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Strong negative effect of alien herbivores on endemic legumes of the Canary pine forest

V. Garzón-Machado [a,*], J.M. González-Mancebo [a], A. Palomares-Martínez [b], A. Acevedo-Rodríguez [b], J.M. Fernández-Palacios [c], M. Del-Arco-Aguilar [a], P.L. Pérez-de-Paz [a]

[a] Departamento de Biología Vegetal (Botánica), Facultad de Farmacia, Universidad de La Laguna, C/Astrofísico Francisco Sánchez s/n, 38071 La Laguna, Tenerife, Islas Canarias, Spain
[b] Parque Nacional de La Caldera de Taburiente, Centro de Visitantes de El Paso, Carretera General de Padrón, 47, 38750 El Paso, La Palma, Islas Canarias, Spain
[c] Departamento de Ecología, Facultad de Biología, Universidad de La Laguna, C/Astrofísico Francisco Sánchez s/n, 38206 La Laguna, Tenerife, Islas Canarias, Spain

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ABSTRACT

We studied the effects of herbivores on populations of four endemic legume species in pine forests in Caldera de Taburiente National Park on La Palma, Canary Islands. Seeds of these species were sown in control and herbivore-exclusion plots. Over the subsequent 4-years period, we assessed the effects of herbivores by counting the number of individual plants that emerged and by following their growth. We assessed growth over time using three plant-size categories. For these four species, we conclude that the presence of herbivores, including barbary sheep (*Ammotragus lervia*), goat (*Capra hircus*) and European rabbit (*Oryctolagus cuniculus*), exerts a strong negative effect on plant establishment. We suggest that the paucity of understory plant species in the pine forests of the Canary Islands may be strongly correlated with the presence of introduced herbivores in this region. We propose urgent conservation measures, such as large fenced areas, control activities and the most effective measure, eradication.

1. Introduction

The archipelago of the Canary Islands, together with Madeira, belongs to the Canary-Madeiran Subregion of the Mediterranean biogeographical region (Rivas-Martínez, 2007). The Canary Islands are part of one of the most remarkable biodiversity hotspots on the planet (Médail and Quézel, 1997; Myers et al., 2000), including over 680 endemic taxa (species and subspecies) of vascular plants (Reyes et al., 2008). Endemic taxa account for more than 50% of the native flora (Santos, 2001).

The distribution of endemic diversity within the Canary Islands is heterogeneous (Reyes et al., 2008). Endemic species richness is irregularly distributed among the major natural potential communities in the Canaries; rupicolous communities contain the largest proportion of endemic species (about 50%). By contrast, pine forests account for a small proportion of endemics (about 10%, excluding rupicolous), some of which are not exclusive to the pine-forest community. Thermo-sclerophyllous forest is the zonal community with the largest (about 20%, excluding rupicolous) (Garzón-Machado et al., in preparation). Previous authors have suggested that this heterogeneity of the endemic flora is related to topographic complexity (Whittaker et al., 2007). However, the effect of herbivores has also been considered to be a highly influential factor in the Canary Islands (Bañares et al., 2003; Nogales et al., 2006); the current endemic richness in rupicolous communities may be related to their inaccessibility.

No native mammalian herbivores are known to occur in the Canary Islands (Izquierdo et al., 2004). The effects of alien herbivores on plants are well known, especially on oceanic islands (Drake et al., 2002; Courchamp et al., 2003). Alien herbivores represent one of the primary threats to endemic island floras and are one of the main causes of biodiversity loss (Vitousek et al., 1997; Wilcove et al., 1998; Mooney and Cleland, 2001; Brooks et al., 2002; Donlan et al., 2002). In the Canary archipelago, several herbivore species have been introduced. These herbivores disturb the substrate and vegetation (Gangoso et al., 2006) and threaten native plants in multiple ecosystems, including pine forests (Nogales et al., 1992; Rodríguez and Rodríguez, 1992). Goats (*Capra hircus* L.) were introduced by the earliest inhabitants of the islands in the pre-Hispanic era (Navarro et al., 1990). European rabbits (*Oryctolagus cuniculus* L.) arrived with the Castilian conquerors in the middle of the 15th century (Cabrera, 1997). Finally, barbary sheep (*Ammotragus lervia* Pallas), which are native to North Africa, were brought to the island in 1972 for hunting (Palomares, 1999). Goat

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[*] Corresponding author. Tel.: +34 922 31 84 36; fax: +34 922 31 84 47.
E-mail addresses: vigarma@ull.es (V. Garzón-Machado), jglezm@ull.es (J.M. González-Mancebo), APalomares@oapn.mma.es (A. Palomares-Martínez), aaceved2@tragsa.es (A. Acevedo-Rodríguez), jmferpal@ull.es (J.M. Fernández-Palacios), marco@ull.es (M. Del-Arco-Aguilar), pperez@ull.es (P.L. Pérez-de-Paz).

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and rabbits are among the world's 100 most invasive alien species (Lowe et al., 2000). In the Canaries, various authors have examined the effects of these herbivores on endemic plants through diet studies (Rodríguez and Rodríguez, 1987; Martín et al., 2003) or direct observation (Nogales et al., 1992; López-Darias and Lobo, 2009).

