Burned and Devoured-Introduced Herbivores, Fire, and the Endemic Flora of the High-Elevation Ecosystem on La Palma, Canary Islands

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Abstract

Novel disturbance regimes (e.g., introduced herbivores and fire) are among the major drivers of degradation in island ecosystems. High-elevation ecosystems (HEEs) on islands might be especially vulnerable to these disturbances due to high endemism. Here, data from an 11-year exclosure experiment in the HEE of La Palma (Canary Islands) are presented where mammalian herbivores have been introduced. We investigate the combined effect of herbivory and fire on total species richness, seedling richness, and seedling establishment on the whole system and a subset of highly endangered species (target species). Total species richness, seedling species richness, and seedling establishment decreased with herbivory. Five out of eight target species were exclusively found inside the exclosures indicating the negative impact of introduced herbivores on endemic high elevation flora. Target species were generally affected more negatively by introduced herbivores and were subject to significantly higher browsing pressure, probably owing to their lack of defense strategies. A natural wildfire that occurred six years before data sampling substantially increased total species richness and seedling richness in both herbivory exclosure and reference conditions. We conclude that species composition of the HEE has been severely altered by the introduction of non-native herbivores, even though fire seems to have a positive effect on this system.

Introduction

Anthropogenic influences have created novel disturbances as well as altered natural disturbance regimes (White and Jentsch, 2001; Hobbs et al., 2006; Catford et al., 2012). Indeed, changes in disturbance regimes are widely recognized as major threats to island biota and ultimately to global biodiversity (Caujapé-Castells et al., 2010). Mammalian herbivores (Courchamp et al., 2003; Campbell and Donlan, 2005), altered fire regimes (Perry et al., 2012; Ramirez et al., 2012), along with land use change, habitat degradation, or climate change (Caujapé-Castells et al., 2010) are of special importance among the threats to native and endemic island biota and insular ecosystems in general. Conservation efforts on islands should have particularly high-elevation (Kier et al., 2009) because of the outstanding position of islands as hotspots of endemic plant species diversity (Kreft et al., 2008).

A high degree of endemic species (Steinbauer et al., 2012) and their ephemeral evolutionary position (Fernández-Palacios et al., 2014) characterize especially high-elevation ecosystems (HEEs) within islands. These ecosystems experience strong environmental (due to increasing climatic harshness with elevation) and geographical isolation (because of increasing distance to comparable ecosystems on other islands or the continent; Steinbauer et al., 2013). As the ocean is an effective filter for terrestrial mammals, most oceanic islands did not possess mammalian herbivores before human colonization. Thus, mammalian herbivory has not influenced the evolution of endemic species on islands (Traveset et al., 2009). As a consequence, endemic plant species have often lost the particular herbivore defense mechanisms and strategies of their continental ancestors due to this lack of selection pressure (Atkinson, 2001). Indeed, evolutionary effects of missing herbivore pressure on plant traits can become apparent even within only decades (Didiano et al. 2014).

Introduced herbivores often profit from the absence of natural enemies, diseases, and pests (Shea and Cheeson, 2002). Thus, introduced mammalian herbivores have not only inflicted damage in the past but continue to inflict great damage on natural island vegetation and endemic plant species (e.g., Campbell and Donlan, 2005; Caujapé-Castells et al., 2010; Irl et al., 2012; Ramirez et al., 2012). Important examples are the feral goat (*Capra hircus*) and the European rabbit (*Oryctolagus cuniculus*), both considered among the world's 100 most invasive species (Lowe et al., 2000).

As an additional driver of change and degradation, human-induced alterations of fire regime (i.e., increased fire frequency or

magnitude) can negatively affect island vegetation, even though it may be naturally adapted to occasional wildfires (Arévalo et al., 2001; Perry et al., 2012, Garzón-Machado et al., 2012; Crausbay et al., 2014). Especially combined changes in both disturbances, introduced mammalian herbivores and altered fire regimes, will likely create negative impacts on vegetation dynamics or species richness. Population structure and community composition can be substantially modified via reduced regeneration success after fire events (Johansson et al., 2010; Ramirez et al., 2012).

In contrast to lower elevation ecosystems, HEEs in oceanic islands are still believed to be largely in a natural or at least semi-natural state. This is reflected in different forms of nature reserves and protection status. High-elevation nature reserves have been established, for instance, on La Palma and Tenerife (Canary Islands, Spain), Pico (Azores, Portugal), Fogo (Cape Verdes), La Réunion (Mascarene Islands, France), and Hawaii and Maui (Hawaii Islands, United States). The exclusion of intensive land use, settlements and infrastructure and the limited direct human impact in general makes it possible to investigate the dynamics of introduced herbivore pressure and altered fire regimes.

