

Climate warming and introduced herbivores disrupt alpine plant community of an oceanic island (Tenerife, Canary Islands)

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Abstract Invasive alien species and climate change are two of the main current threats to conservation of biodiversity worldwide. Their effects have been extensively studied individually, but we know less about their combined effect. This study analyzes the population changes in the plant community of the high mountain legume shrub habitat of Tenerife over 10 years (between 2009 and 2018), using alien herbivore exclusion plots distributed over two sectors with different patterns of climate. Our outcomes show contrasting effects of herbivory and climate in plant communities, with significant shifts in community composition. The dominant species, Teide broom (*Spartocytisus supranubius*), is negatively affected by

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Área de Botánica, Departamento de Ciencias Agroforestales, EU de Ingenierías Agrarias, iuFOR-Universidad de Valladolid, Campus Duques de Soria, 42004 Soria, Spain both climate and alien herbivores, leading to a regression of its abundance. In contrast, a formerly rare species, *Pterocephalus lasiospermus*, is benefiting from warmer temperatures and from herbivore presence owing to its low palatability. Simultaneously, some thermal native species from the neighboring pine forest are invading the alpine ecosystem. We conclude that the alpine habitat is changing very quickly and differently according to whether it is in warmer or colder sectors of the summit of Tenerife. This work reveals the need to simultaneously consider multiple drivers to understand the response of mountain ecosystems to global change.

Keywords Climate change · Ecosystem disturbance · Herbivory · High mountain · Vegetation dynamic

Introduction

The effects of climate change can be observed worldwide, and we know today that it will act as a major cause of extinctions in the near future (Thomas et al. 2004). Climate change is not spatially homogenous, since arctic, alpine and boreal ecosystems are expected to suffer stronger impacts (Thuiller 2007). In alpine habitats the warming signal is amplified with elevation; high mountain environments thus undergo more rapid temperature changes than lowlands (Pepin et al. 2015). This may be particularly dramatic for mountains on oceanic islands, with limited capacity for species movement (Martín et al. 2012; Halloy and Mark 2003; Diaz et al. 2014).

Vegetation responds to climate fluctuations at scales that range from years to decades or centuries (Nogué et al. 2013; García-Cervigón et al. 2019). For example, Brown et al. (1997) described the recent reorganization of an arid ecosystem in response to climate change, with increases in woody shrub density, and shifts in faunal composition. Plants distributions move in response to global warming, shifting their latitudinal and altitudinal ranges (Lenoir et al. 2008). Walther et al. (2005) reported an average upward shift of plants of 27.8 \pm 14.6 m/decade after a century of monitoring the vegetation of the Alps. This can lead to notable problems of habitat loss in summit taxa with "nowhere to go", which explains why mountain species are among the most threatened in temperate and tropical regions (Colwell et al. 2008; Pauli et al. 2012). Higher temperatures may amplify drought events, leading to increased aridization and significant losses of "available habitat" for many species (Jentsch et al. 2007).

Climate change acts synergistically with other global change drivers (Mainka and Howard 2010). On oceanic islands, invasive species and climate change are currently the main drivers of plant species loss and transformation of habitats (Caujapé-Castells et al. 2010). However, there is little research to date on how these two drivers affect plant communities as synergistic feedbacks (Brook 2008). Most studies have focused on the influence of introduced herbivores on the treeline (Cairns and Moen 2004). However, few authors have addressed changes in the assembly of plant communities due to simultaneous pressure from warming and herbivory (McEachern et al. 2009). Moreover, climate warming is driving an upward expansion of both native and invasive species. This may lead to novel species combinations, including, new interactions of alien fauna with plants living at higher altitudes. Underlying the scarcity of research in this line is the complexity of attributing the decline of a native species to more than one driver as the number of potential drivers and their interactive effects increases (Didham et al. 2007).

Understanding the impact of global change drivers on oceanic island mountains is a priority, since these environments combine small population ranges with a high degree of endemism (Fernandez-Palacios et al. 2014, Steinbauer et al 2016). These problems are acute in the Canary Islands, where warming in high mountains is occurring rapidly (0.14 \pm 0.07 °C/ decade on Tenerife summits), twice as fast as the rest of the island (Martín et al. 2012). This pattern has been reported for other temperate (Halloy and Mark 2003) and tropical-subtropical islands (Diaz et al. 2014; McKenzie et al. 2019). Invasive plant species are scarce in the Tenerife high mountain zone, due to the severe environmental constraints (Arévalo et al 2005). First settlers introduced herbivorous mammals 2000 years ago (Nogales et al. 2006), when the aboriginal people herded goats in the highest parts of the island during summer (Machado and Galván 2012). European rabbit (Oryctolagus cuniculus) was introduced later during the fifteenth century by Castilian settlers. Goat grazing was banned in the 1950s after the establishment of the Teide National Park, enabling vegetation recovery (Kyncl et al. 2006; Rodríguez-Delgado and Elena-Roselló 2006). In contrast, the rabbit population was at low levels in 1950 but has increased in recent decades (Martín et al. 2015).

