



# Assessing global warming vulnerability of restricted and common plant species in alpine habitats on two Oceanic Islands

Juana María González Mancebo<sup>1</sup> · Víctor Bello-Rodríguez<sup>1</sup> · Jonay Cubas<sup>1</sup> ·  
Jesús Parada-Díaz<sup>1</sup> · Ángel Bañares-Baudet<sup>4</sup> · Ángel Palomares<sup>2</sup> ·  
José Luís Martín-Esquivel<sup>3</sup> · Marcelino J. del Arco<sup>1</sup>

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## Abstract

Climate change is modifying plant communities and ecosystems around the world. Alpine ecosystems are of special concern on oceanic islands, due to their characteristic higher endemism percentage, small area and undergoing severe climate change impact in the last few decades. During recent decades there has been increasing interest in the effects of climate change on biodiversity and a range of methods have been developed to assess species vulnerability. However, some new insights are necessary to obtain useful information for species management on oceanic islands. Here in the alpine area of two oceanic islands (Tenerife and La Palma) we evaluate the drivers that best explain the vulnerability of 63 endemic species along three scenarios, covering recent past to present and two future projections (2041–2060 and 2061–2080). The selected drivers were: loss of potential area, mismatch index between potential and occupied areas in different scenarios, and adaptive capacity constraints. We assess the influence of potential area size and whether the drivers of risk and the vulnerability for common, restricted and rare species are significantly different. Our results indicate that management must be widely distributed over the species, and not only focus on restricted species. Evidence for this was that drivers directly deriving from climate change showed no significant differences in their impact on the rarity groups identified. Vulnerability depends partially on the potential area size, showing a more complex picture where constraints on the adaptive capacity of the species have a strong enough influence to modify the effects of the characteristic drivers of climate change.

**Keywords** Rarity · Potential area · Occupied area · Endemism · Species range-size · Canary Islands

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## Introduction

Oceanic islands are extremely fragile areas, with features that intensify the impact of global warming (Veron et al. 2019; Russell and Kueffer 2019). In this context, alpine zones have been the focus of many research studies, due to their high endemism percentage within a small surface area (Steinbauer et al. 2016). Indeed, they are undergoing some of the strongest climate change effects in just the last few decades (Pauli and Halloy 2019). In addition, mountaintop species are among the most vulnerable to climate change due to the “escalator effect” (Urban 2018), especially cold-adapted species (Rumpf et al. 2018).

Most species are represented by a few individuals or populations, while most individuals belong to a few common species (Rabinowitz 1981; Flather and Sieg 2007). The pattern of commonness and rarity of the biota inhabiting the ecosystems may be natural (Martín 2009; Enquist et al. 2019). However, it is frequently caused by human disturbances (Flather and Sieg 2007; Otto et al. 2020), which explains why many rare species are also vulnerable or even threatened (Gaston 2003; Ohlemüller et al. 2008). Due to scarce resources dedicated to ecosystem conservation, a common strategy for management has been to focus on threatened species (Flather and Sieg 2007), preventing integral management of the ecosystem. On the other hand, common species are often used for ecological restorations in deeply disturbed areas (del Arco et al. 1992). However, between rare and common species there is a large species pool that is frequently neglected in conservation plans.

Global warming during the last decades is affecting the patterns of the species rarity and commonness. More than 35% of terrestrial plant species are categorized as very rare, and their risk of extinction is increasing due to climate change (Enquist et al. 2019), especially because of the exacerbation of other existing threats (Macinnis-Ng et al. 2021), such as invasive herbivores, the fires or droughts (Del Arco et al., 2018). However, also common species can be threatened by both, intrinsic and extrinsic factors related with global warming (Périé and Blois 2016; Dickson et al. 2019). Climate change can also benefit some species (Somero 2010), including rare species (Cubas et al. 2018; Perera et al. 2018). Thus, there are losers and winners of climate change (Martín et al. 2020, 2021) and common species may also become a priority for conservation (Cubas et al. 2022). The question is whether to continue with the same conservation management strategies or adapted approaches.

