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# Thirsty peaks: Drought events drive keystone shrub decline in an oceanic island mountain



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#### ABSTRACT

Oceanic islands ecosystems are among the most endangered in the world, as the effects of ongoing climate change may potentially combine with other pre-existing drivers of plant population decline. In the Canary Islands, nitrogen-fixing Teide broom (Spartocytisus supranubius) is a keystone species in the Teide National Park high mountain ecosystem. However, recruitment failure due to introduced herbivores and dieback episodes are decimating its populations. We explored the role of climate as a potential driver of Teide broom mortality. We analyzed annual rings of Teide broom to reconstruct the impact of climate on secondary growth, intrinsic water use efficiency (iWUE) and mortality, and to explore the potential for growth rates and levels of resilience to act as indicators of mortality risk. We found that higher precipitation from October to February improved Teide broom secondary growth, whereas iWUE increased with high July-August temperatures. Extreme drought events in 2001 and 2012 strongly reduced secondary growth and resulted in subsequent plant death. Individuals that subsequently died had lower growth rates, poorer capacity for growth recovery after drought events and marginally higher iWUE than those which survived. More frequent recurrence of extreme drought events in the future would increase the frequency of dieback episodes, and the combination of a decline in mature individuals and lower recruitment rates due to exotic herbivore pressure would mean an uncertain future for the Teide broom. Our results indicate how global change may impact keystone species in protected areas and highlight the need for urgent implementation of proactive conservation policies.

#### 1. Introduction

High mountains in oceanic islands are Noah's Arks of biodiversity. The ecological barrier created by their two-fold isolation has fueled evolutionary processes (Steinbauer et al., 2012), leading to a disproportionately large number of endemic taxa in relation to their extent (Cronk, 1997; Kreft et al., 2008; Steinbauer et al., 2012). At the same time, the combination of geographical isolation, small populations and reduced distribution ranges makes these ecosystems particularly susceptible to species extinction (Martín, 2009). Higher historical incidence of extinctions in island ecosystems has already been documented (Diamond et al., 1989); of 80 plant species extinctions documented in the last 400 years, around 50 were from island ecosystems (Sax and Gaines, 2008). Continuation of the ecological heritage of island mountains is considered to be globally threatened by the combination of human activity and invasive species, and this is exacerbated by climate change (Caujapé-Castells et al., 2010; Ferreira et al., 2016;

#### Harter et al., 2015; Triantis et al., 2010).

Tenerife is the largest and highest island of the Canary archipelago. Located in the Atlantic Ocean 300 km away from the African continent, the island is a large volcanic outcrop that peaks in the 3718 m high Teide volcano, which towers over the island just 15 km from the shoreline. Such a steep altitudinal gradient creates a rough orography that is only interrupted on the southern Teide slopes, where a relatively flat area creates an extensive high mountain environment at over 2000 m altitude, where an original biota has evolved. The singularity of this high mountain ecosystem has long been recognized (von Humboldt and Bonpland, 1807) and led to the designation of this area as a National Park in 1954. Since them, Teide has become one of the most visited National Parks in the world, with > 4 million visitors in 2016.

The nitrogen-fixing Teide broom (*Spartocytisus supranubius* (L. f.) Christ *ex* G. Kunkel, Fabaceae) is the keystone species in this ecosystem. Traditional land management involved the intensive use of Teide broom as fodder and fuel, which reduced its abundance until the

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suppression of traditional pastoral activities following designation of the National Park, which prompted a recovery of Teide broom population levels (Elena and Rodríguez, 2005; Kyncl et al., 2006). However, this positive trend ceased in the 1980s due to the onset of dieback episodes, combined with massive recruitment failure following an increase in abundance of the rabbit (*Oryctolagus cuniculus* L.), a non-native herbivore that had been introduced from continental Europe (Garzón-Machado et al., 2010). Measures for controlling rabbits in such a large area (Teide National Park occupies nearly 19.000 ha) have proved insufficient to contain the expansion of the species and its detrimental impact on native flora, and large exclosures are now being planned to promote Teide broom recruitment.