The impact of introduced herbivores on the native flora of the Tenerife high mountain zone has been analyzed in detail (Cubas et al. 2018, 2019). However, the joint action of herbivory and climate remains largely unexplored. It is expected that climate instability alone can produce marked imbalances in the plant community, damaging some species and benefiting others. Nevertheless, we do not know if herbivory could exacerbate the consequences of climate variations or if, on the contrary, it could contribute to mitigating them. It could also be the case that the two drivers do not interact with each other. The purpose of this paper is to answer these questions within the framework of the ecosystems monitoring program of the Teide National Park. Our specific aims were to evaluate: (1) the changes over time in the species abundance and community structure under herbivory pressure, (2) the changes in the abundance of vascular plants and their community structures under climatic pressure, and (3) the combined impact of herbivory and climatic pattern on different sectors of this high mountain ecosystem.

Materials and methods

Study site

The study area is a shrub habitat in the high mountain of Tenerife (Canary Islands), dominated by Teide broom (Spartocytisus supranubius (L. f.) Christ ex G. Kunkel), with numerous endemic species such as Adenocarpus viscosus (Willd.) Webb & Berthel., Andryala pinnatifida Aiton, Argyranthemum teneriffae Humphries, Descurainia bourgeauana (E. Fourn.) O.E. Schulz, Echium auberianum Webb & Berthel., Echium wildpretii Pearson ex Hook. f., Nepeta teydea Webb & Berthel., Pterocephalus lasiospermus Link ex Buch, and Scrophularia glabrata Aiton. This habitat is within the Teide National Park boundaries, above 2000 m altitude (del Arco Aguilar and Rodríguez Delgado 2018). The national park includes the huge caldera of Las Cañadas and the stratovolcano Teide, which rises from its northern rim up to 3715 m elevation. Our study area was limited to the surrounding terrain below 2600 m a.s.l. (Fig. 1).

The shrub vegetation habitat is distributed from the base of the volcano at 2000 m a.s.l., up to 3100 m a.s.l on its lower slopes, on poorly developed soils. This vegetation is surrounded by an endemic pine forest, whose treeline reaches just to the outer edge of the caldera at 2400 m a.s.l., at a higher elevation than the lower limit of the summit shrub. This peculiarity has been explained by the thermal inversion between the interior of the caldera (cooler) and the higher parts of its surrounding walls (Höllermann 1978; Wieser et al. 2016).

This shrub vegetation ecosystem hosts a great number of species adapted to living under extreme conditions (Perera-Castro et al. 2017). Temperature shows high annual and daily variation, in winter months often dropping below 0 °C, while in summer easily exceeding 25 °C. Just above soil level, temperature may range from -10 °C on winter nights to 50 °C in summer daytime (Höllermann 1978). The radiation is very intense (sunshine > 3700 h/year), the humidity is very low (usually less than 30%), and dominant winds are dry. Climate is typically Mediterranean, yearly average rainfall is 350 mm, mostly occurring in winter, when some snow is also possible, and almost null in summer.

There are two meteorological stations managed by the Spanish State Meteorological Agency located at contrasting sites in the study area. These have facilitated the detection of a thermal gradient between the colder NE sector (Izaña; C306E) and the warmer SW (Parador; G406G) (Fig. 2). These two meteorological stations have a very different geographical setting, being Izaña open to the northern winds and Parador sheltered among Teide and Guajara Mountain. The average temperature between 1990 and 2018 was 12.1 \pm 0.3 °C in the SW and 10.3 \pm 0.2 °C in the NE. The rainfall was similar in both sectors, with average values of 382 ± 110 mm in the SW and 345 ± 59 mm in the NE. Rainfall variability was high in the SW, especially in the wet months of February, March and December. The number of dry years, with annual rainfall less than 150 mm, was also higher in the SW (24.1%) than in the NE (10.3%). The average evapotranspiration between 1990 and 2018 was 650 mm/year in the SW and 605 mm/year in the NE.

Sampling methodology

A total of 16 permanent sampling stations were established trying to cover the variety of natural habitats in the area along a gradient from 2000 to 2600 m a.s.l. (Fig. 1). Four of them in 2004 and another twelve in 2009. Each sampling station consisted of an exclusion plot 400 m² in area, surrounded by a 1.50 m high fence reaching 50 cm below ground to prevent the entry of rabbits, and a nearby unfenced control plot.

Number of plants excluding seedlings (abundance), was counted yearly between 2009 and 2018 at the end of the growing season (June-July) within a 10×10 m² area in the 32 plots. In the fenced plots the sampling area was located in the central zone to avoid a potential edge effect caused by the fence. Each plant was classified as juvenile (plants that have survived at least one summer but never flowered) or adult (reproductive individual with the appropriate size to flower). Species were also classified according to their life form (Raunkiaer 1934).