The Canary pine forest is dominated by the endemic *Pinus canariensis* C. Sm. *ex* DC. in Buch, a species of Mediterranean affinity (Millar, 1996), which is the only prevalent tree species. Many authors have described the typical Canary pine forest as a formation that is poor in understory species (Ceballos and Ortuño, 1976; Santos, 1983; Pérez et al., 1994; Bramwell and Bramwell, 2001). Although it has been shown that some endemic species of the pine forest in Gran Canaria (Canary Islands) contribute to the diet of goats (Nogales et al., 1992), the effects of herbivores on the abundance and distribution of endemic species have not been studied, and quantitative studies are lacking.

Fire is the primary natural disturbance agent in the pine forest, apart from tree fall, but anthropogenic wildfires are now frequent. The Canary pine shows fire tolerance. It remains alive after fire and resprouts quickly (Del Arco et al., 1992). Among the species of the pine-forest community, reseeders dominate. The species poorness of the pine forest has been commonly linked to adverse climatic conditions (Ceballos and Ortuño, 1976), topographic position (especially slope) and the maturity and stability of the forest (Del Arco et al., 1992). Other unstudied factors may also play a role, such as the effect of litter accumulation through time, which may impair germination and recruitment. However, in recent years, Palomares (1999, 2004), the Conservation Director of Caldera de Taburiente National Park (La Palma), has suggested that herbivore effects may be stronger determinants of the pine forest vegetation, cover and richness, especially for endemic plants, than the factors listed above. To date, the effects of herbivores have not been quantified in this region. This information would help land managers develop and execute conservation plans.

The aim of this study was to verify whether the endemic species richness in the pine-forest understory is related to herbivore effects by comparing control and exclusion plots. We hypothesized that the abundance of the studied species in the exclusion plots would not be related to the natural abundance of the species in the pine-forest understory in the National Park. In other words, we expected that environmental variables would have less influence than herbivore effects on the distribution and abundance of each species, even for more restricted species. Our study took place in Caldera de Taburiente National Park (La Palma island). This National Park currently contains the most highly protected pine forest in the archipelago (Gobierno de Canarias, 1994), although herbivores have not been eradicated.

2. Materials and methods

2.1. Study area

Caldera de Taburiente National Park is located on the island of La Palma, in the northwest portion of the Canary archipelago (Fig. 1), and contains one of the larger protected sections of pine forest in the Canary Islands (Del Arco et al., 2006). The park