Even within exclosures, however, strong dieback episodes are a major concern for National Park managers. Dieback episodes began at the end of 1980s in the southern part of the Park; they have since extended across the whole of the National Park, but continue to be most intense in the south. These events are characterized by plant wilting that eventually leads to the death of affected individuals, with decaying plants being attacked by different species of pathogenic fungi and phytophagous insects (Lorenzo et al., 1991). Even if the primary factors triggering dieback episodes remain unclear, the onset of this phenomenon in the southern/drier edge of the species' range hints at the possibility that drought stress might be a contributory factor. This hypothesis is supported by evidence that high drought stress levels are a primary cause of dieback episodes for numerous woody species in arid and semiarid environments (Allen and Breshears, 1998; Liu et al., 2013; Marqués et al., 2016; McDowell, 2011). This may be a critical issue in the study area which is experiencing a warming rate (0.14  $\pm$  0.07 °C per decade) closer to the rates experienced in nearby continental regions than to the mean of Canary Islands archipelago (Martín et al., 2012).

Annual growth rings in the secondary xylem provide a valuable proxy to enable reconstruction of growth history and mortality dynamics, and to improve our knowledge about the role of climatic trends and climatic extremes on plant growth and survival (Speer, 2012). The presence of well-resolved annual growth rings in the wood of Teide broom (Kyncl et al., 2006) allows a retrospective analysis of growth patterns and mortality events in this species, in order to determine the importance of water availability and extreme drought events in triggering dieback episodes. In this study we compared the responses to climate shown in the growth rings of living and dead plants in the northern/wet and southern/dry edges of the species distribution in the National Park.

We performed a range of analyses to gain a better understanding of the factors driving Teide broom dieback. Firstly, we determined the effect of climate on secondary growth and intrinsic water use efficiency (iWUE). We then analyzed (a) whether plant mortality was associated with extreme drought events, (b) whether growth rates and iWUE varied between individuals that survived and died, and between wet and dry edge populations, and (c) whether resilience to drought events could serve as an early indicator of predisposition to die.

#### 2. Materials and methods

#### 2.1. Study area

The study area is located at 2055–2340 m a.s.l. in Teide National Park, Tenerife, Canary Islands, Spain (Fig. 1). The climate varies from semiarid continental subalpine in the North to arid in the South, with strong daily variations of temperature. Monthly time series of precipitation and temperature were recorded in the Izaña meteorological station, located within the northern edge of the study area at 2373 m a.s.l. (Fig. 2). Annual mean temperature for the 1961–2015 period is 10.3 °C, the coldest month being January (mean daily minimum temperature of 1.3 °C) and the warmest month July (mean daily maximum temperature of 22.9 °C). Average annual precipitation is 330 mm with a

drought period of six months from May to September. Temperature increases and precipitation decreases towards the southern half of the National Park (Bustos and Delgado, 2000).

Poorly developed soils of volcanic origin dominate in the study area, mainly consisting of volcanic scoria with acidic pH, poor water retention capacity and low organic carbon and nitrogen contents (Rodríguez et al., 2014). Teide broom is the dominant species of a singular vegetation community which includes a variety of plants adapted to dry alpine conditions and numerous endemic species of Tenerife and the Canary Islands (Fernández-Palacios and de Nicolás, 1995).

#### 2.2. Study species

*Spartocytisus supranubius* is a multibranched leguminous shrub endemic to the highest Canary Islands, i.e. Tenerife and La Palma (Fig. 2). This species inhabits mountain areas at elevations from 1400 to 3250 m, with its largest population occurring within the Teide National Park. It can reach 4 m in height and > 10 m in crown diameter with some degree of clonal growth (Kyncl et al., 2006). Diameter growth occurs from the end of April to mid-July (González-Rodríguez et al., 2017). Secondary xylem is semi-ring porous (Fig. 2) with distinct annual rings (Kyncl et al., 2006).

#### 2.3. Sampling design and chronology elaboration

In June 2016, 15 living and 15 dead individuals were sampled from six sites across the Teide National Park (Fig. 1). Three of the sites were in the northern part of the National Park, where adult broom mortality is lower, and three sites were in the southern part, where broom dieback is more intense and death rates higher (Fig. S1). At least one core was extracted from branches of living Teide brooms in areas with active secondary growth, as close as possible to the central stem collar in order to capture individual age. A second core was taken from 5 trees per site for analysis of stable isotope content in the secondary xylem. A stem cross section was obtained with a chainsaw from dead Teide brooms, as close to the plant base as possible. From each stem cross section, we selected the radius with highest growth rate and obtained a complete section of this radius from pith to bark. Comparing cross-sections and branch cores may induce some bias in the result due to different growth rates. Nevertheless, both growth patterns were highly correlated, and no difference in mean growth rates were found before extreme drought events. Cores and sections were dried and both were surfaced with a sliding microtome (Gärtner and Nievergelt, 2010) to observe the cellular structure of the secondary xylem. After visual cross-dating, treering widths were measured to the nearest 0.001 mm using a slidingstage micrometer (Velmex Inc., Bloomfield, NY, US) interfaced with a computer. Individual tree-ring series were statistically compared with a master living trees chronology using the COFECHA program and checked for dating accuracy (Grissino-Mayer, 2001).