Species differ naturally in their range-size and understanding its determinants is essential for identifying risks to species and habitats (Myers et al. 2000), and their sensitivity to anthropogenic climate change (Ohlemüller et al. 2008). Two main components may be distinguished to define the geographical space where a species can grow and expand (Soberon and Nakamura 2009). Firstly, the potential area where a species can occur, mostly characterized by the climatic and other physical factors that might allow their growth (Jackson and Overpeck 2000). Secondly, the area where biotic conditions would allow existence of viable populations (realized niche), are determined mainly by Eltonian processes (Junker et al. 2019), ecological interactions and resource consumption (Jackson and Overpeck 2000). A third component is based on the limited area where the species can maintain effective dispersal or colonization over a sustained time interval (Soberon and Nakamura 2009). This factor is important due to the pressing need for migration, considering this as an adaptive response to global warming (Foden et al. 2019).

Even though other factors can limit a species' distribution, it is generally assumed that climate remains a significant driver (Araújo and Peterson 2012; Barber et al. 2016). How-

ever, assessment of climate change vulnerability must also include species sensitivity and adaptability (Pacifiçi et al. 2015; Foden et al. 2019). Estimations of the speed of climate change (Burrows et al. 2014; Carroll et al. 2015; Barber et al. 2016) provide an idea of the rate at which species need to migrate to maintain an effective response to the climate change occurring over a given interval of time, as part of the adaptive capacity (Beever et al. 2015). However, there may be constraints that reduce or disable this capacity (Harter et al. 2015; Bello-Rodríguez et al. 2019). So, there is a need to consider both climate vulnerability and factors that make the species more sensitive, which explain the realized niche size and species distribution. In this way, the mechanisms underlying a nonlinear ecosystem response to climatic and anthropogenic stresses can be carefully explored (Martín et al. 2021; Wu et al. 2021). This requires considering what actions should be successful in enhancing the species' adaptive capacity, by reducing constraints to shifting the adaptive capacity (Beever et al. 2015).

There have been a great variety of methodological developments that aid in assessing the vulnerability of species to climate change (Felicísimo et al. 2011, 2012; Pacifiçi et al. 2015; Foden et al. 2019). These tools provide essential information on climate change vulnerabilities across different species and habitats and aid in conservation management of those species at highest risks (Heikkinen et al. 2021). However, on oceanic islands additional factors such as their small size, greater endemism rates and an invasive herbivores stress sustained over time, even in the best-preserved areas, need to be considered (Nogales et al. 2006; Caujapé et al. 2010; González-Mancebo et al. 2019).

Together with climate conditions and island area, habitat size is one of the most important factors explaining both richness (Whittaker and Fernández-Palacios 2007; González-Mancebo et al. 2011) and species range sizes (Ohlemüller et al. 2008; Morueta-Holme et al. 2013) on oceanic islands. Habitat size may be correlated with species rarity on islands, but especially in disturbed habitats (Chase et al. 2020). The potential area of the species is highly influenced by island heterogeneity and habitat size (Whittaker and Fernández-Palacios 2007), but occupied area on oceanic islands are frequently limited by invasive herbivores. After several hundred or thousands of years, the structure and composition of the plant communities mostly reflect differences in their palatability (Irl et al. 2014; Cubas et al. 2019). Thus, some less palatable species become dominant in the communities (Garzón et al. 2010; Cubas et al. 2018, González-Mancebo et al. 2019), even when more competitive – usually larger - species coexist with restricted occupied areas (Irl et al. 2012). Thus, rarity and commonness in oceanic island habitats may be highly dependent on introduced herbivores, so the realized niche may be the great unknown for many species. Many species could have unknown potential area, due to the low number of occurrences (current occupied area) that have survived to our days because of various human activities. This not only affects restricted species; today's common species distributions may be the result of the loss of more competitive and highly palatable species due to introduced herbivores. Characteristically, a consequence of anthropogenic activities is that narrow-ranged species become replaced by widespread species (Xu et al. 2019; Staude et al. 2022).