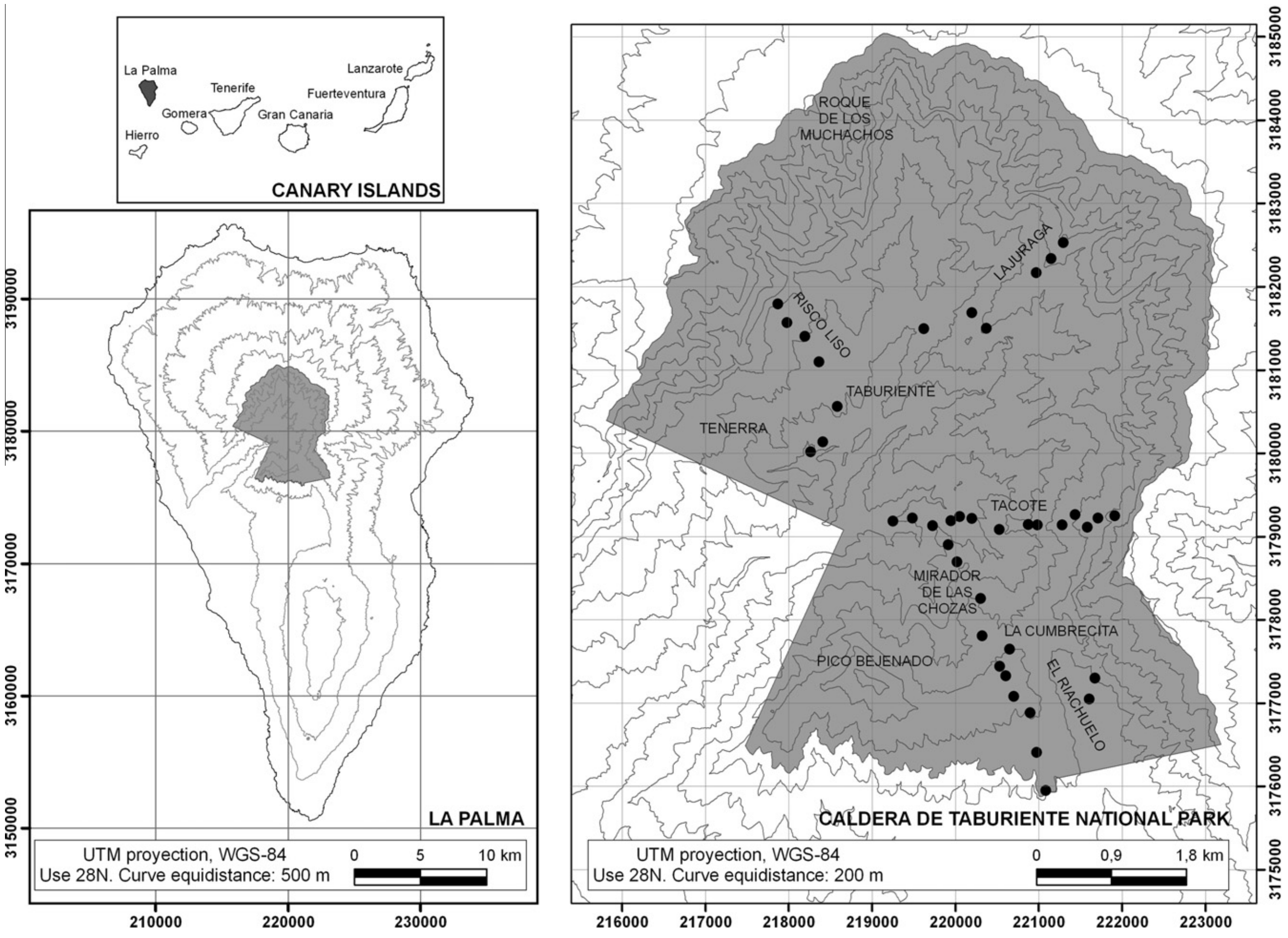

Fig. 1. Locations of plots within Caldera de Taburiente National Park, La Palma, Canary Islands (black points). The gray area represents Caldera de Taburiente National Park.

encompasses a difference in elevation of over 2000 m and occupies around 4690 ha. Its basic characteristics include rough topography, with deep precipices, slopes of greater than 50° inclination and many near-vertical rocky walls (Afonso, 1988). The climate is Mediterranean, with a warm and dry summer and most rainfall occurring in autumn and winter (Del Arco et al., 1999).

The pine forest in the park is dominated by open wooded formations of *P. canariensis*. As mentioned previously, the understory is poor in terms of species richness and abundance. This species poorness contrasts with the diversity and floristic richness of the cliff areas in the interior of the park (Beltrán and Pérez, 2004), which are practically inaccessible to herbivores. The park includes about 390 plant species, 18 of which are Macaronesian endemics, 86 of which are Canary endemics and 28 of which are restricted to La Palma (Santos, 2004). Among the La Palma endemics, 15 species are threatened (Gobierno de España, 1990; Gómez et al., 1996; Bañares et al., 2003).

2.2. Plant material

We chose four endemic legume species with varying abundances and distributions within the park. The selected species were *Chamaecytisus proliferus* ssp. *proliferus* (L.f.) Link, *Teline stenopetala* (Webb and Berthel.) Webb and Berthel., *Spartocytisus filipes* Webb and Berthel. and *Cicer canariense* A. Santos and G.P. Lewis. These species were selected because they are all present in the diets of goats, rabbits and barbary sheep (Pérez et al., 1986; Santos and Lewis, 1986; Rodríguez and Rodríguez, 1987; Nogales et al., 1992; Palomares, 2004; Rodríguez, 2008) and because they all have natural populations in the study area.

C. *proliferus* and *T. stenopetala* are found throughout the park, although they are locally abundant only in isolated, restricted areas that are inaccessible to herbivores. By contrast, *C. canariense* and *S. filipes* have more restricted distributions. *C. canariense* exists only in very small and at-risk populations and has been included in catalogues, atlases and species red lists (Gobierno de Canarias, 2001; Bañares et al., 2003; Moreno, 2008).

C. canariense is an evergreen plant with creeping and climbing stems, while the other three species are evergreen shrubs that reach several meters in height. The time to reach the reproductive stage varies from 1 to 2 years for *C. canariense* and from 2 to 4 years for the other species. These four legume species reseed after fire.

2.3. Experimental design

Initially, we visited natural populations of the four selected species for observation purposes. We recorded the distribution and abundance of each species within the park using a 500-m grid. Inside the park, we used GIS tools (ArcGIS 9, 2006) to mark out 40 monitoring areas (for plot establishment) separated by 100 m in elevation from 550 to 1650 m a.s.l. These areas were located along five transects where the topography allowed optimal conditions for access to and work within the plots. Two additional areas were included, making a total of 40 sampling areas. Two adjacent plots (5 × 10 m each) were installed within each selected area, always at sites without natural populations of the four studied species. One plot was unprotected (control), while the other plot (exclusion) was surrounded by a metal fence and wire that served as a barrier (150 cm in height) to goats (*C. hircus*), rabbits (*O. cuniculus*) and barbary sheep (*A. lervia*).

The inaccessibility of the terrain prevented us from installing plots in some of the areas previously selected using GIS tools. In such cases, we adjusted the positions of the sampling areas slightly (by no more than 50 m from the original position) while maintaining their altitudinal separation (Fig. 1). The location (UTM coordinates), altitude, slope, aspect, thermotype and ombrotype (Del Arco and González, 2004) of each location were recorded using GIS tools (Table 1). These data were also verified through field observations. In addition, we recorded tree cover and the proportion of rock in each plot.

Table 1
Environmental variables used in the study.

Variable	Level/Class
Altitude (m)	550–1650
Slope (°)	5–55
Aspect	Sector 1: (NE) Sector 2: (SE) Sector 3: (SW) Sector 4: (NW)
Tree cover	(1) Low (<25%) (2) Medium (25–50%) (3) High (50–75%) (4) Very high (>75%)
Proportion of rock	(1) Low (<25%) (2) Medium (25–50%) (3) High (50–75%) (4) Very high (>75%)
Thermotype	(1) Thermomediterranean (2) Mesomediterranean
Ombrotype	(1) Dry (2) Subhumid (3) Humid

In February of 2005, 600 seeds of each of the four species (harvested from natural populations within the National Park) were mixed together and sown in each of the protected and unprotected plots. The seeds were previously mixed with a portion of natural soil of each plot, and later spread in their respective plots after we had removed the existing vegetation. After sowing, we visited the plots three times each year (at the end of winter, spring and autumn) for 4 years. During each visit, we counted the number of individuals of each species. We also recorded plant sizes. The times of year selected for monitoring visits coincided with the end of flowering season and most probably recruitment periods. We categorized the plants into three size classes (small, medium and large) based on the relative height of each individual. "Small" plants were those in the earliest growth phase (⩽10 cm for all species). "Medium" plants were young individuals (10–50 cm for *C. proliferus*, *S. filipes* and *T. stenopetala* and 10–25 cm for *C. canariense*). The "large" size class included any plant that had the possibility of having entered in its reproductive phase (⩾50 cm for *C. proliferus*, *S. filipes* and *T. stenopetala* and ⩾25 cm for *C. canariense*). A total of twelve monitoring visits were conducted during our 4-years research period.