Individual ring-width series for living and dead plants were standardized and averaged separately for each group to assess state (living/ dead) and location (north/south) differences in tree-ring width and climatic response. For standardization, raw series were fitted to a spline function that retained 50% of the variance in the original series over periods of 32 years, which was flexible enough to reduce the non-climatic variance by preserving high-frequency climatic information (Cook and Peters, 1981). The residuals obtained by dividing each raw ring width by its fitted spline values were prewhitened by autoregressive modeling, giving dimensionless indices that represent independent records of annual growth for each measured series. Growth indices for each group were averaged on an annual basis into a chronology using a biweight robust mean. Ring-width series were detrended, standardized and averaged with the ARSTAN computer program (Cook and Holmes, 1996). First order autocorrelation (AC1), mean sensitivity (msx), mean inter-tree correlation (rbt), signal-to-noise ratio (SNR) and expressed population signal (EPS) were calculated to



Fig. 1. Geographical location of the Canary Islands (right), study area location (star) in Tenerife Island (upper left), and sampling design within the Teide National Park (bottom left). Northern sites are shown as black circles and southern sites as white circles, the triangle indicates Izaña meteorological station, and the white line represents 2 km. Map source: Google Earth.

assess chronology properties.

#### 2.4. Estimation of water-use efficiency

To assess the annually-resolved iWUE time series, we evaluated xylem  ${}^{13}C/{}^{12}C$  isotope ratios ( $\delta^{13}C$ ) in wood from cross-dated annual tree rings. We created five chronologies: one master living trees chronology including 77 living individuals for the 1992–2015 period, and four independent chronologies for north, south, living and dead

individuals, each based on six individuals for the 1998–2012 period. Annual tree rings from each tree were separated with a scalpel under a binocular lens. Tree rings for each year and group were merged and homogenized using a mill (Retsch MM400). Cellulose was not purified, as several studies show good correlations between  $\delta^{13}$ C in complete wood and in purified cellulose, and therefore both measurements show near identical relationships with atmospheric CO<sub>2</sub> content and climate (Roden and Farquhar, 2012; Taylor et al., 2008). The wood powder was weighed into tin cups and combusted to CO<sub>2</sub> using an elemental



Fig. 2. Spartocytisus supranubius (white flowers) in Teide National Park (upper left); climatogram for Izaña Meteorological Station at 2373 m a.s.l. (upper right), and histological preparation of Teide broom xylem, with lines indicating limits between annual growth rings (bottom).

analyzer interfaced to a continuous flow isotope ratio mass spectrometer (UC Davis Stable Isotope Facility, University of California, Davis, CA). Results were expressed as relative differences in  ${}^{13}C/{}^{12}C$  ratio of tree-ring wood in parts per thousand (‰) relative to the standard V-PDB ( $\delta^{13}C$  plant).  $\delta^{13}C$  plant was used to calculate isotopic discrimination ( $\Delta$ ; Farquhar and Richards, 1984). We then calculated the intrinsic water-use efficiency (iWUE; expressed in µmol of CO<sub>2</sub> per mol of H<sub>2</sub>O), using available data of  $\delta^{13}C$  in atmospheric CO<sub>2</sub> and atmospheric CO<sub>2</sub> concentrations (see McCarroll and Loader, 2004 for a detailed description of iWUE calculation). The iWUE chronology corresponding to living trees was standardized following the same protocol described above for ring-width chronologies.

#### 2.5. Dating of secondary growth cessation

In dead plants we estimated the date of the last year with active secondary growth by dating the individual tree-ring series with the master living trees chronology. We identified unique narrow rings in the ring width series of all studied radii from samples of both living and dead individuals, and used the program COFECHA to identify the correct dating of floating ring-width series from dead individuals. This procedure provided the date of cambial activity cessation on dead individuals.

