and Fernández-Palacios 2007), and particularly the Mediterranean ones (Thompson 2005), are considered among the most fragile from an ecological point of view. Given the strong impacts of introduced ungulates on vegetation structure and composition, and soil system functioning (see for example Farris et al. 2010) extensive controls of the introduced herbivores seem to be necessary, especially on islands (Garzón-Machado et al. 2010).

Tyrrhenian islands (Balearic Archipelago, Corsica, Sardinia and Sicily) are one of the Mediterranean biodiversity hotspots (Médail and Quézel 1997, 1999; Myers et al. 2000). Sardinia, for example, shows a rough estimate of about 2,500 vascular plants (Conti et al. 2005), of which 6.2 % are exclusive to the island and are in need of conservation actions due to a high extinction risk (Pisanu et al. 2009; Fenu et al. 2011, 2012). A large fraction of Sardinian endemic plants (42.3 %) grow in coastal, saline, and rocky habitats (Bacchetta et al. 2012), often on extreme environments like many Mediterranean endemics (Lavergne et al. 2004). Although western Mediterranean islands had a variety of endemic large herbivores due to migratory events during the entire Cenozoic (Palombo 2009), the present island fauna is almost exclusively characterized by continental generalist mammals nowadays (Masseti 2009). As a consequence, the local flora of these islands is now suffering the impact of this foreign interaction.

In the last decades, the introduction of different kinds of alien ungulates took place both for hunting in some areas (i.e., mouflon on the Asinara islet, Sardinia), and for conservation purposes in many other areas like protected spaces. The effect of alien herbivores (ungulates) in Mediterranean protected areas has not been evaluated at a large scale (Courchamp et al. 2003), and very few studies have shown

the potential damage on overall diversity or particular plant species.

In this paper, we focus on the demography of the Mediterranean narrow endemic *Centaurea horrida* Bad. (Asteraceae), a perennial, sea-cliff plant restricted to the North of Sardinia. Over 6 years, we individually monitored hundreds of plants in three out of the five populations of this species, located in two protected and one non-protected areas. In protected areas, ungulates (wild boar, deer and mouflon) have been introduced in the last decades, and now constitute an important component of the ecosystems. Furthermore, domestic ungulates (goats, horses and donkeys) have become feral. Experiments to establish herbivores control and open habitats maintenance for the conservation of *C. horrida* populations have been recently invoked (Farris et al. 2012).

We first describe the current population structure, the frequency of damage at each place, and the long-term population dynamics through matrix models. Then, we evaluate how herbivores affect multiple demographic vital rates (Farrington et al. 2009; Abe et al. 2008; Knight et al. 2009; McEachern et al. 2009; García et al. 2010), using a matrix projection model to compare the long-term dynamics of plants in/out two large mammal exclusions. Finally, we disentangled which vital rates and plant stages best explained differences between stochastic population growth rates of plants in/out exclusions.

The following specific questions were addressed: (1) Does the demographic structure of *C. horrida* populations differ between protected and non-protected areas? (2) Do populations differ in their stochastic population growth rate? (3) To what extent are herbivores a threat for the future of this species? Results will be discussed with the aim to clarify which of the different current management regimes (a—protected space with introduced ungulates; b—protection from ungulates by fencing; and c—non-protected space without ungulates) seems to be better for the persistence of this endangered plant.

Materials and methods

Study species

The genus *Centaurea* L. (Asteraceae) includes roughly 400 species (Susanna and Garcia-Jacas

2009), with many narrow endemics (Kose et al. 2010; Kultur 2010; López-Alvarado et al. 2011). *Centaurea horrida* is endemic of the North of Sardinia (Italy). It is protected by the Berne Convention, listed with priority status in Annexe II of the EU “Habitat” Directive, and considered endangered (EN) on the basis of IUCN criteria. This cushion-forming spiny dwarf plant is self-incompatible and reproduces mainly sexually by means of cross-pollination carried out by insects. The capitula usually flower in the late spring (April–May) and seeds are released in July–August. Seeds have an elaiosome attractive for ants, and seedlings are usually located near the mother plant (Pisanu et al. 2009).

Study sites

Centaurea horrida is restricted to five populations on sea-cliffs, along the coasts of Northern Sardinia, where it grows in both cliff face and cliff plateau (see map in Farris et al. 2012). Because two of the five populations, Piana and Tavolara Islets, are small (87 and 175 individuals respectively), this demographic study was conducted in the other three populations, located in Alghero (AHO), Asinara (ASI) and Stintino (STI; Table 1). We think that environmental conditions and genetic differences among sites are not so high except for herbivores density.

In fact, the bioclimate is always Thermomediterranean dry euoceanic type, and the vegetation is also very similar in the three sites (see Table 38 in Biondi et al. 2001). ASI and STI have the same geological substrate (schist) and AHO is limestone. On the other hand, although all populations showed moderate

levels of genetic differentiation, one of the five populations (AHO) was more strongly differentiated from the other four, suggesting a certain barrier to regular gene exchange (Mameli et al. 2008).

All the three sites are included in the Natura 2000 network, but in Sardinia this does not mean effective protection or specific management. Active management will only occur within protected areas such as National or Regional Parks, or Marine Protected Area and therefore only two of the sites, ASI (Asinara National Park, established 1997) and AHO (Regional Park of Porto Conte, established 1999), will be managed.