2.4. Data analyses

We used a paired *t*-test to determine whether there were significant differences between the two types of plots (control and exclusion) in recruitment and establishment of the four species. We performed separate tests for each monitoring period. The data were log transformed to satisfy the assumptions of normality and homoscedasticity.

We used a bivariate correlation analysis (Spearman) to identify any differences in abundance between each exclusion plot and its respective grid cell within the park.

In addition, we performed a multiple regression (Enter method) to analyze the influence of environmental variables (Table 1) on the establishment of the four species. For this purpose, the mean number of large individuals in the exclusion plots was used. We performed a one-way ANOVA and post hoc Bonferroni's tests to detect differences between groups for variables that were significant ($P < 0.05$) in the multiple-regression analysis. All analyses were performed using the SPSS statistical package (version 15.0).

3. Results

The paired *t*-test revealed significant differences ($P < 0.05$) between control and exclusion plots for all the species except for small individuals (Fig. 2). In the absence of herbivores, the

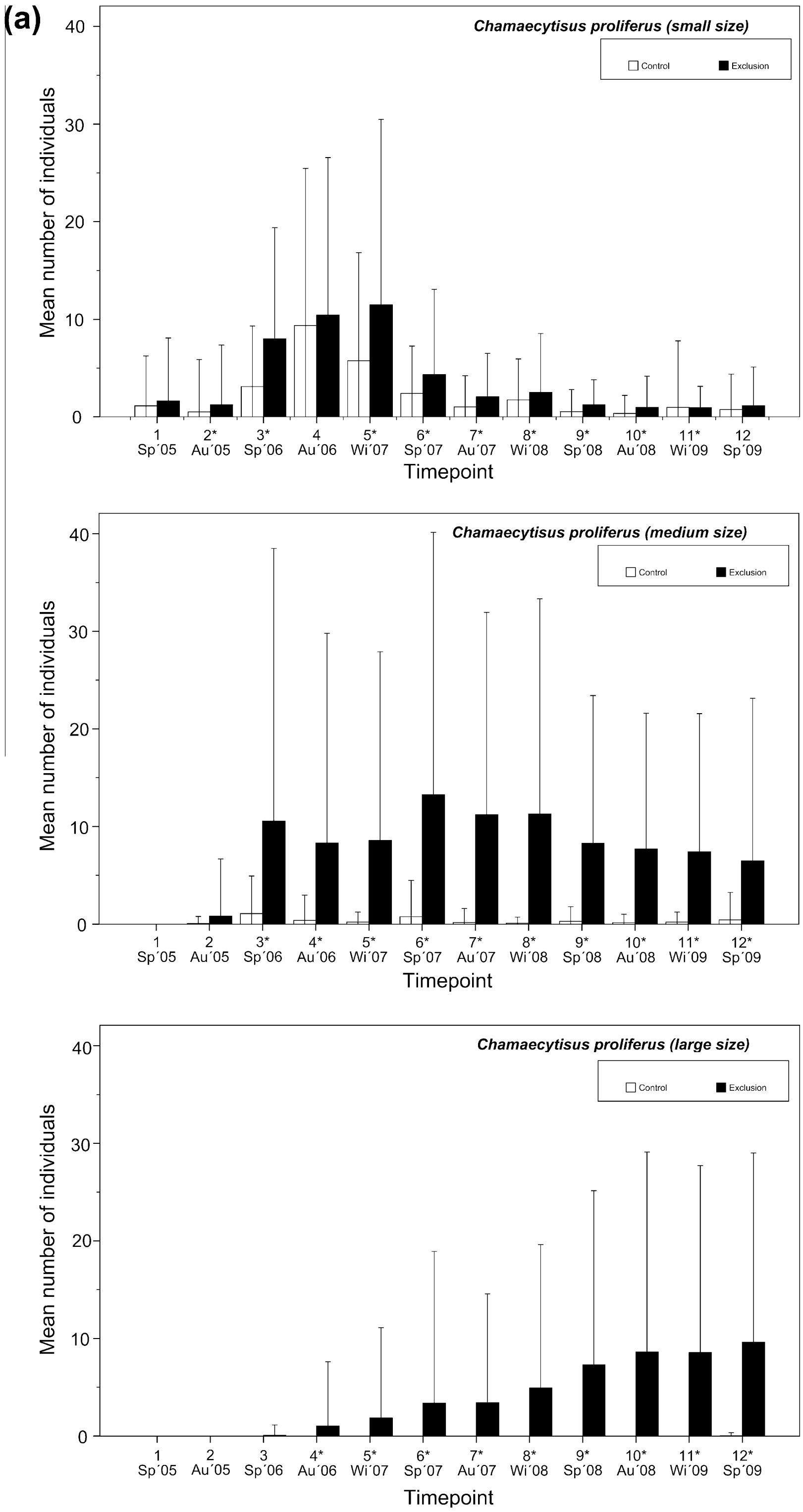

Fig. 2. Differences in mean number of individuals (mean from 40 plots for each monitoring timepoint) between control and exclusion plots (white bars and black bars, respectively). Error bars show two standard deviations. Small, medium and large individuals are differentiated for each species (2a: *Chamaecytisus proliferus*; 2b: *Cicer canariense*; 2c: *Spartocytisus filipes*; 2d: *Teline stenopetala*). *X*-axis legend: Sp = Spring; Au = Autumn; Wi = Winter. *Results are statistically significant ($P < 0.05$) in a paired *t*-test.