Statistical analysis

Climatic classification

Sampling stations were classified according to 39 climatic variables: monthly precipitation (12), maximum monthly temperature (12) and minimum



Fig. 1 Sampling stations in relation to the limits of the Teide National Park (below), and clustered according to their respective climatic parameters between 1980 and 2019 (above)

monthly temperature (12), and their respective annual averages (3), obtained from the data of the "Climaimpacto" project funded by the Canary Islands Government (Santana and Martín 2013, data available at www.climaimpacto.eu). Prior to data analyses, we classified the plots using a cluster analysis based on similarity dendrograms (Euclidean distance) obtained dist with the functions and hclust. with method = "complete", of R-package Stat, that distinguished two groups of eight sampling stations, coinciding with the colder NE and warmer SW sectors of the study area (Fig. 1). The evapotranspiration was analyzed with the R-package Climclass (Eccel et al. 2014).

Changes in species abundance

Abundance trends were calculated for each species individually and for the different life forms, using the non-parametric Spearman correlation between abundance and years (time). The trends were calculated for the whole set of 16 sampling stations, and separately for the stations in each sector.

As the abundance trends of all species or groups of species within each climatic sector were not always statistically significant, we developed an analysis to at least determine possible differences in trends in the warmer sector (SW) with respect to the colder one (NE). For this purpose, we ran a linear mixed effects model with the trends of each sector (NE vs. SW) using the Lme4 R-package (Bates et al. 2014) and considering time (year) and climatic sectors as fixed factors, and plots as a random factor. We assessed the statistical significance of differences between H₀ (taxa ~ sector) and H₁ (taxa ~ sector + year) using a likelihood ratio test with anova function to get Chi square and P value (Winter 2013). Calculations were made considering independently the results of the sampling in the control and exclusion plots. Control plots provided information on the changes under the Fig. 2 Climate characteristics in the NE (blue) and SW (red) sectors. a Temperature and average precipitation between 1990 and 2018, b temperature evolution and trends in NE and SW sectors. Dashed lines represent the linear regression of the period between 1980 and 2018, and dotted lines the sampling period between 2009 and 2018. The shaded area shows the thermal tolerance range of S. supranubius



joint pressure of herbivory and climate, while exclosures only considered the effect of climate.

Diversity and evenness

Diversity was calculated with the Shannon index and its modification to produce a measure of "effective number of species" ($^{1}D = Hill$ index or Shannon effective) in the R-package *Vegan* (Oksanen 2011). To get the confidence interval (variance), the speciesbased group of samples in each sector (NE, SW) was converted into individual-based group of samples before randomization (bootstrapping) with *Boot* R-package (Canty and Ripley 2012). To compare samples between consecutive years, we used random tables in a Monte Carlo process with the command r2dtable() of the *Vegan* R-package.

The Alpha Gambin index (α) provided information about the evenness of community (Ugland et al. 2007). This index summarizes the shape of the species abundance distribution (SAD) in a single number. A community is perfectly even if every species is present in equal proportions, and uneven if one species dominates the abundance distribution. Evenness has been shown to be a key factor in preserving the functional stability of ecosystems (Wilsey and Potvin 2000), since uneven communities are often more susceptible to invasion and less resilient to stresses and disturbances (Wittebolle et al. 2009, Daly et al. 2018). Data were rarefied with 1000 iterations with the R-package *Gambin* (Borregaard et al. 2013).

Results

Climatic trends in the two sectors

Mean annual temperature in the warmer SW sector during 1990–2008 ranged between 10.7 and 13.8 °C, while in the colder NE sector it ranged between 9.0 and 11.6 °C (Fig. 2). Warming trends in this period were different in the two sectors, increasing rapidly in the SW (0.4 °C/decade, $r_s = 0.58$, P < 0.001) but with no significant trend in the NE ($r_s = 0.21$, P = 0.279). If we focus only on the temperature changes in the last 10 years (2009–2018) during which we conducted the study, no significant trend was found in the SW ($r_s = 0.17$, P = 0.638) and it decreased with a marginal statistical significance in the NE ($r_{s.}$ = -0.612, P = 0.066). Precipitation showed no statistically significant trend between 1990 and 2018, probably due to its high variability. Finally, evapotranspiration remained stable in the colder NE but not in the warmer SW, where it grew at a rate of 0.9 ± 0.4 mm/year ($R_s 0.54$, P = 0.003).