Between 1990 and 2010, a total density of 0.24 ungulates ha^{-1} was recorded at AHO: 42 % were deer, 31 % wild boars (they were already present at this site), 17 % feral donkeys, and 10 % feral horses. Roughly, the population of each species increased around 30–40 % every 10 years. At ASI, in the same period, 300 donkeys, 1,000 wild boars, 600 mouflons, 180 horses, and 7,000 feral goats were present on the island (5,200 ha). This means that at ASI the total density of herbivores reached 1.7 individuals ha^{-1} because the ungulates do not have natural predators here, and hunting them is forbidden. No ungulates are present at STI, except wild boars.

All the ungulates, except wild boars at AHO and STI, were introduced few decades ago (before the parks institution) for hunting purpose (ASI) or for reintroduction (deer at AHO), or simply were domestic animals that became feral (goats, donkeys, horses). Only recently some eradication programmes (carried out with the use of harmless traps) have been started to

Table 1 Characteristics of the study sites

Population	Asinara	Stintino	Alghero
Code	ASI	STI	AHO
Coordinates	41°00'N–8°12'E	40°56'N–8°11'E	40°36'N–8°08'E
Geology	Schist	Schist	Limestone
Bioclimate	Thermomediterranean dry euoceanic	Thermomediterranean dry euoceanic	Thermomediterranean dry euoceanic
Inclusion in the Natura 2000 network	ITB010001	ITB010043	ITB010042
Effective management	Asinara National Park	None	Porto Conte Regional Park
Ungulates introduced in the last century	Donkeys, horses, goats, mouflon, wild boars	None	Deer, donkeys, horses
Other ungulates	None	Wild boars	Wild boars

decrease feral goats and wild boars at ASI: from 2007 to 2011 wild boars diminished to 300 and goats to 3,000.

Sampling demographic data

In order to answer question one, four $10 \times 10 \text{ m}^2$ permanent plots were established at each site of study in June 2004, and all the individuals of *C. horrida* within plots were mapped, tagged, and monitored yearly until 2009. We classified individuals of *C. horrida* in three life stages: 1) seedlings (sdl), still with cotyledons (often with one or two pairs of leaves but without stalks); 2) saplings (sap), non-reproductive individuals, usually with a diameter less than 30 cm); and 3) adults, all reproductive individuals. Adults were further assigned to three size-classes depending on maximum diameter: R1 ($\varnothing < 30 \text{ cm}$); R2 ($31 \text{ cm} < \varnothing < 70 \text{ cm}$), and R3 ($\varnothing > 70 \text{ cm}$).

Over the 6 years of monitoring, each individual was recorded as alive or dead, sapling, or adult, and the maximum diameter of the cushion measured with a calliper. Fecundity was calculated as the total seed production, from the total number of capitula (estimated using a grid on the bush surface), and counting capitula in four quadrats and the average number of fertile achenes per capitulum (estimated by collecting at random 3 capitula from each adult plant). All the seedlings found in the annual census after careful inspection within plots were considered as new recruits.

Because our research was limited by population availability and population sizes (a common situation for endangered plant species), site was used as a fixed factor in comparative analyses carried out among specific populations investigated. Two-ways ANOVAs were used to test differences in the relative proportions of each stage of *C. horrida* individuals among sites, and to test differences in seeds production among sites and among adult classes.

For all the ANOVAs performed, the homogeneity of variances was tested a priori using Cochran's *C*-test, and data were appropriately transformed, if necessary. Whenever transformation did not produce homogeneous variances, ANOVA was applied after setting $\alpha = 0.01$ to compensate for the increased likelihood of Type I errors (Underwood 1997). Student–Newman–Keuls (SNK) tests were carried out to compare the mean values of all significant factors (Underwood

1997). ANOVAs were conducted using the GMAV5 software package (University of Sydney).

Matrix parameterization

In order to answer question two, stage-based population-projection matrix models were used to explore the dynamics of populations under current conditions. Each plant was included in one of the five stages above mentioned (sdl, sap, R1, R2, R3), and transition rates between pairs of classes were calculated for each pair of consecutive years.

Since experiments in the greenhouse demonstrated that seeds germinate mostly within the year after being released (Pisanu unpublished), fertility of each class was set as the proportional part of seedlings in $t + 1$, relative to the mean number of seeds released by plants in each class in t (anonymous reproduction, Caswell 2001). A total of 15 annual Lefkovich projection matrices was set for each combination of site (AHO, ASI, STI) and consecutive years (2004–2005, 2005–2006, 2006–2007, 2007–2008, 2008–2009). Matrices were constructed according to the standard procedure of transition probabilities of the life cycle graph (Caswell 2001), from estimates of fertility and transition probabilities among stage classes.

Projection matrices were the basis for linear time-invariant matrix models of the form $n_{t+1} = A * n_t$ (Caswell 2001), where n_{t+1} is a vector with the abundances of stages in the population at time t , and A integrates all the probabilities (a_{ij}) for an average individual plant in class j at a moment t , to be in class i after one year. The dominant eigenvalue (λ) of the projection matrix represents the deterministic population growth of the species at a particular site and time. To construct 95 % confidence intervals for the projected population growth rates, bootstrapping was applied by resampling 2,000 times the observed fates of monitored plants. The bias-corrected percentile method provided the lower and upper bounds (see e.g., McPeck and Kalisz 1993; Caswell 2001). The stochastic growth rate (λ_s) and an approximate 95 % Confidence Interval (CI) was calculated for each population by simulation of 50,000 population growth increments, considering that each matrix had the same probability of occurrence. The arithmetic mean and variance of $\log(N_{t+1}/N_t)$ over all pairs of adjacent years was calculated using the Stoch_log_lam routine of Morris and Doak (2002).