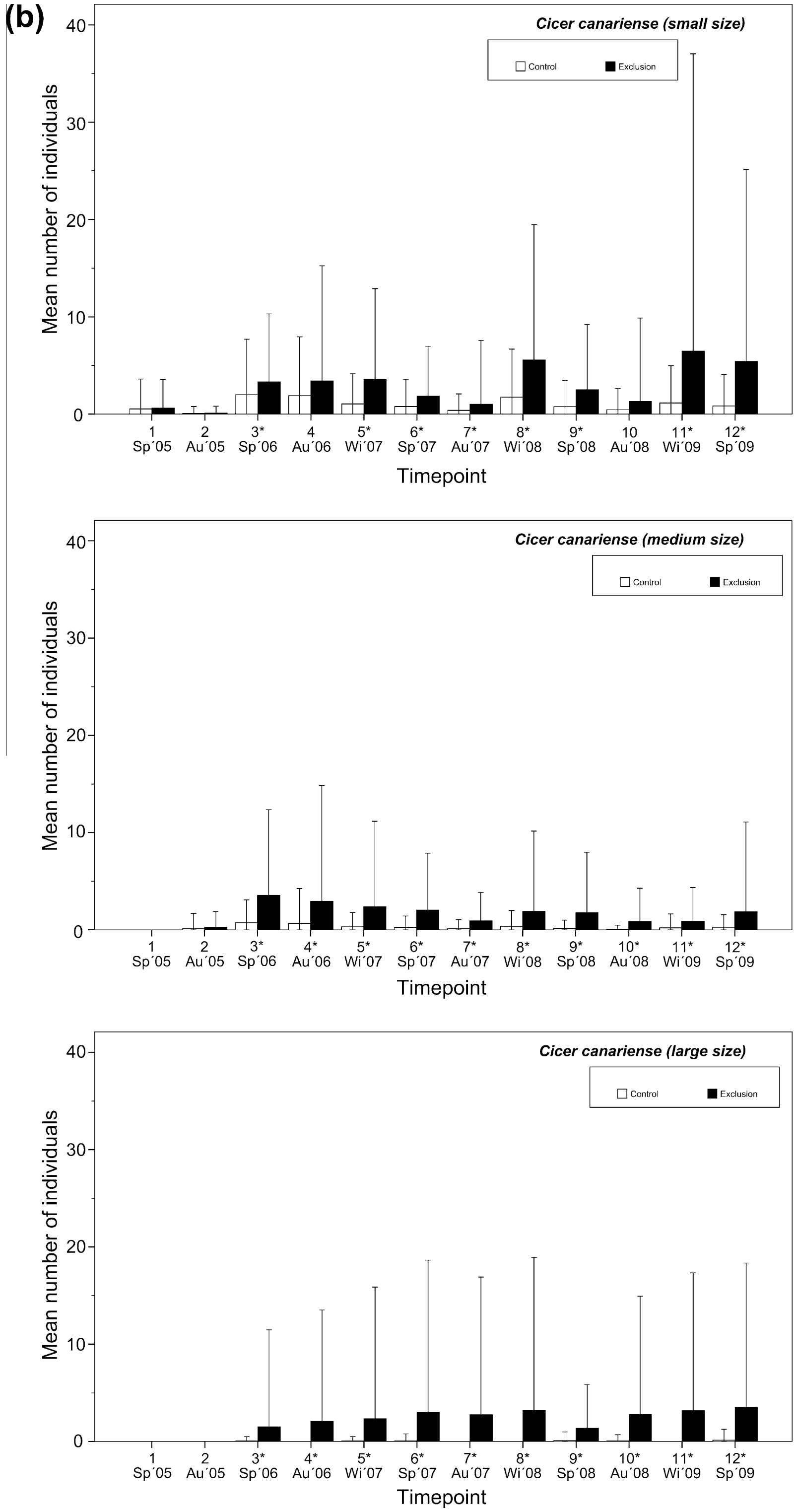

Fig. 2 (*continued*)

number of individuals was significantly greater for all species. These differences in abundance were apparent across all 12 monitoring visits (Fig. 2), except for the first visit (when there were no medium or large individuals in either control or exclusion plots), and became more noticeable over time, especially for large individuals (for which we observed a difference of more than 99% in the number of individuals in control and exclusion plots at the last timepoint).