Community structure

The *effective numbers of species* were higher in the exclusion plots (${}^{1}D = 8.1 \pm 0.6$) than in control plots (${}^{1}D = 6.0 \pm 0.5$) (Table 1). In exclusion plots, the effective numbers of species were higher in the colder NE sector (${}^{1}D = 6.7 \pm 0.4$) than in the SW (${}^{1}D = 5.5 \pm 0.5$), but the opposite occurred for control plots, where they were higher in the warmer SW sector (SW ${}^{1}D = 5.8 \pm 0.4$; NE ${}^{1}D = 3.5 \pm 0.7$). Effective numbers of species in the exclusion plots did not show a significant trend of change in either of the two sectors, whereas a decreasing trend was observed in the NE control plots ($R_{s} - 0.78$, P = 0.01).

Alpha Gambin index was significantly higher (t = 2.26, P < 0.05) in the exclusion plots $(\alpha = 7.04 \pm 1.4)$ than controls $(\alpha = 4.94 \pm 1.0)$. Exclusion plots showed higher values in the NE $(\alpha = 8.1 \pm 1.5)$ than SW $(\alpha = 4.8 \pm 0.9)$, with the reverse seen in control plots (SW $\alpha = 5.2 \pm 0.6$; NE $\alpha = 4.1 \pm 1.5$) (Table 1). Alpha Gambin decreased over time in both treatments (exclusion: $R_{\rm s} - 0.73$, P = 0.021; control: $R_{\rm s} - 0.66$, P = 0.044), but the analysis according to sectors only showed a significant decreasing trend in the colder NE control plots ($R_{\rm s} - 0.65$, P = 0.049). No statistical significance was found in the trends for NE control, SW control, or SW exclusion plots.

Trends in species abundances

A total of 27 species were reported in the sampling plots: 20 in the NE sector and 23 in the SW. The mean number of sampling stations where each species occurred in at least 1 year of the study period was 4.4 ± 1.5 . Nine species were present in six or more sampling stations, and another nine in only one or two (Table 2). *P. lasiospermus* was the most common species, in occurrence and abundance, followed by *S. supranubius* and *Tolpis webbi* (Table 2).

The number of species did not change in control plots but increased in the exclusion plots through the study period (R_s 0.65, P = 0.044). A similar pattern was observed when the number of individuals was considered: no change in control plots and increases in exclusion plots (R_s 0.67, P = 0.039). The increase was significant in the juvenile population, both in the NE (R_s 0.83, P = 0.006) and the SW (R_s 0.77, P = 0.014). The adult population did not show any significant trend in any two sectors taken together, but showed a statistically marginal increase in exclusion plots (R_s 0.61, P = 0.066) (Table 3).

Overall, phanerophytes increased only in exclusion plots (R_s 0.75, P < 0.018), basically due to the increase in NE exclosures (R_s 0.92, P < 0.001), but decreased in NE control plots ($R_s - 0.79$, P = 0.007). Phanerophytes were dominated by two legume species: *A. viscosus* and *S. supranubius*. *A. viscosus* was only sampled in the SW, where its populations decreased in the exclosures ($R_s - 0.73$, P = 0.018) and without statistical significance in control plots ($R_s - 0.56$, P = 0.092). This pattern was due to the progressive disappearance of adult individuals

Table 1 Trends in offective number of encoires			Hill index (¹ D)		Gambin index (a)	
[Hill index (1D)] and Gambin index			Average value	Trend 2009–2018	Average value	Trend 2009–2018
	Exclusion	NE + SW	8.1 ± 0.6	n.s	7.0 ± 1.4	- 0.73
		NE	6.7 ± 0.4	n.s	$8,1 \pm 1.5$	n.s
Rho significance: <i>n.s.</i> not		SW	5.5 ± 0.5	n.s	4.8 ± 1.0	n.s
significant	Control	NE + SW	6.0 ± 0.5	- 0.61	4.9 ± 1.0	- 0.66
***a < 0.0001;		NE	3.5 ± 0.7	- 0.78*	4.1 ± 1.5	- 0.65
** $\alpha < 0.001; *\alpha < 0.01;$ $\alpha < 0.1$		SW	5.8 ± 0.4	n.s	52 ± 0.6	n.s

Table 2Species sampled,indicating number of plotswith at least 1 year ofpresence, averageabundance in each plot, andbiotype