The Canary archipelago presents several interesting characteristics for testing vulnerability to climate change on islands. The alpine ecosystem is well represented, especially on Tenerife with a maximum elevation of 3715 m a.s.l., and a smaller area and a maximum elevation of 2426 m on La Palma. Furthermore, global warming in alpine zones on these

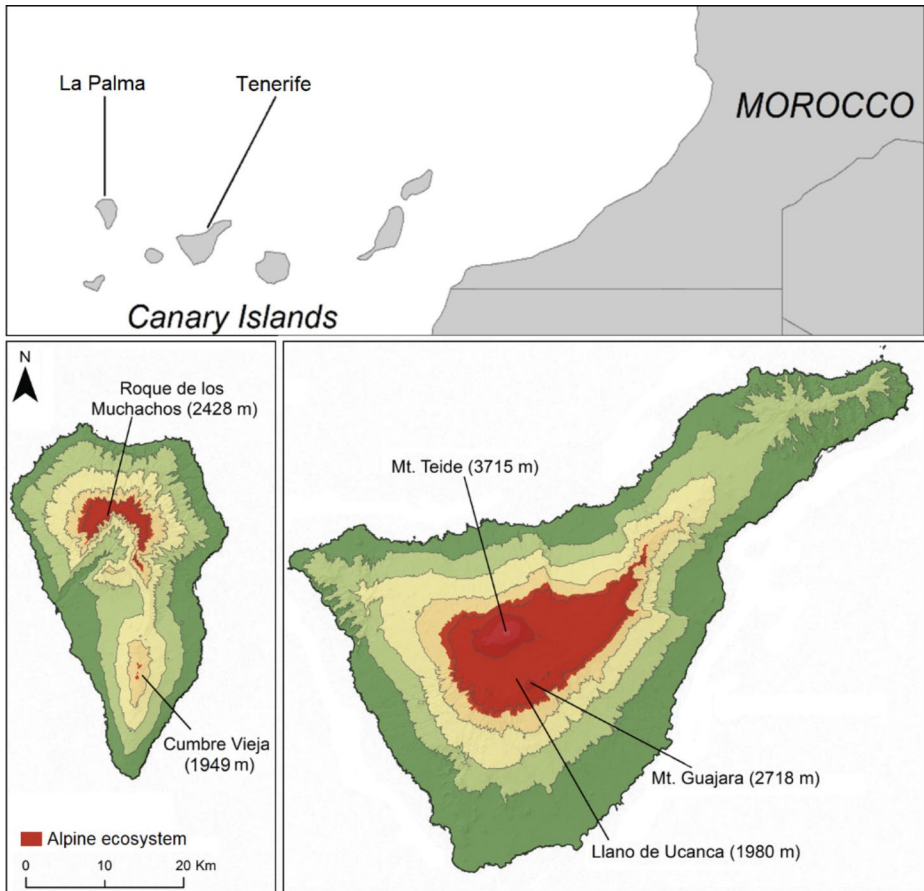
islands is happening fast, notably on Tenerife ( $0.14 \pm 0.07$  °C/decade in the area surrounding its summit (Martín et al. 2012).

Here, we evaluate the drivers (loss of potential area, mismatch of potential and occupied areas between different scenarios, and adaptive capacity constraints limiting the realized niche) that best explain the vulnerability of 63 endemic species in the alpine area of two oceanic islands (Tenerife and La Palma). Three scenarios are examined (present, and two future projections for the periods 2041–2060 and 2061–2080). We hypothesized that vulnerability for rare species depends more on adaptive capacity constraints than on direct drivers of climate change (loss of potential area, mismatch of potential and occupied areas between different scenarios). This could be expected to be consistent with rarity being highly dependent on human disturbance. We also expected negative correlations between the potential area size and species vulnerability, resulting in greater vulnerability at present on the smaller island of La Palma, emphasizing a risk level related to its small size.