The lack of significant differences for small individuals at the last timepoint is related to the rapid germination of the seeds and the absence of new recruitment (in both plots) for all species except *C. canariense*. This species showed several increases in the number of small individuals (at timepoints 3–5, 8 and 11–12). *C. canariense* produces flowers and fruit earlier than the other three species. This difference might also be related to its shorter lifespan. Large individuals produced seeds before they were 2 years old,

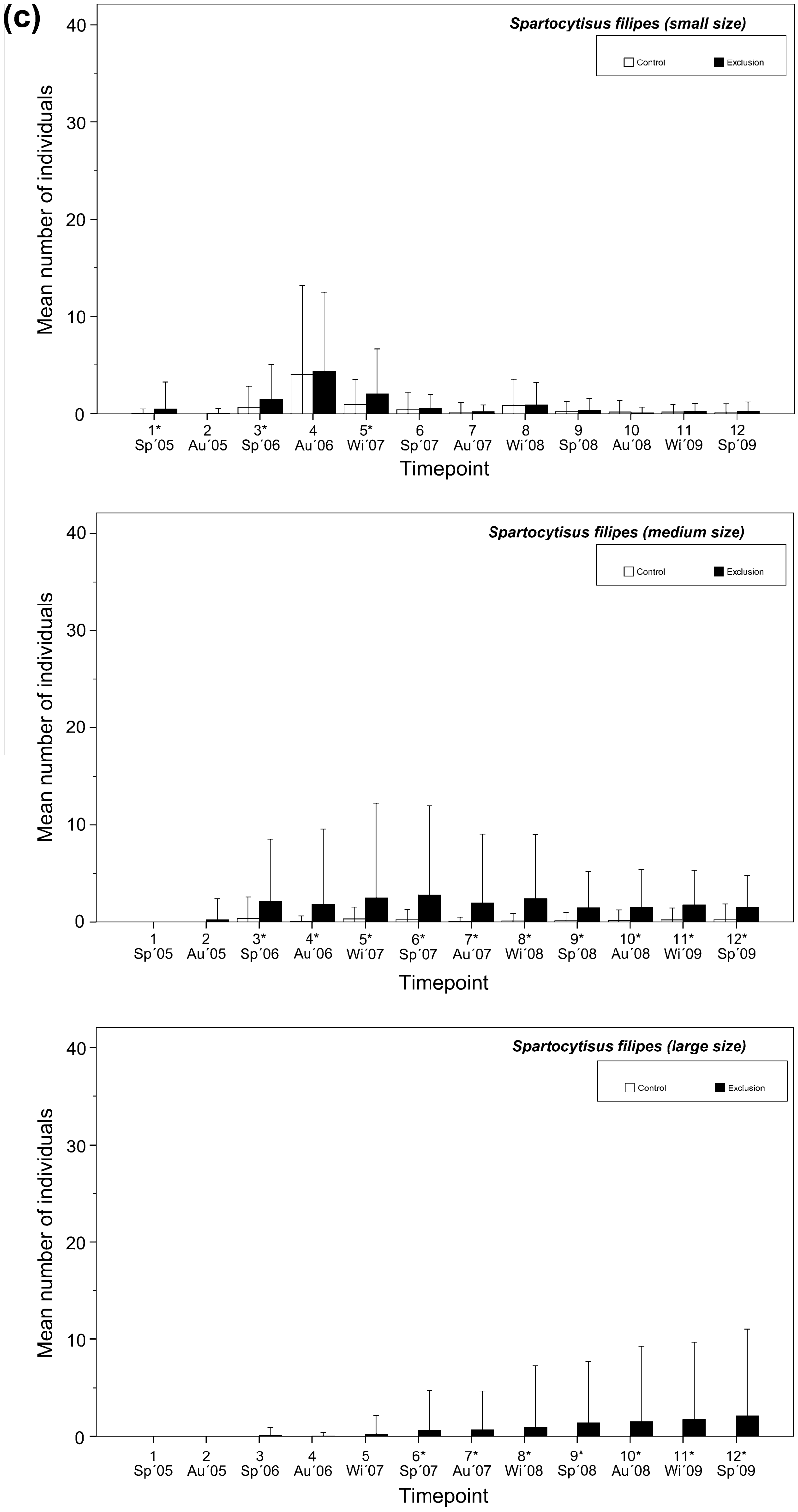

Fig. 2 (*continued*)

generating a second and third generation during the monitoring period. The number of medium-sized *C. canariense* individuals increased at timepoints 3, 8, 9 and 12 and declined at timepoint 7, while the number of large individuals began to increase from timepoint 3 until the end of the study. *C. proliferus*, *S. filipes* and *T. stenopetala* showed another trend across the study period (Fig. 2). For these three species, the total number of small individuals increased between timepoints 3 and 5 and declined slowly across the latest timepoints. The largest numbers of medium-sized individuals were found between timepoints 3 and 8, declining thereafter. The number of large individuals of these three species progressively increased from timepoints 4–5 onward.