Species	North		South		Biotypes	
	Plots	Average abundance	Plots	Average abundance	(life forms)	
Adenocarpus viscosus	_	-	6	10.9	Phanerophyte	
Andryala pinnatifida	_	_	1	0.1	Chamaephyte	
Arenaria leptoclados	2	7.8	1	54.3	Therophyte	
Argyranthemum teneriffae	3	14.6	3	8,7	Chamaephyte	
Arrhenatherum calderae	3	8.8	7	76.0	Hemicryptophyte	
Bromus tectorum	2	12.2	4	37.4	Therophyte	
Carlina xeranthemoides	2	0.3	3	35.4	Chamaephyte	
Chamaecytisus proliferus	1	0.3	1	1.8	Phanerophyte	
Cistus symphytifolius	_	_	1	5.2	Chamaephyte	
Dactylis metlesicsii	1	0.5	_	-	Hemicryptophyte	
Descurainia bourgeauana	5	25.7	3	18.5	Chamaephyte	
Descurainia gonzalezii	_	_	1	7.9	Chamaephyte	
Echium auberianum	2	3.3	1	2.5	Hemicryptophyte	
Echium wildpretii	-	_	1	0.5	Chamaephyte	
Erysimum scoparium	3	4.4	3	3.5	Chamaephyte	
Micromeria lachnophylla	1	70.0	2	0.9	Chamaephyte	
Nepeta teydea	_	_	1	0.1	Chamaephyte	
Pinus canariensis	_	_	2	2.1	Phanerophyte	
Polycarpaea tenuis	1	2.3	1	0.1	Chamaephyte	
Pterocephalus lasiospermus	7	89.8	8	69.2	Chamaephyte	
Schrophularia glabrata	2	0.2	2	3.7	Chamaephyte	
Silene nocteolens	1	90.1	-	-	Geophyte	
Spartocytisus supranubius	5	12.8	7	6.0	Phanerophyte	
Stemmacantha cynaroides	3	23.0	_	-	Geophyte	
Tolpis webbii	4	2.2	8	46.1	Hemicryptophyte	
Vulpia myurus	1	0.6	_	_	Therophyte	
Walhenbergia lobelioides	1	1.6	2	9.5	Hemicryptophyte	

(exclusion: $R_s - 0.93$, P < 0.001; control: $R_s - 0.69$, P = 0.028). S. supranubius showed a complex response to treatments (Fig. 3). Number of individuals showed a strong increase in NE exclosure plots (R_s 0.92, P < 0.001) but decreased in the control plots of both sectors (NE $R_s - 0.76$, P = 0.012; SW $R_s - 0.75$, P = 0.013). Juveniles increased in exclosures in both sectors (NE R_s 0.73, P = 0.021; SE R_s 0.73, P = 0.016), but recruits were absent in the control plots. Simultaneously, there was a decreasing trend of S. supranubius adults ($R_s - 0.82$, P = 0.004). The time elapsed between installing the fence and the last sampling did not allow recruits to become adults, explaining the decrease in adults in both control (NE

 $R_{\rm s} - 0.82, P = 0.004$; SW $R_{\rm s} - 0.73, P = 0.016$) and SW exclusion plots ($R_{\rm s} - 0.76, P = 0.01$) (Table 3).

Total chamaephyte population increased both in exclusions ($R_s 0.67$, P = 0.039) and controls ($R_s 0.74$, P = 0.014 and was also significant for the exclosures in each sector individually (NE $R_s 0.67$, P = 0.039; SW $R_s 0.73$, P = 0.021). The chamaephyte P. *lasiospermus* had a significant rising in their populations (Fig. 3), increasing in exclosures ($R_s 0.70$, P = 0.031) and control plots ($R_s 0.66$, P = 0.044) in the NE sector. In the SW sector this pattern was not significant in either exclusion ($R_s 0.56$, P = 0.096) or control plots ($R_s 0.60$, P = 0.066). Other chamaephyte species increased their populations: *Carlina xeranthemoides* L. f. (exclusion: $R_s 0.68$, P = 0.035;

Table 3 Temporal pattern of species abundance between 2009 and 2018 in exclusion and control plots