La Palma is a subtropical volcanic-oceanic island with strong environmental gradients (Irl and Beierkuhnlein, 2011). It is inhabited by several globally relevant introduced mammalian herbivores such as the feral goat (*C. hircus*) and the European rabbit (*O. cuniculus*; Garzón-Machado et al., 2010; Irl et al., 2012) but also the recently introduced Barbary sheep (*Ammotragus lervia*) originally from northern Africa. The selective grazing of these herbivores has been shown to cause the virtual mono-dominance of a single shrub species (i.e., the single-island endemic subspecies *Adenocarpus viscosus* subsp. *spartioides*), even though climatically better-adapted shrub species are present in the natural HEE flora (Irl et al., 2012). Fires occur naturally in the subalpine scrub due to the close vicinity to the endemic fire-promoting Canary Pine forest that forms the treeline (Höllermann, 2000; del Arco Aguilar et al., 2010). Both disturbances, fire and herbivory, have been individually studied on the Canary Islands and specifically on La Palma (see Höllermann, 2000, but also Garzón-Machado et al., 2010, or Irl et al., 2012), but an integrative approach to identify the combined effects of both introduced herbivores and altered fire regime with focus on the unique characteristics of HEEs is still missing.

We aimed at exploring the effects of two major disturbances—herbivory and fire—on the high elevation vegetation of La Palma, Canary Islands. Using an 11-year fenced exclosure experiment and nonfenced counterparts we take the HEEs of La Palma and the transition zone with the Canary Pine forest as a case study. We hypothesize that (1) introduced herbivores negatively affect total species richness, seedling species richness, and seedling establishment; (2) additional fire reduces total species richness, seedling richness, and seedling establishment; and (3) introduced herbivores selectively browse on endemics due to their lack of adaptation to herbivory.

Material and Methods

STUDY AREA

The Canary Islands are situated off the northwestern coast of Africa in the Atlantic Ocean. All islands are of volcanic origin (Carracedo et al., 2002). La Palma is located in the NW of the archipelago. At approx. 1.7 Ma it is the second youngest island, spanning an area of 706 km^2 (Carracedo et al., 2002). The HEE of La Palma—also referred to as the subalpine summit scrub (Irl and Beierkuhnlein, 2011; Irl et al., 2012) or summit broom scrub

(Garzón-Machado et al., 2011)—is most prominent on the outer flanks of the Caldera de Taburiente complex, ranging from about 2000 to 2400 m a.s.l. It covers an area of 14.3 km^2 (see Fig. 1). The treeline ecotone consists of a transitional zone of the HEE and the Canary Pine forest and ranges between 1800 and 2000 m a.s.l. The inner cliffs of the caldera are too steep for closed vegetation cover. Above the trade-wind induced cloud bank the climatic conditions are characterized by high solar radiation, extensive arid periods of up to 6 months in summer, high diurnal temperature amplitudes, and harsh winter conditions with snow and ice storms at irregular frequencies and magnitude (Garzón-Machado et al., 2013).

No mammalian herbivores exist or have ever existed naturally on the Canary Islands (Traveset et al., 2009). However, aboriginal inhabitants brought the feral goat (*C. hircus*) to the Canary Islands more than 2000 years ago as archaeological studies have shown (Zöller et al., 2003), whereas the Castilian conquerors introduced the European rabbit (*O. cuniculus*) in the 15th and 16th century to the archipelago. Today, rabbits are partially controlled by hunting (Cabrera-Rodriguez, 2006) but are still relatively abundant throughout the whole island. As recently as the 1970s, the Barbary sheep (*Ammotragus lervia*) was deliberately introduced to the Caldera de Taburienta National Park (NP) (Nogales et al., 2006) by the National Institution for Environmental Conservation (ICONA) to stimulate big game hunting as a new economical field.

Forest fires spread upslope from the fire-adapted Canary Pine forest into the HEE at irregular intervals and intensities (del Arco Aguilar et al., 2010), generally affecting the lower HEE regions more than the higher ones. Fire frequency has increased in the last decades (Climent et al., 2004; Palomares Martínez et al., 2004; Garzón-Machado et al., 2012).

The HEE of La Palma is dominated by endemic legume shrub species (Fig. 1; del Arco Aguilar et al., 2010). It has already been shown that, although climatically better adapted legume shrub species such as *Genista benehoavensis*, *Spartocytisus subpranubius,* or *Chamaecytisus proliferus* subsp. *proliferus* are potentially present, the selective grazing of introduced herbivores strongly favors the legume *Adenocarpus viscosus* subsp. *spartioides* (Irl et al., 2012). In order to halt extinction dynamics of several very rare and highly endangered endemic plant species the administration of the Caldera de Taburiente NP has established a variety of conservation measures specifically for these endangered endemics, including large-scale fenced exclosures and massive aerial seed dispersal (Palomares Martínez et al., 2004). These endangered endemic species are considered our *target species* (Table 1). All other species are *non-target species*.