## Materials and methods

### Study area and target species

The study area consisted of the summit areas of the Canary Islands La Palma and Tenerife (Fig. 1). On La Palma they include the highest part of Caldera de Taburiente National Park in the north of the island, and the Cumbre Vieja (1949 m) ridge in the south. On Tenerife, it mostly coincides with Teide National Park. The alpine ecosystem on both islands (supra-, and oromediterranean thermotypes) is characterized by shrubby vegetation communities: *Spartocytisetum supranubii* (Tenerife) and *Genisto benehoavensis-Adenocarpetum spartioidis* (La Palma) (del Arco & Rodríguez-Delgado 2018). Target species in this study included 63 endemic species (33 to Tenerife and 30 to La Palma. Among these 19 are single island endemics to Tenerife and 13 to La Palma and only one endemic from La Palma and Madeira islands), 16 being common on both islands (see Table S1, supplementary material). Among these, 31.74% are threatened (Bañares et al. 2004). The species were selected to obtain a wide range of abundance, from the most common to the rarest. Habitat size varies among species, 80% occur exclusively above 1800 m, while others (La Palma nine species and Tenerife four) showed a wider distribution area including lower elevations, although with higher frequency higher up. Occurrence data were compiled from the data bases of the National Parks, the Canary Islands Biodiversity Databank (Gobierno de Canarias 2021) and our own surveys. Data from the Government of the Canary Islands were compiled from the regional atlas of 500×500 m cells (Gobierno de Canarias, <https://www.biodiversidad-canarias.es/biota/>). All these data were revised, and detected errors were removed. In addition, we used data provided by the Teide National Park, which are in cells of 250×250 m (Hernández 2016). We also used species occurrences of high precision provided by the Caldera de Taburiente National Park and our own field inventories. This fact allows working at the desired resolution, since it is higher than the error measurement of the GPS coordinate sensor (Sillero and Barbosa 2021). All species occurrences were carefully downscaled to a 200×200 m grid using our extensive knowledge about the current species distribution, since a 500×500 m resolution is too coarse and can cause mismatch between observed and predicted species distributions (Aranda & Lobo, 2011).



**Fig. 1** Location of the alpine zones (brown colour) on the islands of La Palma and Tenerife, with detail of the main elevational features. Isolines are represented each 500 m

Although the alpine ecosystems on both islands are included within protected areas, they are subject to several types of disturbances. The European rabbit, an invasive herbivore, was introduced on these islands about 500 years ago, but its population has increased in the Teide National Park during the last few decades (Martin et al. 2021), in accordance with the rising minimum temperatures due to global warming (Martin et al. 2012). During recent decades these factors are causing a striking new change in the species composition of this ecosystem (Martin et al. 2020) and has led to the alpine ecosystem of La Palma being dominated now by *Adenocarpus viscosus*, the least palatable species in this habitat (Irl et al. 2012). Fortunately, over the last 30 years, a successful management action sowing threatened species within herbivore exclusion fences revealed a different potential community structure and composition of this ecosystem (Irl et al. 2012; González-Mancebo et al. 2019). On Tenerife, the establishment of Teide National Park in 1954 halted shrub harvesting and the grazing. However, in 1968 the *Corsican muflon* was introduced (*Ovis muflon*), which is still present, but controlled by the National Park managers.

## Rarity index

We distinguished three species groups (rare, restricted and common) using a combination of the number of occurrence cells in the 500×500 m grid described above and the percentage of the potential area occupied by each species (which was derived using species distribution models, details see below): rare species ( $\leq 50$  occurrence cells), restricted species (51–150 occurrence cells or 35–55% cells in PA), and common species ( $> 150$  cells or  $> 75\%$  cells in PA). We used 500×500 cells, instead of 200×200 to avoid overestimation in national parks, due to the large abundance of occurrence data within them. Additionally, the size of the potential area (PA size) was used as a variable in the PCA analyses (see supplementary (S3) data).