	Control plots (<i>r</i> _s)			Exclusion plot	(r_s)		
	Whole	NE	SW	whole	NE	SW	
Total individuals	n.s	n.s	n.s	0.67*	0.77*	0.59	
Abundance of juveniles	0.75*	0.56	0.77*	0.82**	0.83**	0.77*	
Abundance of adults	n.s	n.s	n.s	0.61	n.s	0.59	
Chamaephytes	0.74*	0.57	0.62	0.67*	0.67*	0.73*	
Abundance of juveniles	0.73*	0.66*	0.78**	0.78*	0.84**	0.73*	
Abundance of adults	n.s	n.s	n.s	n.s	n.s	n.s	
Phanerophytes	n.s	- 0.79**	n.s	0.75*	0.92***	n.s	
Abundance of juveniles	n.s	n.s	n.s	0.72*	0.73*	n.s	
Abundance of adults	- 0.82**	- 0.82**	- 0.75*	n.s	n.s	- 0.96**	
Hemicryptophytes	n.s	n.s	n.s	0.67	0.77**	0.64	
Geophytes	n.s	_	_	n.s	_	n.s	
Therophytes	n.s	n.s	n.s	n.s	n.s	n.s	
Pterocephalus lasiospermus	0.61	0.66*	0.60.	0.64*	0.70*	0.56	
Abundance of juveniles	0.73*	0.66*	0.71*	0.75*	0.75*	0.72*	
Abundance of adults	n.s	0.73*	n.s	n.s	0,64	n.s	
Spartocytisus supranubius	- 0.77**	- 0.76*	- 0.75*	0.95***	0.92***	n.s	
Abundance of juveniles	0.59.	0.7*	n.s	0.73*	0.73*	0.73*	
Abundance of adults	- 0.82**	- 0.82**	- 0.73*	n.s	n.s	- 0.76**	
Descurainia bourgeauana	0.58.	n.s	n.s	n.s	n.s	n.s	
Abundance of juveniles	0.75*	0.71*	n.s	n.s	n.s	n.s	
Abundance of adults	n.s	n.s	- 0.62*	n.s	n.s	n.s	
Descurainia gonzalezii	0.60.	_	0.60	n.s	_	n.s	
Abundance of juveniles	n.s	_	n.s	n.s	_	n.s	
Abundance of adults	0.60	_	0.60	n.s	_	n.s	
Arrhenatherum calderae	n.s	n.s	n.s	n.s	0.69*	n.s	
Micromeria lachnophylla	n.s	n.s	n.s	0.76*	0.78**	n.s	
Adenocarpus viscosus	- 0.56	_	- 0.56	- 0.73*	_	- 0.73*	
Abundance of juveniles	n.s	_	n.s	n.s	_	n.s	
Abundance of adults	- 0.69*	_	- 0.69*	- 0.93***	_	- 0.93**	
Carlina xeranthemoides	0.76*	_	0.76*	0.68*	_	0.68*	
Abundance of juveniles	0.68*	_	0.68*	0.66*	_	0.66*	
Abundance of adults	0.59.	_	0.59	0.66*	_	0.66*	
Ervsimum scoparium	ns	ns	n s	n s	ns	0.78**	
Pinus canariensis	0.66*	_	0.66*	0.70*	_	0.70*	
Echium auberianum	n s	ns	_	0.87***	0 87***	_	
Stemmacantha cynaroides	n s	n s	_	0.80**	0.80**	_	
Abundance of juveniles	0.55	0.55	_	0.76*	0.00		
Abundance of adults	0.55 n s	0.55 n s	ne	0.70 n.s	n.s	ne	
Arovranthemum teneriffae	0.75*	0.66*	0.75*	0.75*	0.75*	ns	
Abundance of inveniles	0.75	0.85*	0.75	0.75 n c	0.75 n c	n.o	
Abundance of adults	0.55	0.57	0.72	0.60	0.77*	n.s	
Tolnis webbii	0.00 ⁻	0.57	0.70 ²	0.60	0.77°	0.62	
Seronhularia alabrata	11.5 n.c	0.01	11.5 n.c	- 0.56	n.s	_ 0.72*	
	11.5	11.5	11.5	- 0.50	11.5	-0.72^{*}	

Table 3 continued

	Control plots (<i>r</i> _s)			Exclusion p	Exclusion plots (r_s)		
	Whole	NE	SW	whole	NE	SW	
Bromus tectorum	n.s	n.s	n.s	n.s	0.68*	n.s	

Signification of Rho/deviance: *n.s.* not significant

*** $\alpha = 0.000$; ** $\alpha = 0.001$; ** $\alpha = 0.01$; $\alpha = 0.1$



Fig. 3 Temporal evolution of the populations of *Spartocytisus supranubius* (squares) and *Pterocephalus lasiospermus* (circles) in the exclusion (a) and control (b) plots, in the NE (blue) and SW (red) sectors. The abundance axis is represented in logarithmic scale

control: $R_s 0.76$, P = 0.016), Argyranthemum teneriffae (exclusion: $R_s 0.75$, P = 0.018; control: $R_s 0.75$, P = 0.012) and SW population of Erysimum scoparium (Brouss. ex Willd.) Wettst. in exclusion plots (R_s 0.78, P = 0.008). The juvenile population of Descurainia bourgeauana increased in the NE controls (R_s 0.71, P = 0.022), while in the SW it remained stable. In contrast, the adult population decreased with marginal statistical significance in the SW controls ($R_s 0.62$, P = 0.056) and was stable in the NE. Remarkably, its congeneric Descurainia gonzalezii Svent., only sampled in one SW location, showed a marginal statistical significant increase in the adult population ($R_s 0.60$, P = 0.066) (Table 3).

Finally, hemicryptophyte population increased in NE exclosures (R_s 0.77, P = 0.009) (Table 3). Three hemicryptophytes showed a positive trend in abundance. Two of them increased their populations in NE exclusions: Arrhenatherum calderae A. Hansen (R_s 0.69, P = 0.028) and Echium auberianum (R_s 0.87, P < 0.001), and the third, Tolpis webbii Sch. Bip. ex Webb & Berthel., showed a positive trend marginally significant in SW exclosures (R_s 0.62, P = 0.06).