Effects of herbivores

In order to answer question three, we first evaluated the occurrence of damage on *C. horrida* populations: in 2006, we randomly established four $2 \times 20 \text{ m}^2$ transects at each site of study. Each plant included in transects was assigned to one of the above-mentioned stages, and to one of the following categories of injury: (1) mechanical damage (MD, damage mainly caused by trampling of horses, donkeys, deers, wild boars, and goats); (2) browsing (BR); (3) unthreading (UN, breaking of single branches caused by deers and goats: this differs from browsing because the last implies only a surface damage on the cushion plants; whereas the unthreading means damage of a single branch that is cut from the internal part of the plant); and (4) no damage (ND). Differences in the frequency of damaged plants among populations and classes were tested by Generalized Linear Models (GLM; *glm* procedure with logit link function; R statistical software version 2.11.1; R Development Core Team 2010).

Second, we tested the overall effect of herbivores on *C. horrida* performance using a demographic approach based on exclosures to ungulates at site ASI. Two $10 \times 10 \text{ m}^2$ plots were fenced in December 2005 (thereafter “fenced plots”), and two open $10 \times 10 \text{ m}^2$ control plots were established nearby (thereafter “control plots”). All plants in the four plots were monitored as in permanent plots.

Two-way ANOVA was used to test differences in seed production between treatments (Fenced vs Control) and adult size classes. Generalized Linear Models (GLM; *glm* procedure with logit link function; R statistical software version 2.11.1; R Development Core Team 2010) were used to test the effect of “fencing” on the survival of seedlings, saplings, and adult plants, after pooling all the transition events across years.

The long-term effect of herbivores was evaluated by matrix models, and a total of 6 annual Lefkovich projection matrices was constructed from this exclusion experiment: one for each combination of treatment and year (control vs fenced, 2006–2007, 2007–2008, 2008–2009). The stochastic growth rate (λ_s) and an approximate 95 % Confidence Interval (CI) were calculated for each treatment following the same procedure described above. In order to quantify the contribution of each matrix element (a_{ij}) to the observed variation in λ between fenced and control

plots (overall effect of herbivores), we used a one-way life table response experiment analysis (LTRE, Caswell 2001). This analysis takes into account differences in the values between pairs of the same matrix element (each one provided by the average matrix of each treatment), and its sensitivity evaluated at the average matrix.

Results

Population structure

There were no significant differences between the three sites in the relative proportion of individuals in each stage ($F_{2,8} = 8.84, P = 0.9991$). Adults were the prevalent life stage in all three sites and during all the period of study ($F_{2,8} = 15.88, P < 0.0001$): on average, the density of seedlings was 3.8 ± 0.47 individuals 100 m^{-2} , saplings were 12.9 ± 1.84 individuals 100 m^{-2} , R1 adults reached an average density of 16.5 ± 2.65 individuals 100 m^{-2} , R2 were 25.2 ± 3.33 individuals 100 m^{-2} , and R3 had a density of 19.8 ± 2.37 individuals 100 m^{-2} . On average STI showed densities 2–3 times higher than AHO and ASI. For the saplings, STI showed double density in comparison to the other two sites, whereas seedling variability among sites was very low (Fig. 1).

The differences in seed production were highly significant among adult classes: R1 produced on average 65.6 ± 6.23 seeds, R2 produced 627.1 ± 53.13 , and R3 produced $2\,915.1 \pm 184.92$ seeds ($F_{2,4} = 25.44, P < 0.0001$) (Fig. 2).

Population trends

None of the 15 yearly matrices produced deterministic lambdas significantly below one (see Appendix 1). On the contrary, some values were significantly above one (the CI did not intercept $\lambda = 1$), indicating that some years some populations were growing up to a maximum of 2.4 % (AHO 2005–2006; Fig. 3). Temporal variability of deterministic lambdas was larger in AHO ($\sigma^2 = 0.038$) and lower in STI (0.016; see also Fig. 3). The stochastic population growth showed that populations were growing over the study period at a rate of 0.17 % (AHO), 0.54 % (ASI), and 1.12 % (STI). Thus, STI showed the highest population growth rate which also varied less through time.