## Species vulnerability index

Three components of vulnerability were considered, to obtain the vulnerability index of the species in each scenario. The first two refer to direct exposure to local climate change: (1) percentage of loss of suitable potential area (PA loss, see Sect. 2.2.1), (2) mismatch index (vulnerability index of Felicísimo et al. 2012, see Sect. 2.2.2.), including both, potential area and occurrence cells, and (3) adaptive capacity constraints (ACC, see Sect. 2.2.3.). We follow a specific combination of methods used by other researchers (Felicísimo et al. 2012; Barber et al. 2016; Young et al. 2015) but adding or emphasizing some specific vulnerability drivers for small island habitats (loss of potential area, small size potential area) as explained later. The sensitivity and adaptive capacity of the species were analyzed according to the exposure to climate change and adaptive constraints (Foden et al. 2019; Comer et al. 2019). The vulnerability index was calculated as follow (each of the three components ranges between 0 and 1): Vulnerability index = ((Potential area loss/100) + (Mismatch index) + (Adaptive capacity constraints/100))/3.

The vulnerability index encompassed six risk categories: 0–1: low ( $< 0.25$ ), intermediate (0.25–0.45), high (0.45–0.60), very high (0.60–0.75), critical (0.75–0.90) and very critical ( $> 0.90$ ).

## Species distribution models and loss of suitable potential area

Most vulnerability studies have been conducted at a rather coarse scale (Heikkinen et al. 2021) whereas small-scale data are necessary on small islands (Segal et al. 2021). To evaluate the climatic vulnerability of the species, we obtained data about the potential area they occupy through distribution models, using MaxEnt 3.4.1 (Phillips et al. 2006). As dependent variable, we introduced the presence of the selected species (200×200 m as was mentioned in the 2.1 section) and as predictor variables the mean temperature, the maximum and minimum temperatures of the warmest and coldest month and annual precipitation were considered, although we only used in each model variables that weren't highly correlated ( $R^2 < 0.7$ ). These layers were calculated through interpolations at a scale of 200×200 m based on weather stations data provided by the Spanish National Meteorological Agency (AEMET), which we homogenized with the R package 'climatol' (Guijarro 2019) for the period 1959–2019. Those data were divided into a first period from 1959 to 1989 and a second one from 1990 to 2019 (present), so it was possible to evaluate both present and

recent past scenarios (Bello et al., 2023). Interpolations for obtaining these layers were performed in R Studio 1.3.1093, using multiple linear regression algorithms for temperature and random forest (*randomForest* package, Liaw and Wiener 2018) for precipitation, as they resulted to be the best fitting models in each case. For the future scenarios, we adapted the anomalies from international layers to the Canary Islands (Karger et al. 2017), including different feasible climate change scenarios for the periods 2041–2060 (future I, FI) and 2061–2080 (future II, FII). We considered several Representative Concentration Pathways (RCP), but focused only on the most pessimistic (RCP 8.5).

With the species distribution models obtained we estimated the size of the potential area occupied by each species in hectares (ha). For that purpose, we selected the threshold of the 10th percentile with which we were able to transform the suitability maps of each species in presence-absence maps with 1 and 0 values (Bello et al., 2023). We selected it over other similar parameters offered by Maxent as it showed moderate values (neither too restrictive or permissive). We then counted all the pixels with value 1 in ESRI ArcGIS 10.1 and transformed that data into hectares, so we were able to obtain the potential area for each species and scenario, and the consequent increases or decreases in response to the climate change.

### Mismatch of the potential area and present occurrence cells between scenarios

Following Felicísimo et al. (2012), we calculated the mismatch index (MI; vulnerability index in Felicísimo et al. 2012) for each scenario, using the following formula:

$$MI = 1 - ((PA_{t_2} \cap OA_{t_1}) \cdot (PA_{t_2} \cap PA_{t_1})).$$

where  $PA_{t_2}$  is the potential area at time  $t_2$  (i.e., 1990–2019 for the present scenario, 2041–2060 for FI, and 2061–2080 for FII; in the following referred to as “future potential area”),  $OA_{t_1}$  is the occupied area at time  $t_1$  (i.e., 1959 to 1989 for the present scenario, and 1990–2019 for FI and FII, respectively; “current occupied area”), and  $PA_{t_1}$  is the potential area at time  $t_1$  (“current potential area”), all ranging from 0 to 1.