SAMPLING DESIGN

A paired approach of thirty 20 × 20 m plots (15 pairs) in the presence and absence of introduced herbivores was implemented in this study to assess total species richness, seedling species richness, and establishment success of all vascular plant species of the HEE and transitional zone of La Palma (Fig. 1). The plots are situated outside of the actual Caldera de Taburiente NP but administrated by the park authorities on the outer flanks of the caldera. The first plot of each pair was a fenced exclosure in order to prohibit the access of introduced herbivores (*herbivory exclosure plot*; fence height 1.20 m), The exclosures were established by the Caldera de Taburiente NP in 2000. During the establishment of the herbivory exclosure plots, all aboveground vegetation was removed and eight target species were sown within this area. Target species were sown in equal quantities per plot but differing quantities per spe-
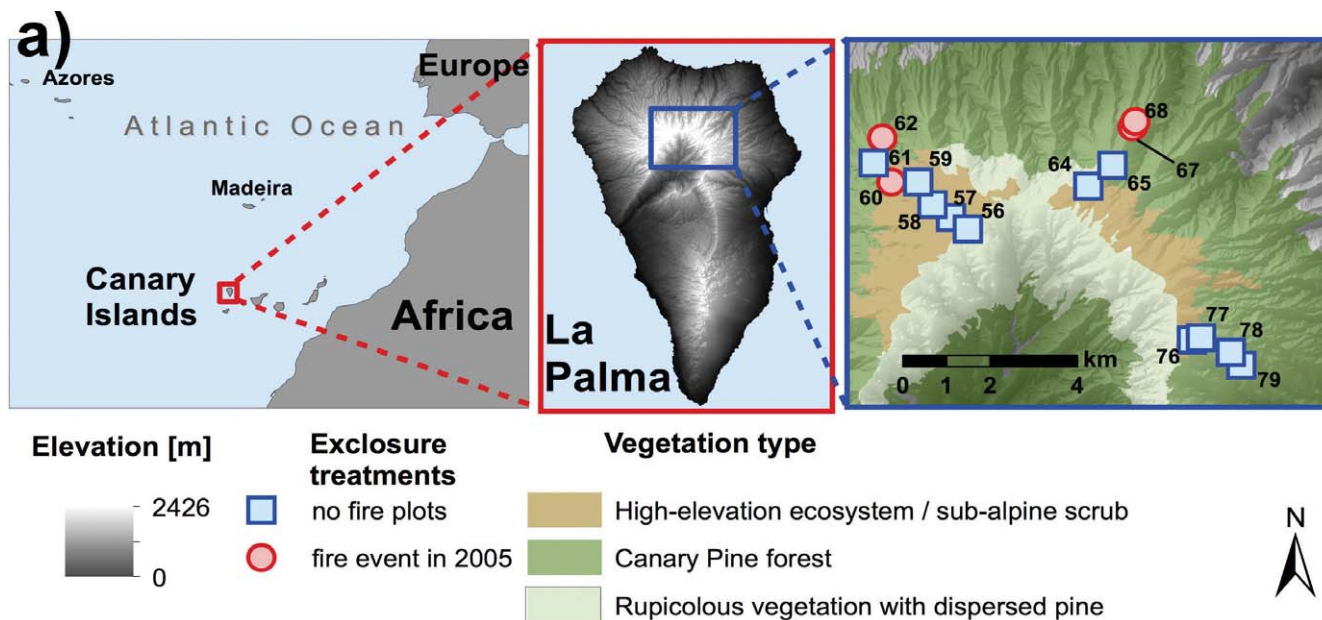
FIGURE 1. (a) Map of the Canary Islands, La Palma, and the study area. (b) A view of the rim of the Caldera de Taburiente from the highest plot (56) at 2400 m a.s.l. The study area is located on the northern part of the island (a, central panel). The symbols depict the sites of exclosures (*herbivory exclosure*) and their respective *herbivory reference* pairs: squares = unaffected by 2005 fire and circle = affected by 2005 fire (created with ArcGIS 10, ESRI Inc.). The species inside the exclosure are two of our target species, i.e. *Spartocytisus supranubius* (dark green) and *Genista benehoavensis* (grayish green). Around the telescopes a mono-dominant stand of *Adenocarpus viscosus* subsp. *spartioides* can be seen. Photo by Gesche Blume-Werry.

cies because germination success varied greatly between species (see experimental germination tests done by Palomares Martínez, 1993). See Appendix A1 for the sown seed quantity per species. We assumed that seeds of species, which were not sown, were present in the soil seed bank as these species are more or less widely distributed throughout the study area.

The reference plot of each pair was an unfenced plot permitting full access for introduced herbivores (*herbivory reference plot*). The herbivory reference plot was situated directly next to the herbivory exclosure counterpart and possessed the same size. It was established under comparable site conditions (inclination, soil conditions, fire regime; in the transitional zone, this also in-

cluded tree cover, etc.), although vegetation was not removed in the herbivory reference plots. Each herbivory reference plot is situated downslope from its herbivory exclosure pair to ensure effective and continuous seed dispersal from within the herbivory exclosure plots. Dispersal ability differs between species, but the Caldera de la Taburiente NP undertook an additional seed rain in 2006 throughout large parts of the study area due to massive aerial seed dispersal of target species. Most target species reach their reproductive age after 2 to 5 years (Palomares Martínez, 1993), indicating that natural seed dispersal from the herbivory exclosure plots to the herbivory reference plots has been possible for a maximum of 6 to 9 yr.