Fig. 1 Mean densities \pm SE (individuals 100 m^{-2} ; $N = 4$) of seedlings, saplings, and adults of three size classes at three study sites monitored for 6 years

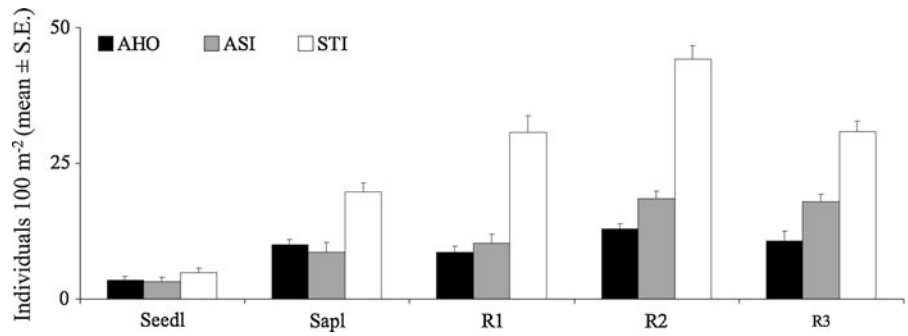


Fig. 2 Mean values (\pm SE) of seeds per each adult class evaluated on all the individuals belonging to the three size classes at the three study sites monitored for 6 years

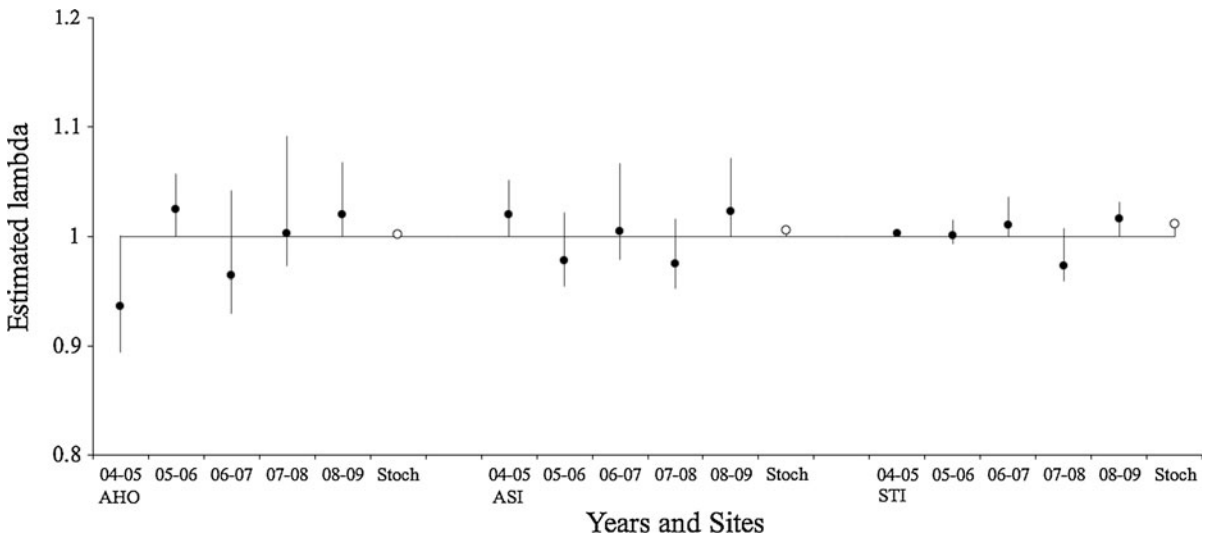
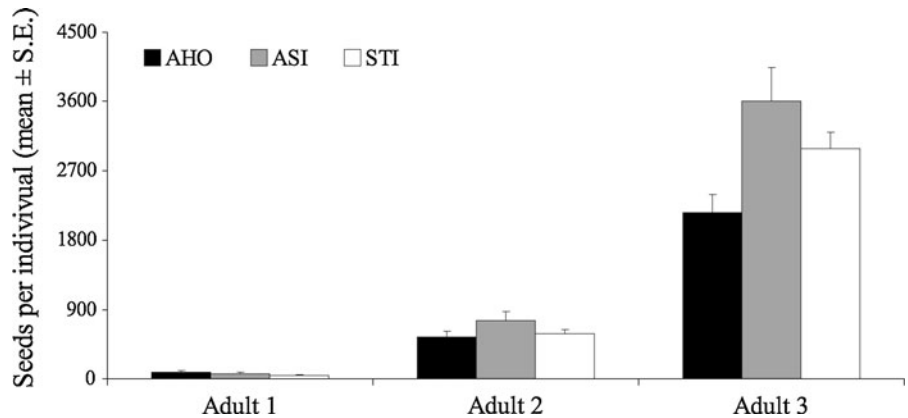


Fig. 3 Stochastic population growth rate (λ_s) in the three study sites. Empty dots correspond to the stochastic population growth rate

The effects of herbivores

All three studied populations of *C. horrida* showed signs of damage by herbivores, although the density of

damaged individuals was highest in protected populations (ASI: 26.7 ± 3.2 damaged individuals 40 m^{-2} ; AHO: 16.2 ± 2.7 damaged individuals 40 m^{-2}) and only occasional in the non-protected

population (STI: 0.7 ± 0.5 damaged individuals 40 m^{-2}). Adults suffered the highest incidence of damage, and mechanical damage was the prevalent type. Seedlings and saplings were affected only by MD (Fig. 4).

There were significant differences in the frequency of individuals damaged by herbivores among populations, STI having a significant lower proportion than AHO ($Z = 6.796$; $P < 0.001$) and ASI ($Z = 8.285$, $P < 0.001$). Such difference was due to the lower proportion of damaged adults in STI relative to AHO ($Z = 6.25$; $P < 0.001$) and ASI ($Z = 8.43$; $P < 0.001$), whereas the proportion of seedlings and saplings damaged did not differ among populations.