The MI also ranges from 0 to 1, with 0 and 1 indicating complete and no overlap, respectively, between potential area at time  $t_2$  and both potential and occupied area at time  $t_1$ . Thus, lower values mean that the species is more likely to maintain its niche despite climate change.

### Adaptive capacity constraints

For the calculation of the vulnerability index the ACC component was considered as proportion of the number of constraints present (from 1 (20%) to  $\geq 5$  (100%)). However, for the PCA analyses (see [statistical methods](#) section) an index (0–5) was used for each of the six adaptive constraints (the binary variable habitat specificity was not used in the PCA analyses, since it was only found in two species).

### Indirect climate exposure

- a. **(a) Habitat fragmentation** was considered when there is habitat discontinuity, either due to natural (e.g. orographic, including climate discontinuity) or anthropogenic causes (e.g. agricultural or urbanized areas). The index (0–5) used for the PCA analysis

- was established according with the number of population fragments (0=without fragmentation to 5=5 or more fragments).
- b. **(b) Habitat specificity.** Species with a low tolerance range (specialized niche requirements) tend to migrate less easily. This constraint was considered for species restricted to habitats underrepresented in the Canary Islands such as lithological (salic substrates) or freshwater habitats.
  - c. **(c) Small potential area.** The fragility of the insular biota due to their characteristically small island size may involve an extreme risk in their smallest potential habitats (Simberloff 2000), where the species may run out of habitat. Here, size of potential area was considered as a constraint to species expansion, when its area did not exceed 5% that of the entire island in question. The index (0–5) used for the PCA analysis was established between 1000 and 3000 ha on La Palma and 3500–10.500 on Tenerife, using a proportional distribution of the data at each island (Table S3).

### Species sensitivity

- d. **(d) Index of herbivory damage.** Invasive herbivores are a great threat to species expansion and persistence, and consequently the ability to migrate in response to climate change (Bello-Rodríguez et al. 2019; Martin et al. 2020; Kappes et al. 2021). To assess the impact of introduced and feral herbivores (European rabbit, Corsican mouflon, Babary sheep and domestic sheep-goats), an exhaustive field analysis was carried out. For this purpose, three localities of each species were selected, with a great effort to ensure they were as climatically or ecologically contrasting as possible. The species present on both islands were studied separately on each island. Rabbit damage is easily distinguishable from that caused by other mammalian species (rats and mice) because fresh droppings are frequently found around damaged plants. Characteristic rabbit damage marks are also left on herbaceous plants and shrubs, such as oblique cuts on branches and twigs, gnawed bark and a foliage height-line at 40–50 (70) cm above ground level (Cooke et al. 2008). Intensity of damage by rabbits, mouflons, goat-antelope and feral goats was assessed by applying the index (0–5) of Cooke et al. (2008).
- e. **(e) Small populations** refer to when the species has few occurrence cells (<20) or a low number of individuals (<250) in the localities where the species occurs. The index (0–5) used for the PCA analysis is included in the supplementary material (Table S4).
- f. **(f) Drought** was considered as a migration constraint when detected in more than 50% of the individuals selected for productivity analysis (see later) in any of the 3 locations assessed on each island. Individuals were considered as suffering from drought when they had more than 50% dry branches, or their flowering rate was less than 25% and attributable to drought stress. The index (0–5) used for the PCA analysis is included in the supplementary material (Table S5).
- g. **(g) Potential dispersal ability.** Biotic velocity of climate change (m/year) for each scenario was analysed in combination with the potential dispersal distance of each species. Biotic velocity of climate change was the mean distance in meters the species needs to migrate in each scenario to maintain the same climate conditions, calculated from past to present and from the present to the different futures, divided by the length of the period. A modified version of the Hamann et al. (2015) algorithms provided distance



maps for each species in each scenario, only considering the pixel values in which there was movement, from presence to absence and from absence to presence. To evaluate whether species potential dispersal capacity allowed it to cover this mean distance (m/year), three aspects were considered using the expert criteria based on: (a) potential seed dispersal distance, (b) seed production, and (c) regeneration rate (see supplementary S6, to know the 0–5 index used in the PCA analyses).