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TABLE 1

Total species list including the abbreviations used in the Figures 3 and 4, a classification of their endemism status (SIE = single-island endemic; AE = archipelago endemic; other status = native or non-native), growth form, and the species status as target species.

Species	Abbr.	SIE	AE	Other status	Woody species	Target species
Adenocarpus viscosus subsp. *spartioides*	A.vis	x	x		x	
Asteraceae spec. (2 species)	Ast.	—	—	—		
Bencomia exstipulata	B.exs		x		x	x
Bystropogon origanifolius	B.ori		x		x	
Chamaecytisus proliferus subsp. *proliferus*	C.pro		x		x	x
Cistus symphytifolius	C.sym		x		x	
Descurainia millefolia	D.mil		x		x	
Echium gentianoides	E.gen	x	x		x	x
Echium wildpretii subsp. *trichosiphon*	E.wil	x	x		x	x
Galium spec.	Gal.	—	—	—		
Genista benehoavensis	G.ben	x	x		x	x
Lactuca palmensis	L.pal	x	x			
Lactuca viminea	L.vim			native		
Orchis canariensis	O.can		x			
Pinus canariensis	P.can		x		x	
Pterocephalus porphyranthus	P.por	x	x		x	
Scrophularia glabrata	S.gla		x		x	
Sonchus hierrensis	S.hie		x		x	
Spartocytisus supranubius	S.sup		x		x	x
Teline stenopetala subsp. *sericea*	T.ste	x	x		x	x
Tolpis calderae	T.cal	x	x		x	
Valerianella dentata	V.den			non-native		
Viola palmensis	V.pal	x	x			x

Besides herbivory, a second treatment was present. A wildfire consumed the vegetation of several plot pairs in 2005 (*n* = 4 *herbivory exclosure* plots; *n* = 4 *herbivory reference* plots), thus enabling the assessment of the combined effects of herbivory and fire on total species richness, seedling species richness, and seedling establishment success (Fig. 1). This resulted in a two-factorial sampling design (Table 2).

The plots are distributed throughout the whole HEE reaching from 1800 to 2400 m a.s.l.. They are located at three major aspects (i.e., NW, NE, E) as shown in Figure 1. The distribution of the plots follows the main elevational and aspect gradients and aims at reaching from the transitional zone to the caldera rim. Data sampling took place in April 2011.

BIOTIC MEASUREMENTS

Total species richness was recorded within each of the thirty 20 × 20 m plots. All additional biotic measurements took place in 10 × 1 m² randomly distributed subplots within each of the thirty 20 × 20 m plots (see Table 2). In each of the ten 1 m² subplots seedling identity and abundance of all seedling individuals per species were recorded. Here, we define seedling as a plant individual that has not

Table 2

All possible combinations of the two-factorial design implemented in our sampling design. The number of plots per treatment type is indicated by "n."

	Treatment types			
	Herbivory reference	*n*	Herbivory exclosure	*n*
No fire	Herbivory reference, no fire	11	Herbivory exclosure, no fire	11
Fire	Herbivory reference, fire	4	Herbivory exclosure, fire	4

yet lignified (except for *P. canariensis,* where maximum growth height of 10 cm was chosen as threshold, and the herbaceous *Lactuca palmensis,* which was classified to be juvenile if only juvenile leaves were present). In addition, the absence of flower buds or branch ramifications was mandatory to be considered as seedling. Seedling species richness was calculated by summing up all seedling species. Seedling density (as a measure of seedling establishment success) was calculated by dividing the number of seedlings per species through the total subplot area (i.e., 10×1 m^2).

In addition, we measured species-specific browsing intensity of introduced herbivores. Rabbits were able to enter temporarily due to storm-associated fence damage (plot # 56, 59, 77, 78; Fig. 1) in four herbivory exclosure plots. Temporary rabbit presence did not significantly change total species or seedling richness when compared to the other herbivory exclosure plots (Wilcoxon signed rank test). All plant individuals (i.e., seedlings and adults) were used to identify browsing intensity. Browsing intensity was classified by estimating the percentage of total browsed plant tissue (Table 3).

STATISTICAL ANALYSIS

For comparison of total species richness (measured on the 20 × 20 m plot level) and seedling species richness (i.e., integrating all subplots of one plot) between herbivore and no herbivore plots, paired Wilcoxon signed rank tests (R-package *stats*, version 3.1.0) were used. The effect of fire treatments on total species richness and seedling species richness was tested using a mixed-effects model (package *lme4* version 1.1.6; Bates et al., 2014) with herbivory as random effect.

TABLE 3

Classification of browsing intensity used in Figure 4.

Class	Browsing intensity
0	0% to 5%
1	6% to 25%
2	26% to 50%
3	51% to 75%
4	76% to 95%
5	95% (i.e. lethal damage)

Seedling density was compared between herbivory exclosure and herbivory reference plots for all species separately by using mixed-effects models. Subplots were grouped within pairs by adding a random site factor. The analysis was repeated for all species combined with the factor "species" as an additional random effect.

Model assumptions for mixed-effects models (normality of residuals, homogeneity of variances among treatments) were tested by visual inspection and were not met in all cases. The models were thus repeated with rank transformed data. Results did not differ qualitatively. In the following, results based on the untransformed data are reported.