Seed production in fenced plots was significantly higher than in control plots (on average 664.4 ± 200.58 vs 370.6 ± 83.16 seeds per individual. $F_{1,6} = 11.66$, $P = 0.0142$). The R3 plants produced significantly more seeds than the other two reproductive classes ($F_{1,6} = 62.53$, $P = 0.0001$). The highest

contribution to the difference between fenced and control plots was due to class R3, which produced on average 1572.6 ± 74.80 seeds within fenced plots and 717.1 ± 22.16 seeds in the control plots ($F_{2,6} = 10.26$, $P = 0.00116$).

The survival of seedlings ($Z = -3.303$, $P < 0.001$) and adults ($Z = -3.475$, $P < 0.001$) was significantly lower in control plots than in the exclusions. The presence of herbivores, therefore, significantly increased mortality of some stage classes.

None of the ASI population growth rates was significantly different from $\lambda = 1$ except 2007-fenced, that was significantly higher than one (see Appendix 2). Demographic models confirmed that herbivores had a negative effect, given that the stochastic growth rate in control plots was 3.6 % lower than that in fenced plots: λ_s control = 0.9490 [95 % CI = 0.9485–0.9495], λ_s fenced = 0.9851 [95 % CI = 0.9849–0.9854] (Fig. 5). LTRE analysis showed that survival of the largest plants (R3), either in the form of stasis (48.4 %) or

Fig. 4 Percentage of individuals damaged at each study site and for each kind of damage: AHO Alghero, ASI Asinara, STI Stintino, SEEDL seedlings, SAPL saplings, AD adults, MD mechanical damage, UN unthreading, BR browsing, and ND not damaged

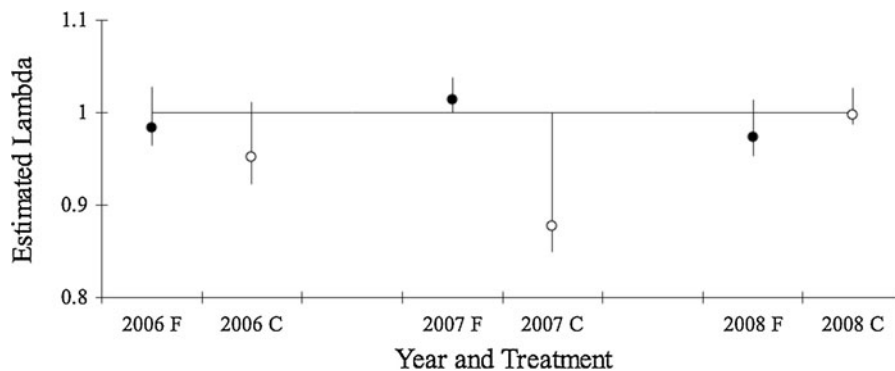
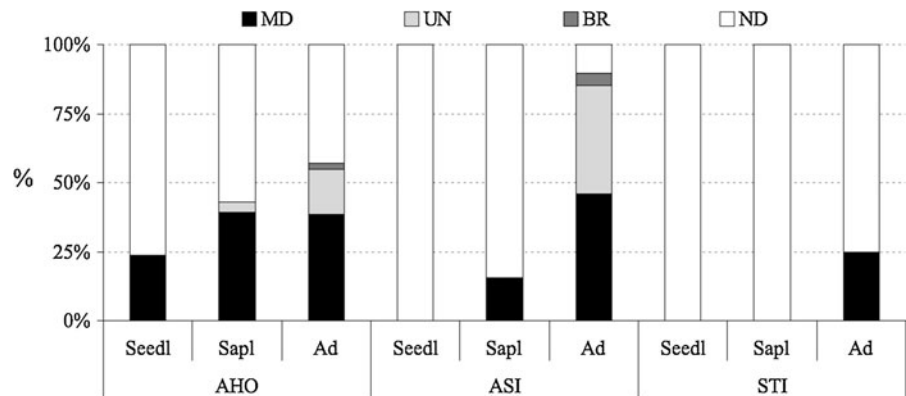


Fig. 5 Deterministic population growth rates and 95 % CI intervals, of fenced (F) and control (C) plots in ASI. Each dot corresponds to a different combination of treatment (Fenced: black dots; Control: white dots) and transition years (2006, 2007 and 2008)

retrogression (13.4 %), and growth of the R2 plants (24.6 %), had the highest responsibility for enhancing the population growth rate of this species when herbivores are excluded.

Discussion

This study provided, for the first time, information on the current structure and long-term dynamics of a narrow endemic plant exclusive to an island of the Mediterranean basin, and evaluated the effect of an anthropogenic threat present in two of the three populations analyzed: the introduction of alien ungulates.

Given the environmental and genetic differences among populations we expected a pattern of response variables like $ASI = STI \neq AHO$, whereas a pattern like $ASI = AHO \neq STI$ could result from differences in management because of the strong differences in the density of wild ungulates. Our results better fit the second scenario. Although a number of biotic and abiotic factors not considered in this study could be involved in the remarkable among population differences found for *C. horrida* in terms of density and population structure (in particular the higher density of adults and saplings at STI), these differences can at least partially be explained by three of our findings: the higher population growth rate of the non-protected population, the negative effect of herbivores on the survival of adult plants and on the stochastic long-term population growth rate.