#### 2.6. Growth resilience estimates calculation

We calculated different components of growth resilience (Lloret et al., 2011) to check for differences in the response of secondary growth to extreme drought events between northern and southern locations, and between living and dead trees. We calculated resistance as the ratio between drought and pre-drought growth, recovery as the ratio between post-drought and drought growth, and resilience as the ratio between post-drought and pre-drought growth. Pre- and postdrought periods were calculated as the mean secondary growth over the three years prior to and after drought events. We calculated these parameters for 2001 and 2012, corresponding with the most intense droughts in the period studied (Fig. S2).

#### 2.7. Statistical analysis

We identified the climatic factors that limit Teide broom secondary growth by correlating ring-width chronologies with climatic parameters. Pearson's correlations were calculated between ring-width chronologies and monthly mean maximum temperature and precipitation, over the period from September of the previous year to October of the growth year. Climate time series for the period 1992–2015 were obtained from Izaña meteorological station. When climatic response was significant over several consecutive months, Pearson's correlation between the chronology and the mean (temperature, relative humidity) and accumulated (precipitation) monthly values for the significant period was calculated. This analysis was performed for both ring-width and iWUE chronologies from living plants.

We employed the Standardized Precipitation-Evaporation index (SPEI) (Vicente-Serrano et al., 2010), available at http://spei.csic.es/ database.html, to evaluate the differential effect of soil water availability at different time-scales over the analyzed chronologies. SPEI analysis considers different time-scales, exploring the multiscale response of vegetation to drought (Vicente-Serrano et al., 2014). Reference evapotranspiration used to calculate the SPEI was obtained by means of the Hargreaves equation (Hargreaves and Samani, 1985) using maximum and minimum temperature and extraterrestrial solar radiation. Pearson's correlations between the chronologies and SPEI at different temporal scales were calculated.

We ran a linear mixed-model to detect any relationship between growth rates over the 1997–2012 period and either location (north or south) or current status (living or dead). The fixed part of the model included status, location, and their interaction. To define the structure of the random part, we included year as a random factor to consider the variation of secondary growth caused by difference in climatic conditions occurring in different years, as well as a first order autocorrelation term. We also ran a linear model with the same fixed structure to assess the effect of status and location on iWUE in the 1998–2012 period.

Using the secondary growth dataset, we ran separated linear models to test the relationship between current status and location and the three components of growth resilience, i.e. resistance, recovery, and resilience. In a first set of models, we evaluated whether status, individual age, and their interaction affected resilience to 2001 drought. In a second set of models, we evaluated whether location affected the growth response of living trees to 2001 and 2012 droughts. This model included location, year of drought, and their interaction as factors.

#### 3. Results

## 3.1. Climatic constraints of secondary growth and intrinsic water use efficiency

A total of 77 plants and 91 cores were included in the master living trees chronology, which covered the period 1975-2015. A robust chronology with adequate replication (AC1 = -0.004, ms<sub>x</sub> = 0.22,  $r_{bt} = 0.31$ , SNR = 13.53, EPS = 0.931) could be established for the 1992-2015 period. Climatic response (Fig. 3) revealed that autumnwinter precipitation exerted a strong control over secondary growth (October to February accumulated rainfall, r = 0.79, P < 0.001). In contrast, temperature was inversely related to seconda1ry growth, with high maximum temperatures during winter having a detrimental effect on secondary growth (December to January maximum temperature: r = -0.45, P = 0.026). SPEI results confirmed this relationship, with a maximum signal from October to February (r = 0.86, P < 0.001), suggesting that the combination of cool and wet conditions during late autumn and winter favoured secondary growth. When the individual tree-ring chronologies were analyzed, they indicated reduced secondary growth in southern and dead individuals (Table S1). However, no remarkable differences in climatic signal were observed between northern/southern or living/dead Teide brooms (Fig. S3).

iWUE increased at a rate of 0.91% per year from 1992 to 2015 (see Fig. 4). This trend showed a significant inter-annual variability that could be partially explained by climate (Fig. 3). iWUE increased in years with high maximum July and August temperatures (r = 0.63, P < 0.001), and March maximum temperature also exerted a marginal positive effect on iWUE. Precipitation played a minor role in determining inter-annual iWUE, with only a minor negative signal of previous September and previous November rainfall (Fig. 3).

Teide broom mortality was linked to low growth rates during significant drought periods (Fig. 5). As much as 22.6% of the dead individuals ceased secondary growth during the extreme 2012 drought event (when October to February precipitation was 23.8 mm only 9.8% of the average). In the 2001 drought (October to February precipitation 66.4 mm; 27.2% of the average), secondary growth cessation did not coincide with the drought in the same way, but mainly occurred the following year. This result should be treated with some caution, however, due to the lower sample size for that period, and the advanced state of decay of much of the sapwood by the time of sampling.