Browsing intensity between target species and non-target species was tested using the Mann-Whitney U-test.

Illustrations were created with SigmaPlot 7.0 (Systat Software Inc., 2001) and R version 3.1.0 (R Development Core Team, 2014). The latter was used for all statistical analyses.

Results

EFFECTS OF INTRODUCED HERBIVORES ON SEEDLING ESTABLISHMENT

A total of 24 species was identified in the study sites; 79% (*n* = 19) of species in the data set were archipelago endemics, 38% La Palma endemics (*n* = 9; Table 1). The majority of the species were woody perennials (67%).

Total species richness was significantly higher inside the *herbivory exclosure* plots (7.8 ± 5.1; mean ± standard deviation [SD]), when compared to the *herbivory reference* plots (4.9 ± 4.2; paired Wilcoxon signed rank test *p* < 0.01; Fig. 2, part a). The difference is even more distinct for seedling species richness (paired Wilcoxon signed rank test *p* = 0.002; Fig. 2, part b; herbivory exclosure*:* 5.1 ± 3.5; herbivory reference: 3.1 ± 3.4).

Plots facing the 2005 fire event were characterized by a significant increase in the total species richness and seedling species richness inside and outside the exclosures (total species richness: 12.3 ± 4.8; seedling species richness: 8.5 ± 2.9) compared to non-fire plots (total species richness: 4.2 ± 2.6; seedling species richness: 2.5 ± 2.1; mixed-effects model *p* < 0.001 in both cases, Fig. 2). However, the effect of fire is statistically not distinguishable from vegetation type (summit scrub vs. transition zone) or elevation because all burnt areas are situated in or close to the transition zone with the fire-prone pine forest at lower elevations.
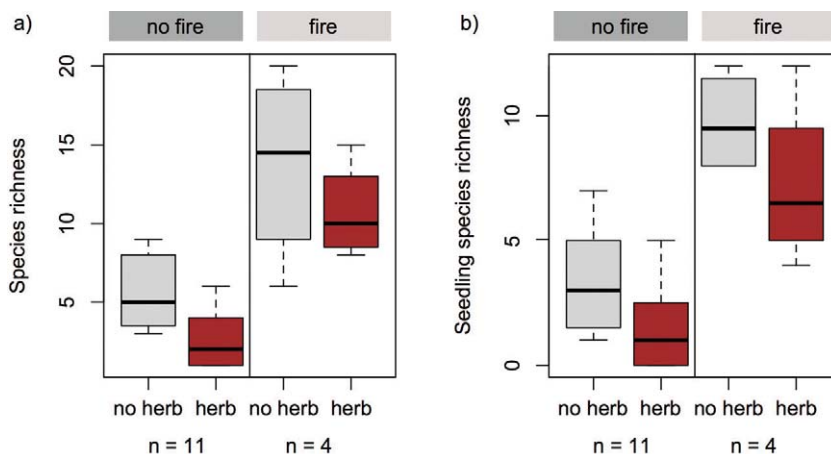

FIGURE 2. **(a) Total species richness and (b) seedling species richness varied significantly according to herbivory (*herbivory reference* = herb; *herbivory exclosure* = no herb) and fire treatment. Note that the effect of herbivory was tested in a paired *t*-test (including all plots) and the effect of fire in a mixed-effects model (herbivory as random effect, including all plots).**
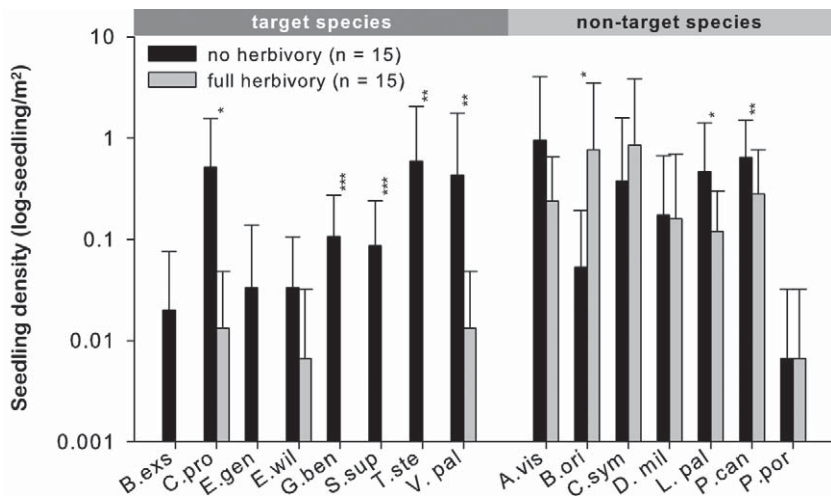
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FIGURE 3. Seedling density per target species and nontarget species in the 1 m² subplots of the herbivory exclosure (black bar; *n* = 15 plots, 150 subplots) and herbivory reference plots (gray bars; *n* = 15 plots, 150 subplots). For species abbreviations see Table 2. Significant differences (indicated as asterisks with *p*-values as *p* < 0.05 = *, *p* < 0.01 = ** and *p* < 0.001 = ***) were assessed using mixed effect models on the subplot data comparing each species individually with a random site factor.