Populations of *Centaurea horrida* are dominated by adults, who together with the slow growth of the plants (frequency of stasis) suggest that *C. horrida* behaves as a typical long-lived Mediterranean endemic plant: low colonization ability (Colas et al. 1997) and high local persistence (Lavergne et al. 2004; Thompson 2005). Although none of the studied populations of this endangered plant seems to be declining, and population sizes are large enough to not consider the species under extreme concern in the short-term, the detection of threats is of vital importance for narrow endemics, in particular if migration of current populations or the foundation of new populations seems quite unfeasible, as it is the case of old endemics restricted to islands.

Many Mediterranean plants evolved a suite of defences to withstand natural herbivory (Carmona et al. 2011), and show different defense mechanisms

against large herbivores that influence plant palatability (see e.g., Vicari and Bazely 1993) and depend on plant functional traits (Papanikolaou et al. 2011). Although *C. horrida* is naturally defended against herbivores by spines, our study shows that it is affected by browsing and particularly mechanical damage from large herbivores that have been introduced only recently on the island on which it occurs.

Studies that have examined the effect of deer herbivory on population growth of perennial plants have found that it has a measurable impact on long-term population dynamics (Knight 2004; McGraw and Furedi 2005). Typically, effects of deer herbivory on understory plants have been examined experimentally using fenced exclosures (e.g., Alverson et al. 1988; Augustine and Frelich 1998; Augustine et al. 1998; Anderson et al. 2001; Townsend and Meyer 2002). These studies show large positive effects of herbivores exclusion on the growth, survival and reproduction of plants. Our results provide similar conclusions. Adult plants of *C. horrida* were the most affected class by ungulates in terms of frequency and survival, and demographic analysis demonstrated that fencing plants to protect them from herbivores enhanced the long-term population dynamics by almost 4 % in the last 5 years. Our analysis also demonstrated that such reduction was due to the lower probability of stasis and shrinkage (survival) of large adults, the class that suffered most damage by herbivores at that place, and the one releasing more seeds (Farris et al. 2012).

To assess which of the different current management regimes could promote the persistence of this endangered plant, it is noteworthy that, even if this study demonstrated the detrimental effects of herbivores on the long-term dynamics of *C. horrida*, other previous studies showed that its seed germination totally depends on the presence of bare soil, and therefore, on gaps and other open spaces created and maintained by disturbance (Farris et al. 2009). Furthermore, we have observed that browsing events on *C. horrida* were concentrated mainly during summer months, after pastures were completely grazed and before the germination period. This is congruent with the findings of Miranda et al. (2011), demonstrating that in season-dependent habitats, such as Mediterranean pasturelands, herbivores tend to occupy alternative patches (e.g., scrubland) when pastures are not productive, i.e., during summer drought.

We therefore argue that the complete disappearance of herbivores might not be, however, a desirable option for the conservation of *C. horrida*. In Mediterranean areas, a crucial role in maintaining the spatial heterogeneity of agro-pastoral systems has been traditionally played by sheep livestock, now decreasing or disappearing in many coastal areas, and replaced by mass tourism. The abandonment of historical practices is favouring the spreading of shrub and forest evergreen vegetation (Farris et al. 2009), whereas pastures and dwarf plant communities are dramatically decreasing (Falcucci et al. 2007; Farris et al. 2010). Unlike large ungulates, sheep are less able to browse on spiny plants and cause mechanical injuries to single plant individuals, at the same time maintaining open spaces suitable for seeds germination and seedlings establishment, as demonstrated also by some experiments conducted on other plants, such as *Gentiana nivalis* L. (Miller et al. 1999). Consequently, a possible management regime for *C. horrida* would be the complete eradication of the most heavy browsers as goats (Campbell and Donlan 2005; Simbaña and Tye 2009), the reduction of the other herbivores (deer, mouflon, horses, and donkeys) to densities compatible to the herbaceous biomass grown each year at each site (Donlan et al. 2002; Miranda et al. 2011), and the maintenance of low controlled densities of sheep (Miller et al. 1999).

Since protected areas are devoted to the conservation of all aspects of biodiversity, some conflicts can emerge when trying to protect animals and plants whose management strategies are in contrast (Gangoso et al. 2006; Fornara and du Toit 2008; White and Goodman 2009). Our study constitutes a clear example on how the protection of alien large mammals (moreover, considered as flagship species by protected areas managers) has a negative effect on a single plant species, paradoxically amplified by the lack of any attempt of active conservation of the local plant biodiversity.

Overall, this study has shown that the presence of alien ungulates may have negative effects on the long-term population dynamics of endangered plant species (Bastrenta 1991; Ehrlén 1995; Rydgren et al. 2001) in a protected space designed to preserve overall biodiversity. Although the evaluation of the responses of endangered plant populations to multi-specific

assemblages of alien herbivores seems particularly helpful to conservation biologists and land managers, we believe that successful management schemes can only be projected on the basis of future manipulative experiments, disentangling species-specific interactions between a protected plant and a single alien herbivore species.