#### 3.2. Location and status effect on growth and functional parameters

Growth rate strongly depended on plant status and location, particularly after 2001 (Fig. 6). Linear mixed model identified lower secondary growth in dead plants ( $-0.787 \pm 0.222 \text{ mm year}^{-1}$ , P < 0.001) and in individuals from southern locations ( $-0.606 \pm 0.217 \text{ year}^{-1}$ , P = 0.006) compared to northern locations. However, no significant interaction effect between status and location was found ( $0.129 \pm 0.327 \text{ mm year}^{-1}$ , P = 0.69).



**Fig. 3.** Correlations between climate and *Spartocytisus supranubius* residual chronologies for secondary growth (black bars) and iWUE (white bars) for the 1992–2015 period. Previous year months are capitalized. Dotted lines indicate P < 0.05, thin solid line P < 0.01 and thick solid line P < 0.001.



**Fig. 4.** Temporal variation of water use efficiency annual values for living individuals for the 1992–2015 period. Thin dotted line indicates lineal trend ( $r^2 = 0.81$ , P < 0.001).



Fig. 5. Residual chronology of *Spartocytisus supranubius* secondary growth (black solid line) and proportion of dead individuals ceasing secondary growth each calendar year (grey dashed line).

Survivors and dead Teide brooms had shown similar growth resistance to the 2001 drought, although survivors showed better recovery and resilience (Table 1). When the effects of the 2001 and 2012 droughts on the growth of Teide broom survivors were evaluated simultaneously, individuals in the southern part of the National Park showed similar resistance and recovery rates, but poorer resilience rates. Analysis revealed the 2012 drought had a greater impact, with more intense effects on growth resistance, recovery and resilience.

Individuals in the southern part of the National Park showed higher iWUE (effect estimate = 6.66, P < 0.01) with marginally lower iWUE values for living plants (effect estimate = -3.46, P = 0.059), and no significant effect of location per status interaction (effect estimate = -2.54; P = 0.31) (Table S2).

#### 4. Discussion

Teide broom secondary growth depended on the replenishment of soil reserves by winter precipitation. Extreme drought events caused a severe reduction of secondary growth and were associated with cambial activity cessation and, subsequent plant death. Plants that died showed lower growth rates, poorer recovery and resilience following extreme drought events and marginally higher iWUE than survivors. Similar differences were observed when dry (southern) and wet (northern) populations were compared.

Optimal thermal and hydric conditions for secondary growth are

decoupled in the Teide broom. Threshold temperature for xylogenesis initiation (Rossi et al., 2008) is reached in mid-April in the study area with basal area increment occurring from the end of April to mid-July (González-Rodríguez et al., 2017). Thus, almost all cambial activity occurs during a period of drought, and secondary growth is therefore sustained by soil water reserves accumulated during the previous autumn-winter. This inference is supported by two pieces of evidence from our study: (1) the high correlation between radial growth and October to February accumulated precipitation (r = 0.79; P < 0.001), and (2) the lower correlation with precipitation in individual months, which indicates the cumulative effect of autumn-winter precipitation in replenishing soil water reserves. The inclusion of evaporative demands during autumn-winter (SPEI) improved substantially the interpretation of the observed climate-growth relationship, highlighting the detrimental impact of warmer winter temperatures on the soil water balance.

Cell wall lignification is critical for carbon fixation and immobilization as organic compounds, and for xylem properties (Cuny et al., 2015; Olano et al., 2012, 2014). Cell wall lignification, like plant growth in general, is partially supported by recently acquired photosynthates (Richardson et al., 2013). Thus, the carbon isotopic ratio in the cell wall contains information on the factors limiting photosynthetic activity during the lignification process, with higher <sup>13</sup>C/<sup>12</sup>C ratios (higher iWUE) occurring in years with high July-August temperature signals. The timing of this climatic signal implied that Teide broom xylem cell lignification extended until August. Additionally, the positive relationships between iWUE and maximum temperatures indicated that higher iWUE occurred in warm summers. A plausible mechanism for this signal is that warmer conditions during July-August induced stomata closure, reducing CO<sub>2</sub> partial pressure in the leaf mesophyll, promoting higher <sup>13</sup>C uptake. Similar mechanisms have been described in other water-limited environments (Olano et al., 2014; Shestakova et al., 2017).