In general, the seedling density (as a proxy for seedling establishment) was higher inside the exclosures than outside (*p* < 0.001; mixed-effects model on subplot level including all species). On average, the herbivory exclosure subplots have a higher seedling density of 0.33 seedlings per m² than the herbivory reference subplots. For the majority of target species, this negative effect of herbivory on seedling density was also detectable if analyzed individually (Fig. 3). The same trend is visible for the target species where no significant difference was detectable. However, significance is likely not reached due to very low numbers of individuals. Seedlings of five out of eight target species were exclusively found inside the herbivory exclosure plots (Fig. 3).

SELECTIVE BROWSING ON ENDANGERED ENDEMIC PLANT SPECIES

The target species *T. stenopetala* and *S. supranubius* showed highest browsing damage, followed by *C. proliferus* subsp. *proliferus* and *G. benehoavensis* (Fig. 4). Non-target species such as *B. origanifolius* and *L. palmensis* showed a high variability in browsing damage, from no visible browsing marks up to serious damage. Herbivores did not browse *A. viscosus* subsp. *spartioides*. Target species were significantly more heavily browsed than non-target ones (Mann-Whitney U-test: W = 1067.5, *p* < 0.001).

Discussion

NEGATIVE IMPACT OF INTRODUCED HERBIVORES ON SEEDLING RICHNESS

Our findings indicate that total species richness, seedling species richness as well as seedling density in insular HEE decreases significantly if introduced herbivores are present (i.e., feral goats, rabbits, or Barbary sheep). Even if plant individuals have reached a certain growth height (i.e., most species of the HEE have a shrubby growth form), rabbit browsing can still cause severe damage, although it remains mostly non-lethal (see Fig. 5). However, under severe drought conditions when other food sources are lacking, the rabbits can turn to browsing the bark of adult shrub individuals (e.g., *G. benehoavensis*, *C. proliferus* subsp. *proliferus*, *B. exstipulata*, *S. supranubius*, *T. stenopetala* subsp. *sericea*) even causing the shrub's death (Palomares Martínez et al., 2011).

Both endangered target and the other non-target species are mainly single-island or—at least—archipelago endemics, in that case mostly restricted exclusively to the two corresponding Canarian HEEs (Acebes Ginovés et al., 2010; del Arco Aguilar et al., 2010). This high degree of endemism is typical for HEEs within an archipelago (Fernández-Palacios et al., 2014). However, some of the non-target species such as *A. viscosus* subsp. *spartioides* possess a variety of alkaloids possibly functioning as herbivore deterrents (Irl et al., 2012, and references therein), while others are rich in essential oil (e.g. *B. origanifolius* [Economou and Nahrstedt, 1991] and *P. canariensis* [Dob et al., 2005]), or other compounds potentially suitable as herbivore deterrents (e.g., *C. symphytifolius* [Calabuig et al., 1981]). Therefore, these species might have a competitive advantage over the target species. However, recent studies indicate that intraspecific herbivore defense decreases with elevation due to low temperatures and less herbivore pressure (Pellissier et al., 2014).
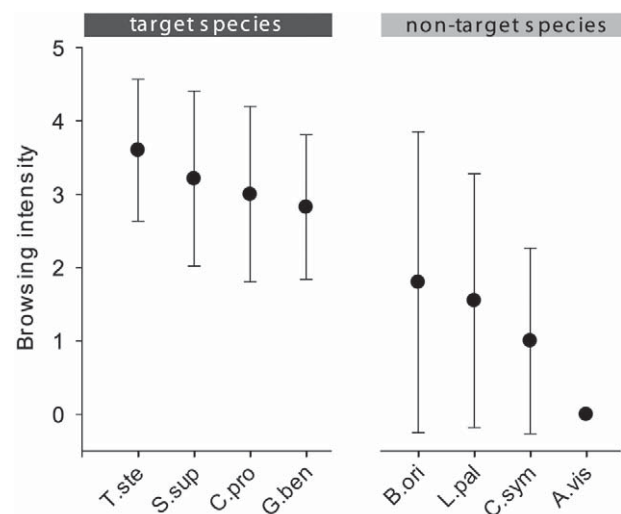

FIGURE 4. Selective grazing indicated by species-specific browsing intensity of introduced herbivores on target and nontarget species present in the herbivory exclosure plot temporarily entered by rabbits. Whiskers indicate the 0.95-confidence interval. Browsing intensity was significantly higher for target species than nontarget species (Mann-Whitney U-test: W = 1067.5, *p* < 0.001). For browsing classification, see Table 3; for abbreviations, Table 1.

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FIGURE 5. Example of selective browsing of introduced herbivores on the single-island endemic *Genista benehoavensis*. The individual at the top is protected from herbivores situated within an exclosure and displaying a vital and healthy growth (growth height about 3.5 m), while the lower individual of the same species has been heavily browsed, reacting with compensational growth (growth height about 0.5 m). Photos by (a) Severin D.H. Irl and (b) Carl Beierkuhnlein.