Based on the grid sampling, the four species showed notable differences in their distributions and abundances in the park (Table 2). *C. proliferus* and *T. stenopetala* were the species with the highest frequencies. *S. filipes* showed a low frequency but high

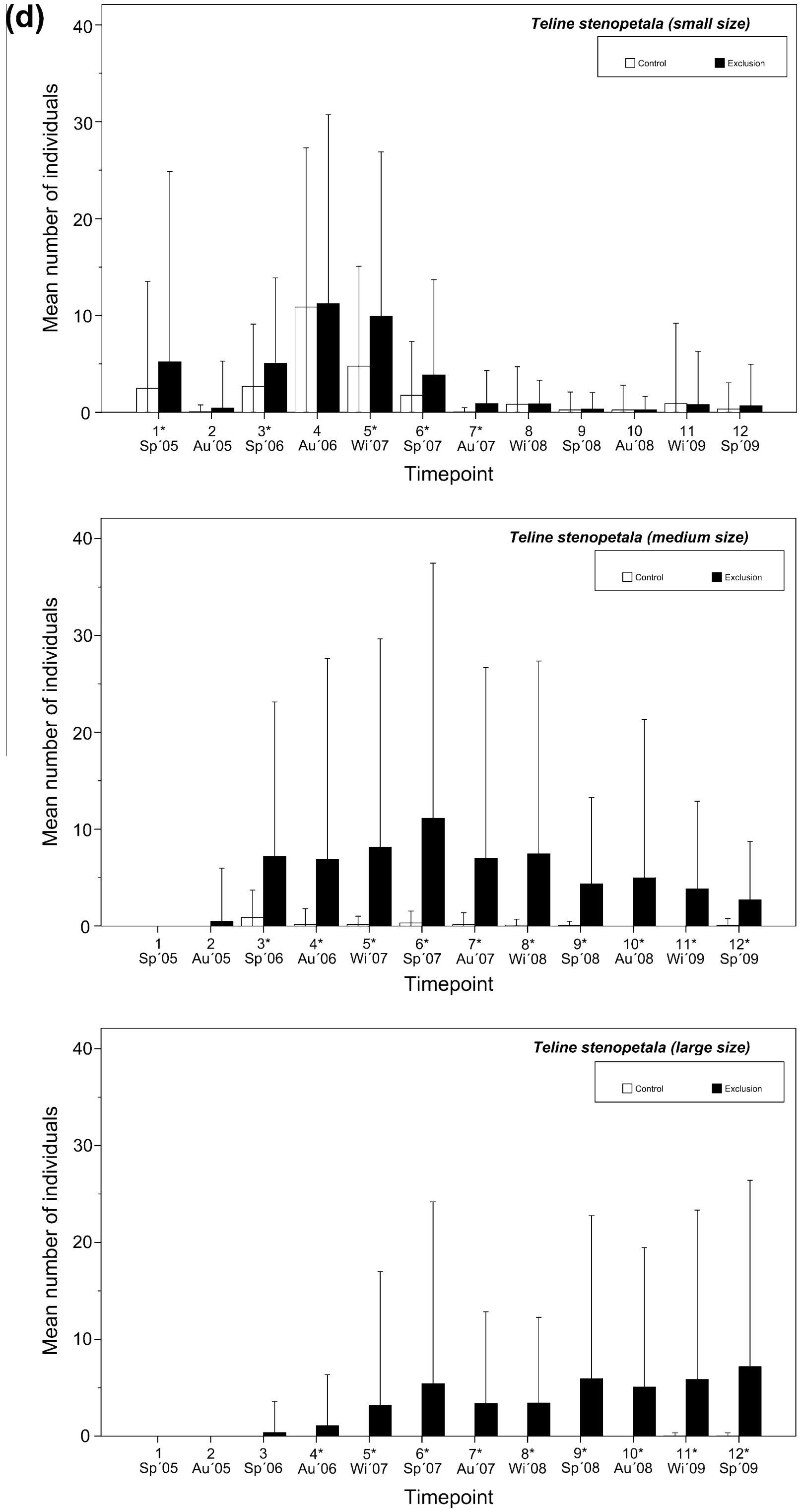

Fig. 2 (*continued*)

abundance, while *C. canari*ense was the only species with notably low abundance within the park grid. The Spearman analysis showed no correlation between abundance in the grid cells and abundance in the experimental plots for any species (*C. proliferus*: $r = 0.262$, $P > 0.05$; *C. canariense*: $r = 0.147$, $P > 0.05$; *S. filipes*: $r = 0.050$, $P > 0.05$; *T. stenopetala*: $r = 0.080$, $P > 0.05$). Thus, the abundance of each species in the exclusion plots was not correlated with its abundance and distribution in the park. This result suggests that the current distribution and abundance of these species in the pine forest is more strongly related to herbivore pressure than to other environmental variables, even for the most restricted species, *C. canariense*.

The environmental variables considered did not influence the multiple regression models for *C. proliferus* and *T. stenopetala* ($F = 1.384$, R^2 adjusted = 0.121, $P > 0.05$ and $F = 1.580$, R^2 adjusted = 0.172, $P > 0.05$, respectively). However, the models were significant for *C. canariense*

Table 2
Distribution and abundance of four endemic legume species, within Caldera de Taburiente National Park.

Species	[a]Distribution	[b]Abundance
Chamaecytisus proliferus	85.08	277
Cicer canariense	9.39	45
Spartocytisus filipes	17.13	250
Teline stenopetala	76.80	252

[a] Percentage of analyzed grids in which the species appears.
[b] Mean number of individuals on the grids in which the species appears.

and *S. filipes* ($F = 8.909$, R^2 adjusted = 0.740, $P < 0.05$ and $F = 4.306$, R^2 adjusted = 0.543, $P < 0.05$, respectively). The variable "ombrotype" was the only variable with a significant influence in the latter case. A one-way ANOVA showed significant differences among the three classes of ombrotypes for *C. canariense* ($F = 44.08$; df = 2; $P < 0.01$) and for *S. filipes* ($F = 16.27$; df = 2; $P < 0.01$). Post hoc tests showed that the abundance of these species was correlated with the humid ombrotype ($P < 0.01$).