Comparative trends in abundances between climatic sectors

Linear mixed models revealed that comparative trend abundances between sectors in control plots showed significant differences in four cases (Table 4): *P. lasiospermus* (χ^2 20.99, *P* < 0.001), *A. teneriffae* (χ^2 16.08, *P* < 0.001), *S. supranubius* adult individuals (χ^2 5.39, *P* = 0.02), and *D. bourgeauana* juveniles (χ^2 10.53, *P* = 0.001). The comparative trend in abundances between sectors in exclusion plots showed significant differences in six cases: *P. lasiospermus* (χ^2 30.29, *P* < 0.001), *S. supranubius* (χ^2 20.21, *P* < 0.001), *A. calderae* (χ^2 7.20, *P* = 0.007), *E. scoparium* (χ^2 7.48, *P* = 0.006), and *A. teneriffae* (χ^2 9.42, *P* < 0.002) (Table 4).

Discussion

Our monitoring revealed sharp changes in the community composition of Teide National Park during the 2009–2018 period. The exclosure treatment increased community richness, favoring the abundance of key species such as *S. supranubius*. However, a shift also occurred in community composition unrelated to exclosure treatment, indicating a potential climate effect. In fact, species abundances and community response differed between both sectors of the National Park indicating future divergence in community composition. Climate and herbivores have been driving changes in community diversity, altering the abundances of some plant species. The effective number of species and evenness tended to decrease over time in the colder NE sector, while in the warmer SW, both parameters remained stable. Populations also experienced differential changes between sectors, when their populations evolved asymmetrically between NE and SW, sometimes even in opposite directions, depending on local climate conditions. Our mixed linear model also showed asymmetry in the changes over time between sectors, suggesting that differences between NE and SW could be much more noticeable in a near future. For example, A. teneriffae increased in the NE but not in the SW control plots. The respective abundances in the two sectors of T. webbii increased in exclusion plots of both sectors, but at different rates. E. scoparium and Micromeria lachnophylla Webb & Berthel. only showed positive trends in one of the two sectors. Finally, changes over time between sectors of the two most abundant species, P. lasiospermum and S. supranubius, were more evident. These patterns show that the climatic differences between the two sectors affect the whole

Table 4 Difference in time evolution of abundances		χ^2 control plots	χ^2 exclusion plots
between sectors (NE vs SW)	Pterocephalus lasiospermus	20.99***	30.29***
	Juveniles	27.61***	34.23***
	Adults	10.29**	11.05***
	Spartocytisus supranubius	n.s	20.21***
	Juveniles	3.15.	22.45***
	Adults	5.39*	n.s
	Arrhenatherum calderae	_	7.20**
	Juveniles	_	_
	Adults	_	5.46*
	Descurainia bourgeauana	n.s	n.s
	Juveniles	10.53**	n.s
	Adults	n.s	n.s
	Micromeria lachnophylla	n.s	4.40*
	Erysimum scoparium	n.s	7.48**
Signification of deviance: n.s. not significant *** $\alpha < 0.0001;$	Argyranthemum teneriffae	16.08***	9.42**
	Juveniles	16.29***	4.31*
	Adults	11.86***	6.28*
** $\alpha < 0.001$; ** $\alpha < 0.01$; · $\alpha < 0.1$	Tolpis webbii	n.s	7.00**

community composition, especially in the exclusion plots, where herbivory effects are removed.

Species tolerance to warming may determine future community structure. Species with lower tolerance to warming will behave as climate losers, while those with higher tolerance to high temperatures will behave as climate winners (Somero 2010). Under this point of view, P. lasiospermum is the most conspicuous representative of the winner group. Its population increased during the study period in both sectors and in both treatments, in concordance with a two-fold cover increase reported for the 2002-2017 period, based on aerial photography (Ibarrola-Ulzurrun et al. 2019). The expansion pattern of P. lasiospermus is even more remarkable if we consider that in the middle of the last century, it was an extremely rare taxon (Sventenius 1946). Currently, P. lasiospermum is the most abundant in the summit shrub vegetation and the trend indicates that its dominance could become even greater in the future. P. lasiospermum is a thermophilic species (Perera-Castro et al. 2017, 2018), with great wind-dispersal potential. Moreover, it has a low palatability to rabbits, thus being unaffected by them. In fact, the extra nutrient contribution from the rabbit latrines may stimulate its growth (Cubas et al. 2018, 2019). The current population expansion of P. lasiospermum is an example of how climate variation might turn some native species into invaders in their own habitat.

Climate warming also appears to be favoring other species formerly restricted to pine forests, such as Pinus canariensis Sweet ex Spreng., C. xeranthemoides and D. gonzalezii. Our study has not sampled P. canariensis with enough intensity, but Bello-Rodríguez et al. (2019) report on how the treeline is expanding upward in the SW sector. D. gonzalezii is a particularly interesting case. It was only detected at a single sampling station a few hundred meters away from the upper limit of the pine forest. In the first 4 years of sampling, the only species present there was the alpine D. bourgeauana, but since 2014, it was replaced by D. gonzalezii. A visual prospection around the site indicates that the former distribution area of D. bourgeauana has retracted due to the expansion of D. gonzalezii.