Similar to the results given by Garzón-Machado et al. (2010) for the Canary Pine forest of La Palma, a large share of target species was exclusively found inside the exclosures in our study area, indicating that introduced herbivores reduce seedling establishment to nearly zero. On the one hand, it cannot be fully excluded that the sampling design (i.e., total vegetation removal and sowing of target species only in the herbivory exclosure plots but not in the herbivory reference twin) might bias our results. On the other hand, aerial seed dispersal by the NP administration (Palomares Martínez et al., 2004) as well as many years of possible seed rain of target species from inside the exclosures to the herbivory reference plots in direct proximity to the exclosures (Palomares Martínez, 1993) should have ensured the possibility of target species to establish also outside of the exclosures. Obviously, this is not the case. In addition, the nonremoval of vegetation in the herbivory reference plots should actually facilitate seedling establishment during the critical period of establishment compared to the herbivory exclosure plots because the removal of the vegetation in the herbivory exclosure plots increases solar radiation and drought stress, and excludes facilitative effects common for high stress HEEs (Anthelme and Dangles, 2012), all affecting seedling establishment and survival negatively.

Extremely few to no seedlings of the target species were found in the *herbivory reference* plots, indicating the poor adaptation of island species to introduced herbivory (Bowen and Van Vuren, 1997). Interestingly, seedlings of some non-target species (e.g., *B. origanifolius*) are significantly more abundant or do not differ (*A. viscosus* subsp. *sparitoides*, *C. symphytifolius*, *Descu-*

rainia millefolia, and *Pterocephalus porphyranthus*) if introduced herbivores are present, probably profiting from chemical compounds acting as herbivore deterrents, reduced interspecific competition, or increased resource availability outside the exclosures. However, some non-target species were also negatively affected (*Lactuca palmensis* and *P. canariensis*).

Our data suggest that the environmental niches made available by reducing plant species diversity through introduced herbivores are filled by native and endemic species, and not by non-native plant species commonly associated with disturbed systems at lower elevations (Merlin and Juvik, 1992). Thus, even though this ecosystem is subject to substantial changes in plant species composition and diversity, there is no indication that non-native species abundant in lower elevations of the Canary Islands (Arévalo et al., 2005) are able to fill the available niches. Exceptions are roadside communities often identified as invasion pathways for non-native plant species (Arévalo et al., 2005; Pauchard et al., 2009) but also for endemics (Irl et al., 2014) into high elevations.

POST-FIRE EFFECTS WITH AND WITHOUT PRESENCE OF INTRODUCED HERBIVORES

Our findings indicate that the legacy of fire has an overall positive effect on total species richness and seedling richness. The negative effects of herbivory seem to be comparable to non-fire conditions. This can result from ameliorated growing conditions owing to the enhanced availability of soil nutrients and the opening of the canopy associated with post-fire conditions, the reduced habitat suitability for introduced herbivores, or population decline of herbivores during the fire (Keeley and Fotheringham, 2000). However, the positive effect on total plant species richness and seedling species richness cannot be separated from elevation or vegetation type.

Herbivore impact is still effective as only 37.5% of the target species that occur in no herbivore conditions were actually recorded in the *herbivory reference* plots and then only in very low abundances in post-fire conditions. A single shrub species (i.e., *A. viscosus* subsp. *spartioides*) creates almost mono-dominant stands if introduced herbivores are present (Irl et al., 2012). Our data suggest that the effect of introduced herbivores acts on the complete species composition of the entire HEE flora. In addition, fire probably has a positive impact on plant species richness, even though the fire regime is considered an anthropogenically altered disturbance regime mainly due to its elevated reoccurrence frequency (Garzón-Machado et al., 2012).

IMPLICATIONS FOR CONSERVATION AND RESTORATION MANAGEMENT

Under natural conditions, that is, in the absence of large mammalian herbivores, other species than *A. viscosus* subsp. *spartioides* will probably have played a more important role in the HEE of La Palma, but the reconstruction of pre-human ecosystems remains speculative. Indeed, recent discoveries suggest that a *Juniperus cedrus* woodland might have existed above the Canary Pine forest, which would have encompassed large parts of the current summit scrub (Nogales et al., 2014). Also, even small reductions in species abundance and distributions are likely to have a big impact on the function and structure of species-poor systems such as the HEE of La Palma (sensu the insurance hypothesis; Naeem and Li, 1997).

The definition of a potential natural state of vegetation and ecosystems is difficult if not impossible when environmental conditions and pressures have changed (Chiarucci et al., 2010). Garzón-Machado et al. (2011) assumed that *G. benehoavensis* might be an important species next to *A. viscosus* subsp. *spartioides* in this system, which is confirmed by our data. However, other species such as *C. proliferus* ssp. *proliferus* and *T. stenopetala* subsp. *sericea*, performed well, too. This indicates that these species should also play a vital role in future considerations of conservation and habitat restoration for hypothetical HEEs without introduced herbivores. Also *S. supranubius,* which is very common in the HEE of Tenerife (Kyncl et al., 2006), might be an important species for the highest elevations of La Palma because it seems to be optimally adapted to the harshest HEE conditions (Irl et al., 2012).