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References

- Abe T, Wada K, Nakagoshi N (2008) Extinction threats of a narrowly endemic shrub, *Stachyurus macrocarpus* (Stachyuraceae) in the Ogasawara Islands. *Pl Ecol* 198:169–183
- Alverson WS, Waller DM, Solheim SL (1988) Forests too deer—edge effects in northern Wisconsin. *Conserv Biol* 2:348–358
- Anderson RC, Corbett EA, Anderson MR, Corbett GA, Kelley TM (2001) High white-tailed deer density has negative impact on tallgrass prairie forbs. *J Torrey Bot Soc* 128:381–392
- Augustine DJ, Frelich LE (1998) Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. *Conserv Biol* 12:995–1004
- Augustine DJ, Frelich LE, Jordan PA (1998) Evidence for two alternate stable states in an ungulate grazing system. *Ecol Appl* 8:1260–1269
- Bacchetta G, Farris E, Pontecorvo C (2012) A new method to set conservation priorities in biodiversity hotspots. *Plant Biosyst.* doi: 10.1080/11263504.2011.642417
- Bastrenta B (1991) Effect of sheep grazing on the demography of *Anthyllis vulneraria* in southern France. *J Ecol* 79:275–284
- Biondi E, Filigheddu R, Farris E (2001) Il paesaggio vegetale della Nurra. *Fitosociologia* 38:3–105
- Campbell K, Donlan CJ (2005) Feral goat eradications on islands. *Conserv Biol* 19:1362–1374
- Carmona D, Lajeunesse MJ, Johnson MTJ (2011) Plant traits that predict resistance to herbivores. *Funct Ecol* 25:358–367
- Caswell H (2001) Matrix population models, 2nd edn. Sinauer Associates, Massachusetts
- Colas B, Olivieri I, Riba M (1997) *Centaurea corymbosa*, a cliff-dwelling species tottering on the brink of extinction: a demographic and genetic study. *Proc Natl Acad Sci* 94:3471–3476

- Conti F, Abbate G, Alessandrini A, Blasi C (eds) (2005) An annotated checklist of the Italian vascular flora. Palombi, Roma
- Courchamp F, Chapuis JL, Pascal M (2003) Mammal invaders on islands: impact, control and control impact. *Biol Rev* 78:347–383
- Cyr H, Pace ML (1993) Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature* 361:148–150
- Dolman PM, Waber K (2008) Ecosystem and competition impact of introduced deer. *Wildlife Res* 35:202–214
- Donlan CJ, Tershy BR, Croll DA (2002) Islands and introduced herbivores: conservation action as ecosystem experimentation. *J Appl Ecol* 39:235–246
- Ehrlén J (1995) Demography of the perennial herb *Lathyrus vernus*. II. Herbivory and population-dynamics. *J Ecol* 83:297–308
- Ehrlén J (2002) Assessing the lifetime consequences of plant–animal interactions for the perennial herb *Lathyrus vernus* (Fabaceae). *Perspect Plant Ecol Evol Syst* 5:145–163
- Falcucci A, Maiorano L, Boitani L (2007) Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. *Landscape Ecol* 22:617–631
- Farrington SJ, Muzika RM, Drees D, Knight TM (2009) Interactive effects of harvest and deer herbivory on the population dynamics of American ginseng. *Conserv Biol* 23:719–728
- Farris E, Filigheddu R (2008) Effects of browsing in relation to vegetation cover on common yew (*Taxus baccata* L.) recruitment in Mediterranean environments. *Plant Ecol* 199:309–318
- Farris E, Pisanu S, Ceccherelli G, Filigheddu R (2009) Effects of the management regime on the performance of the endangered Mediterranean *Centaurea horrida* Badarò (Asteraceae). *J Nat Conserv* 17:15–24
- Farris E, Filigheddu R, Deiana P, Farris GA, Garau G (2010) Short-term effects on sheep pastureland due to grazing abandonment in a Western Mediterranean island ecosystem: a multidisciplinary approach. *J Nat Conserv* 18:258–267
- Farris E, Pisanu S, Ceccherelli G, Filigheddu R (2012) Variability at local scales and between habitats in population structure and reproductive traits of the Mediterranean plant *Centaurea horrida*: implications for management. *J Coastal Res* 28:193–198
- Fenu G, Mattana E, Bacchetta G (2011) Distribution, status and conservation of a critically endangered, extremely narrow endemic: *Lamyropsis microcephala* (Asteraceae) in Sardinia. *Oryx* 45:180–186
- Fenu G, Mattana E, Bacchetta G (2012) Conservation of endemic insular plants: the genus *Ribes* L. (Grossulariaceae) in Sardinia. *Oryx* 46:219–222
- Fornara DA, du Toit JT (2008) Community-level interactions between ungulate browsers and woody plants in an African savanna dominated by palatable-spinescent *Acacia* trees. *J Arid Environ* 72:534–545
- Gangoso L, Donazar JR, Scholz S, Palacios CJ, Hiraldo F (2006) Contradiction in conservation of island ecosystems: plants, introduced herbivores and avian scavenger in the Canary Islands. *Biodivers Conserv* 15:2231–2248
- García MB, Goñi D, Guzmán D (2010) Living at the edge: local versus positional factors in the long-term population dynamics of an endangered orchid. *Conserv Biol* 24:1219–1229
- Garzón-Machado V, González-Mancebo JM, Palomares-Martínez A, Acevedo-Rodríguez A, Fernández-Palacios JM, Del-Arco-Aguilar M, Pérez-de-Paz PL (2010) Strong negative effect of alien herbivores on endemic legumes of the Canary pine forest. *Biol Conserv* 143:2685–2694
- Hawkes CV, Sullivan JJ (2001) The impact of herbivory on plants in different resource conditions: a meta-analysis. *Ecology* 82:2045–2058
- Jenkins MA, Webster CR, Rock JH (2007) Effects of chronic herbivory and historic land use on population structure of a forest perennial, *Trillium catesbaei*. *Appl Veg Sci* 10:441–450
- Knight TM (2004) The effect of herbivory and pollen limitation on a declining population of *Trillium grandiflorum*. *Ecol Appl* 14:915–928
- Knight TM, Caswell H, Kalisz S (2009) Population growth rate of a common understory herb decreases non-linearly across a gradient of deer herbivory. *Forest Ecol Manag* 257:1095–1103
- Kose YB, Ocak A, Erkara IP (2010) *Centaurea cadmea* subsp. *pontica* subsp. nov. (Asteraceae) from northwest Anatolia. Turkey. *Nord J Bot* 28:475–478
- Kultur S (2010) *Centaurea nerimaniae* sp. nov. (Asteraceae) from south Anatolia. Turkey. *Nord J Bot* 28:613–616
- Lavergne S, Thompson JD, Garnier E, Debussche M (2004) The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos* 107:505–518
- López-Alvarado J, Sáez L, Filigheddu R, Guardiola M, Susanna A (2011) *Centaurea tripontina* (Compositae), a new species from the Pre-Pyrenean mountains, Spain. *Plant Biosyst.* doi: 10.1080/11263504.2011.608736
- Mameli G, Filigheddu R, Binelli G, Meloni M (2008) The genetic structure of the remnant populations of *Centaurea horrida* in Sardinia and associated islands. *Ann Bot* 101:633–640
- Maron J, Crone E (2006) Herbivory: effects on plant abundance, distribution and population growth. *Proc Roy Soc B-Biol Sci* 273:2575–2584
- Masseti M (2009) Mammals of Mediterranean islands: homogenisation and the loss of biodiversity. *Mammalia* 73:169–202
- McEachern AK, Thomson DM, Chess KA (2009) Climate alters response of an endemic island plant to removal of invasive herbivores. *Ecol Appl* 19:1574–1584
- McGraw JB, Furedi MA (2005) Deer browsing and population viability of a forest understory plant. *Science* 307:920–922
- McPeck MA, Kalisz S (1993) Population sampling and bootstrapping in complex designs: demographic analysis. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments. Chapman and Hall, New York, pp 232–252
- Médail F, Quézel P (1997) Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. *Ann Mo Bot Gard* 84:112–127
- Médail F, Quézel P (1999) Biodiversity hotspots in the Mediterranean basin: setting global conservation priorities. *Conserv Biol* 13:1510–1513