Among the climatic losers, there are two emblematic taxa, the legumes *S. supranubius* and *A. viscosus*, the first with an appreciable regression throughout its range in the high mountains of Tenerife and the second only in the SW sector, where it was sampled. S. supranubius was the most abundant plant in the summits of Tenerife until a few decades ago, when it was surpassed in coverage by P. lasiospermus (Cubas et al. 2018). During the period 2002-2017, S. supranubius lost 17.5% of its cover in the National Park (Ibarrola-Ulzurrun et al. 2019). Decline of both legume species could have a strong impact, since they play an engineering role in the shrub community, fixing nitrogen in this nutrient-poor environment (Kyncl et al. 2006; Cubas et al. 2018). Considering that the presence of other legume species in this habitat is scare, the regression of S. supranubius and A. viscosus could affect the total productivity and carrying capacity (biomass) of the summit shrub habitat. Some evidence suggests that the ongoing warming may be displacing the current S. supranubius population from its optimal thermal envelope. In the past century, Fernandez-Palacios (1992) established that the optimal thermal range of S. supranubius was between 10.2 and 11.9 °C, but during our study period, the temperature was often above the upper threshold of that range (Fig. 2b). This effect was observed to be more intense in the warmer sector. Indeed, this species is particularly sensitive to high evapotranspiration demand (González-Rodríguez et al. 2017), with drought leading to massive mortality events that affect mainly low-growing SW individuals (Olano et al. 2017). Moreover, our monitoring showed that S. supranubius recruitment was restricted to exclosures. Therefore, S. supranubius is suffering a double jeopardy due to warming and herbivory. Current protection measures aimed at the reduction of rabbit populations and the creation of large exclosures are critical to preserve this species, but they may not suffice for SW populations where adult mortality is occurring at a faster pace.

Although our study has been limited to a short period of 10 years, insufficient to conclude a direct relationship with global warming, that the patterns observed in the plant community are consistent with the response that could be expected due to climate change. In addition, this summit region has been undergoing an acute warming process for more than a century (Sanroma et al 2010). Climate warming is affecting the warmer SW sector more intensely (see Fig. 2), where species replacement is already occurring, in line with what would be expected from the exposure of the ecosystems to higher temperatures. The strong warming in the SW sector has reduced the intensity of internal thermal inversions (unpublished data), raising minimum temperatures and facilitating colonization by pine forest species. This could drive replacement of legume shrub by pine woodland (del Arco et al. 2006; del Arco 2008; Garzón Machado and del Arco 2012), but this process might be delayed by limiting conditions such as soil characteristics, herbivore presence, thermal adaptability, and propagule arrival (Walther 2003, 2010; Bello-Rodríguez et al. 2019). Palaeoecological and current ecological evidence suggests that species migrate individually and at different speeds in response to climate change (Graham and Grimm 1990). Some react quickly and others have a much lower response capacity. In fact, the time lag in vegetation responses to climate has been an ecological constant in the past (Alexander et al. 2017). Most likely, the reorganization of the plant community in terms of species composition and their relative proportions could lead to a different community being formed (Keith et al. 2009). Some pine forest species are increasing in abundance, and although some taxa of the legume shrub habitat are in decline, others are increasing, especially those less palatable for rabbits. This may result in a non-analogous community, with a more diverse novel species assemblage dominated by chamaephytes (instead of phanerophytes), with P. lasiospermus as key species (instead of S. supranubius) and with some scattered P. canariensis.

A general decrease in the evenness of the park's plant community is foreseeable at the short term, being more noticeable in the cold NE sector than in the warm SW sector. In the warmer sector, the losses in species number could be partially offset by the arrival of chamaephytes from the surrounding pine forest. This would be rarer in the NE sector where herbivory is causing an acute impoverishment of its flora, with recruitment impaired outside the fenced areas. Although the temperature of this sector has not increased during the 10 years of our study, data from the last 100 years reveal a long-term warming pattern. It is likely that in the coming years, warming will continue in this sector; in fact, 2019 was the sixth warmest on record in the last 100 years. It is plausible to think that in the medium term, the plant community of the NE sector would follow the same path as the current plant community of the SW sector.

Our 10-year monitoring shows that the alpine habitat of Tenerife is changing rapidly, due to the

synergy between introduced herbivores and the warmer and drier conditions. These stressors could drive key species to collapse due to the combination of adult mortality and lack of recruitment, whereas formerly rare species may become dominant. Facing this challenge is complex and difficult. While herbivory pressure can be partially mitigated through the construction of large exclusion fences and more effective control of the species, climate change is beyond local managers' control. Current results suggest that community change would go beyond a shift in elevation, probably leading towards a non-analogous plant community, as may have happened in the past in several parts of the planet during earlier climatic changes.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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