Due to their specific growth form and morphology, the La Palma endemics *E. gentianoides* and *E. wildprettii* subsp. *trichosiphon* are not able to dominate the vegetation structure. Yet, their conservation should have top priority because their global distribution is confined to the relatively small area of the HEE of La Palma (Acebes Ginovés et al., 2010; del Arco Aguilar et al., 2010). Interestingly, *A. viscosus* subsp. *spartioides* does not seem to play such a dominant role without introduced herbivores.

All in all, insular HEEs are islands within islands dominated by range-restricted endemics (Fernández-Palacios et al., 2014), and therefore these ecosystems and their species should be considered with high conservation priority. This might become especially relevant because additional pressure is likely exerted on the diversity of island HEEs and their endemic species by anthropogenic climate change, which has the potential to increase the extinction risk of these species (Greenwood and Jump, 2014).

STRONG SELECTIVE BROWSING INFLUENCES PLANT COMMUNITY DYNAMICS

In the HEE of La Palma, introduced herbivores selectively browse on the different species present. Selective browsing is characteristic for many mammalian herbivores (e.g., Rafferty and Lamont, 2007; Traveset et al., 2009; Johansson et al., 2010). In non-adapted systems, it can induce substantial alterations of plant community dynamics and structure (Ramirez et al., 2012). In the HEE of La Palma, several plant species, especially the endangered ones, are heavily browsed, while others are less damaged or even remain completely unaffected. Plant species with defense mechanisms possess a competitive advantage, because unprotected species, even though they are rare, are more likely to be browsed severely than abundant species possessing defense mechanisms (Bryant et al., 1991). In our model system on La Palma this phenomenon can be observed as well. Rare species such as *T. stenopetala* subsp. *sericea*, *S. supranubius*, *C. proliferus* subsp. *proliferus,* or *G. benehoavensis* are preferred by introduced herbivores, while common and widespread species are significantly less damaged. Current rarity, however, reflects the long-lasting legacy of introduced herbivore pressure.

We suppose that the vegetation we see today in the HEE of La Palma strongly deviates from the former "natural" vegetation. As HEEs are very isolated, no introduced or invasive plant species has entered these communities. However, shifting dominance patterns and a local decrease of diversity have likely caused impoverished and almost mono-dominant stands of plants that can cope with current herbivore pressure. Today, many species that can be expected to have been abundant under "natural" conditions (i.e., without mammal herbivory) only occur in refugial locations (e.g., on cliffs or rocky outcrops; nowadays also in large exclosures established for conservation purposes by the

Caldera de Taburiente NP) and are highly threatened to become extinct (Palomares Martínez et al., 2004).

Very likely the present ecosystems have been altered by centuries of goat herding and cyclic burning. Such kinds of intense past impacts and land use history can have a long-lasting legacy in local plant species occurrence even after its abolishment (Heubes et al., 2011). In addition, the presence of introduced herbivores has been shown to prevent the recuperation of natural vegetation (Merlin and Juvik, 1992).

Conclusion

The results presented from an 11-yr exclosure experiment offer the unique opportunity to identify the long-term impact of introduced mammalian herbivores on an insular HEE in combination with reoccurring fire events. Presumably, the presence of introduced herbivores has substantially altered the species richness and vegetation composition, leading to a strong degradation of this system. This resulted, among others, in a massive coordinated conservation program initiated by the Caldera de Taburiente NP administration to protect the various endangered single-island or archipelago endemics of this system (Palomares Martínez et al., 2004).

Now, the long-term goal should be to preserve the endangered species, create habitats and "safe sites" for these species to expand their current ranges, and, if possible, restore the HEE to a natural state. A necessary step in this direction would be to monitor and strictly control the population of all major herbivores (especially feral goats, rabbits, and Barbary sheep) as well as create awareness among the population about the damages caused by human-induced fires. However, no matter how successful total eradication programs have previously been in enabling the full recovery of natural island vegetation (e.g., Caujapé-Castells et al., 2010, and references therein), it seems unrealistic to achieve this conservation goal on such a large and inhabited island as La Palma that relies heavily on rural and traditional agricultural practices. Nevertheless, total eradication of introduced herbivores from the whole island of La Palma should be the long-term goal from a conservation perspective to sustainably protect the unique native endemic flora and enable its survival and reestablishment. In the meantime, however, more and larger fenced exclosures might be a promising conservation method to preserve the most endangered species and create patches of restored natural vegetation.

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APPENDIX

TABLE A1

List of sown seed quantity for each of the eight target species.

Species	Sown seed quantity per species
Bencomia exstipulata	30.000
Chamaecytisus proliferus subsp. *proliferus*	2.000
Echium gentianoides	3.000
Echium wildpretii subsp. *trichosiphon*	3.000
Genista benehoavensis	3.000
Spartocytisus supranubius	3.000
Teline stenopetala subsp. *sericea*	2.000
Viola palmensis	3.000