4. Discussion

Our results indicate that alien herbivores in Caldera de Taburiente (*A. lervia*, *C. hircus* and *O. cuniculus*) have a highly negative impact on the abundance and distribution of the species studied. The highly significant differences between control and exclusion plots and the lack of a correlation between each species' abundance in the exclusion plots and its distribution and abundance under natural conditions suggest that the Canary Islands pine-forest understory may be impoverished due to alien herbivores. More restricted species (*C. canariense* and *S. filipes*) were partly influenced by differences in humidity among the study sites. Herbivore effects represent a greater challenge to these species because humidity also appears to restrict their distributions. Habitat-generalist species may persist longer under continuous herbivore effects than more restricted species (Jenkins et al., 2007).

Although further studies are needed to examine the possible influence of other factors, such as the effect of litter deposition in the germination process, our results indicate that the Canary pine forest has been severely impoverished by herbivore activity, at least for the legume species studied. These are the first data that suggest a relationship between the current species poorness in the understory of this forest community and anthropogenic causes. Many previous studies carried out in the pine forest, such as those on the effects of fire on the vegetation (Arévalo et al., 2001) or soil properties (Rodríguez et al., 2009), may have been influenced by this previously unconsidered factor. Therefore, the results of previous studies might be highly biased.

Our results (differences of 99% between control and exclusion plots) suggest that the effects of alien herbivores are much stronger that has previously been considered. As on other oceanic islands (Coblentz, 1978), the flora of the Canary Islands has evolved, in most cases, over long periods of isolation from mainland herbivores. This evolutionary history may have led to an absence of efficient strategies to defend against herbivore activity (Atkinson, 2001). At the same time, the populations of invading herbivores have increased as they enjoy an abundance of nutritional resources; plant communities of oceanic islands are mainly composed of species that are highly palatable and vulnerable (Holdgate, 1967). Furthermore, alien species are highly adaptable because of the absence of natural predators and enemies (Shea and Cheeson, 2002). The main consequence is a reduction in plant species abundance that, in some cases, has been so drastic that urgent measures have been necessary to prevent widespread extinction (Bañares et al., 2003). In addition, herbivore pressure may lead to a progressive replacement of native plants with numerous exotic herbs and grasses that are more resistant to grazing (Holmgren, 2002).

4.1. Conservation implications

This study supports the results of other authors in suggesting that the introduction of herbivores is a serious threat to insular ecosystems, causing persistent and even irreversible qualitative and quantitative changes in plant communities (Donlan et al., 2002; Courchamp et al., 2003).

One management option that may be helpful in the recovery of threatened species and insular ecosystems is the eradication of alien species (Simberloff, 2001; Genovesi, 2005). Eradication is a key tool in conservation and is considered by the Convention on Biological Diversity (CBD) to be the best alternative when prevention fails (Genovesi, 2005). Introduced herbivores have been eradicated from many islands throughout the world (Saunders and Norton, 2001; Burbridge and Morris, 2002; Tershy et al., 2002). Eradication projects in the Galapagos Islands are remarkable for the large area of the islands where they have been implemented. For example, Pinta Island (5940 ha) has been declared to be free of goats (Campbell et al., 2004), and Santiago Island (58,465 ha) and Alcedo Volcano (74,103 ha) are free of feral donkeys (Carrion et al., 2007).

Although the influence of herbivores is closely related to the current threat stage of some species (Sventenius, 1946), no strategies to eradicate wild alien herbivores have been adopted. This failure to act may be explained by the only recent recognized connection between herbivore pressure and threats to endemic species. In fact, only 27 endemic plants are considered to be threatened or critically threatened by wild alien herbivores (Bañares et al., 2003). In archipelagos like the Canaries, which exhibit a high percentage of endemic flora [680 taxa (species and subspecies) according to Reyes et al., 2008], the number of species considered to be threatened by herbivores is probably too low. In addition, as mentioned above, the effects of herbivores on species abundance and ecosystem changes have not been considered. On the other hand, the most important reason for the lack of eradication projects is public opposition, as has occurred in other European areas (Genovesi, 2005). Proposals to eradicate barbary sheep (*A. lervia*) on La Palma Island or mouflon sheep (*Ovis ammon* L.) on Tenerife Island have resulted in conflicts with relevant social groups, such as hunters (Marrero-Gómez et al., 2003).

Our results show the need for total eradication of barbary sheep (*A. lervia*), goats (*C. hircus*) and European rabbits (*O. cuniculus*) from Caldera de Taburiente National Park. However, an additional problem is that the park represents only 7% of the total area of the island. Thus, eradication should take place throughout the island. Such a project legally depends on several institutions with different interests, making it difficult to control the adoption of conservation strategies by the administration of the National Park (Gangoso et al., 2006). For these reasons, we recommend control actions and efforts to preserve natural understory conditions as an emergency measure. One urgent measure is to carry out specific actions to protect the most sensitive and restricted species studied, *C. canariense*, to guarantee its survival. The positive impacts of herbivore exclusion on species that are not rare, such as *C. proliferus* and *T. stenopetala*, also suggests the importance of extensive control of the herbivores in the area. Therefore, we propose the creation of large fenced pine-forest areas, called "micro-reserves" (Laguna et al., 2004), where the flora will be able to grow freely in the absence of herbivores.

Although control measures may be temporary, they are the only option that can be carried out immediately. However, total eradication is the only effective long-term solution to the problem.

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