Enhanced  $CO_2$  levels may enable Teide broom to operate successfully under more unfavourable water balances. In fact, the impact of  $CO_2$  fertilization would be greater at high altitudes, since lower atmospheric pressure makes  $CO_2$  more limiting (Körner and Diemer, 1994). Accordingly, iWUE gain was very high during the study period, with a 0.91% annual increase rate. Nevertheless, the marginally higher iWUE found in dead plants and the higher iWUE at the drier edge of the species range in Tenerife suggests that iWUE gain might not compensate for the detrimental effect of increased drought intensity.

Drought events often have a strong impact in species, such as Teide



Fig. 6. Spartocytisus supranubius mean radial growth for the 1990–2015 period. Black line for northern individuals, grey line for southern individuals, solid line for living individuals and dashed line for dead individuals. Error bars indicate  $\pm 1$  standard deviation.

#### Table 1

Linear models assessing *Spartocytisus supranubius* resistance, resilience and recovery to extreme drought events. A) Effect of 2001 drought on status (living/dead) and location (north/south) and B) effect of 2001 and 2012 droughts on living plants from different locations (north/south). Values in parentheses indicate basal levels. Significant tests in bold.

А	Intercept	Location (north)	Status (dead)	Location * status
Resistance Recovery	0.587; P < 0.001 1.222;	0.086; P = 0.14 0.030;	-0.086; P = 0.64 0.321;	-0.098; P = 0.21 -0.126; P = 0.47
Resilience	P < 0.001 1.034; P < 0.001	P = 0.79 0.008; P = 0.51	P = 0.011 0.330; P = 0.005	-2.177; P = 0.032
В	Intercept	Location (north)	Drought (2001)	Drought * location
Resistance	0.305; P < 0.001	-0.081; P = 0.19	-0.104; P = 0.041	-0.006; P = 0.94
Recovery	0.481; P < 0.001	0.025; P = 0.67	-0.131; P = 0.004	-0.007; P = 0.92
Resilience	1.380; P < 0.001	-0.282; P = 0.017	-0.313; P = 0.001	0.185; P = 0.25

broom, that rely heavily on current year precipitation for growth and performance, driving drastic reductions in secondary growth. Droughts can cause the cessation of cambial activity and ultimately may trigger plant death, as shown by cambial cessation in dead plants being disproportionally concentrated in years with extreme drought events such as 2012, but also in years of moderate drought such as 2008. These results point to drought as the primary stress factor behind massive Teide broom dieback, with other described symptoms such as wilting or phytophagous insect infestation being contributing factors that increased dieback severity (sensu Manion, 1991).

The probability of Teide broom death was higher in individuals that displayed lower secondary growth rates and poorer resilience to, and recovery from, previous drought events. Interestingly, the comparison between drier and wetter (south and north, respectively) populations revealed the same pattern. The dry zone population showed lower secondary growth rates and poorer resilience to drought than the wetter zone population. We can interpret these results as early warnings of probable future diebacks in the drier part of the species range under a global warming scenario (Camarero et al., 2015); this is further evidence of the reported greater sensitivity to global warming of the plant populations located at the drier edge of their species range (Jump et al., 2006).

Drought events drive plant mortality (Allen et al., 2010), and have the potential to induce shifts in species distribution (Adams et al., 2009). Lower growth rates and a limited resilience to drought events could be interpreted as early-warning signals of the decline of Teide broom populations from the dry edge of their range (Marqués et al., 2016). Increased iWUE due to  $CO_2$  fertilization might not be enough to mitigate the predicted increase in regional drought (Expósito et al., 2015), threatening the Teide broom's current distribution range. The topographic configuration of Teide National Park presents a limited amount of land occurring at higher altitudes, thus constraining the potential of an altitudinal shift of this endemic species to compensate for the decline of the dry edge population. Moreover, the combination of higher adult mortality due to a drier climate with a higher recurrence of extreme drought events (IPCC, 2014), and the recruitment limitation due to exotic herbivore pressure (Garzón-Machado et al., 2010), indicate a difficult future for Teide broom. Facilitation of recruitment through the control of exotic herbivores and the creation of large-scale herbivore-free exclosures are critical to maximize the chance of local adaptation to novel climatic conditions (Jump and Peñuelas, 2005). Our results indicate how global change may impact keystone species even in strictly protected areas, and show the need for the urgent implementation of proactive conservation policies.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.biocon.2017.09.008.

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