- Miller GR, Geddes C, Mardon DK (1999) Response of the alpine gentian *Gentiana nivalis* L. to protection from grazing by sheep. *Biol Conserv* 87:311–318
- Miranda M, Diaz L, Sicilia M, Cristobal I, Cassinello J (2011) Seasonality and edge effect determine herbivory risk according to different plant association models. *Plant Biol* 13:160–168
- Morris WF, Doak DF (2002) Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates Inc., USA
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kents J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858
- Palombo MR (2009) Biochronology, paleobiogeography and faunal turnover in western Mediterranean Cenozoic mammals. *Integr Zool* 4:367–386
- Papanikolaou AD, Fyllas NM, Mazaris AD, Dimitrakopoulos PG, Kallimanis AS, Pantis JD (2011) Grazing effects on plant functional group diversity in Mediterranean shrublands. *Biodiversity Conserv* 20:2831–2843
- Pisanu S, Filigheddu R, Farris E (2009) The conservation status of an endemic species of northern Sardinia: *Centaurea horrida* Badarò (Asteraceae). *Plant Biosyst* 143:275–282
- Rydgren K, de Kroon H, Økland RH, van Groenendael J (2001) Effects of fine-scale disturbances on the demography and population dynamics of the clonal moss *Hylocomium splendens*. *J Ecol* 89:395–405
- Simbaña W, Tye A (2009) Reproductive biology and responses to threats and protection measures of the total population of a critically endangered Galàpagos plant, *Linum cratericola* (Linaceae). *Bot J Linn Soc* 161:89–102
- Spear D, Chown SL (2009) Non-indigenous ungulates as a threat to biodiversity. *J Zool* 279:1–17
- Susanna A, Garcia-Jacas N (2009) The tribe Cardueae. In: Funk VA, Susanna A, Stuessy T, Bayer R (eds) Systematics, evolution and biogeography of the Compositae. IAPT, Vienna, pp 293–313
- Thompson JD (2005) Plant evolution in the Mediterranean. Oxford University Press, Oxford
- Townsend DS, Meyer AD (2002) Rapid recovery of witch hazel (*Hamamelis virginiana* L.) by sprouting, following release from white-tailed deer (*Odocoileus virginianus* Zimm.) browsing. *Nat Area J* 22:290–295
- Underwood AJ (1997) Experiments in ecology: their logic design and interpretation using analysis of variance. Cambridge University Press, Cambridge
- Vicari M, Bazely DR (1993) Do grasses fight back—the case for antiherbivore defences. *Trends Ecol Evol* 8:137–141
- White AM, Goodman PS (2009) Differences in woody vegetation are unrelated to use by African elephants (*Loxodonta africana*) in Mkhuzi Game Reserve, South Africa. *Afr J Ecol* 48:215–223
- Whittaker RJ, Fernández-Palacios JM (2007) Island biogeography. Oxford University Press, Oxford