Potential seed dispersal distance was considered according to the published data for a subset of the species, and our own estimations according to the type of fruit and seed and dispersal vectors. We identified shorth (less than 10 m), middle (25–50 m) and longer distances. Shorth distance was identified in all species where barochory was the most common dispersal type, while seeds dispersed by birds were considered as longer distance (Nogales et al. 2013). Mean distance was identified for species with wind dispersal seeds, or even with zoochory by lizards, including not only fleshy fruits, but also dry fruits (González-Castro et al. 2015).

The same three localities and individuals used to estimate herbivory damage (see above) were also used to evaluate seed productivity. At each, the numbers of flowers were estimated on 15 randomly selected individuals of each species. Efforts were made to visit the populations at the peak of blooming or seed production. To estimate the reproductive effort/success (number of flowers, fruits and seeds), height and two perpendicular diameters were measured in every individual. All flowers per individual were counted in the field for species with flowers easily counted. When the flowers were too small to be count in the field (e.g., Asteraceae, Boraginaceae) only the number of inflorescences was counted in the field and these were collected, and their flowers were counted in the laboratory (15 inflorescences/locality). For large shrubs, five quadrats/individual were selected (100–2500 cm<sup>2</sup>) to count the number of flowers in the field. A mean of these numbers was then extrapolated to the total number of quadrats with flowers in bloom in every individual. For the species with heterogeneous fruit/seed production, 15 fruits/locality were collected, counting seed numbers to obtain mean seed production/fruit. When we detected substantial losses of flowers without fruit production, a correction factor was applied to estimate seed production.

The regeneration rate was estimated by the ratio between adults/juveniles based on 30 individuals randomly selected per locality.

## Statistical methods

To evaluate whether there were significant differences between the analyzed variables for common, restricted and rare species, we performed a Kruskal–Wallis test and a Dunn post-hoc test (Oksanen et al. 2018). Boxplots were realised using the function ‘boxplot’, applying the statistical software R (R Core Team 2020).

Principal Component Analysis (PCA) was conducted for each scenario (present, FI and FII) and species group (all combined, common, rare, restricted, Tenerife and La Palma) in R software (R Core Team 2020) using ‘prcomp’ function. All variables analyzed (vulnerability index, rarity, ACC, potential area loss, MI, potential area; Table S3) were standardised and included as input dataset. The least significant variables were removed until the explained variance of principal components 1 and 2 stabilized, ensuring a minimum of five input

variables for each PCA. Spearman's correlation tests were also applied to the relationship between the principal component factors, input variables and vulnerability indices.

## Results

Among the 63 endemic flowering plant species assessed in the alpine zone of the Canary Islands there were currently 65% at low risk (vulnerability index 1 and 2), 33.3% at high risk (vulnerability index 3 and 4) and 1.6% at critical risk (vulnerability index 5) (Table 1). A progressive increase in risk occurred in 55.5% of species through the period. Currently on Tenerife, 24% of species are at high risk, while on La Palma reaches 43.3%. In near future (FI) La Palma may show slightly higher vulnerability (high risk) (33.0%) than Tenerife (36.5%). This tendency increases in future II (FII) (Tenerife: 60% of species at high risk, and La Palma: 40%). Critical species have similar percentages (20% and 21.2%) in F II on both islands.

Common and restricted species showed ca. 80% of species currently at low risk (Table 1). High risk was detected in 15.4% and 20% of common and restricted species, respectively. In contrast, rare species showed only 31.8% of species at low risk and 63.64% with high

**Table 1** Number of species in each vulnerability category and percentage of species at risk (low: 1–2 vulnerability index, high (3–4) and critical (5–6), for three scenarios, present: (1990–2019), future I: (2041–2060) and future II: (2061–2080)

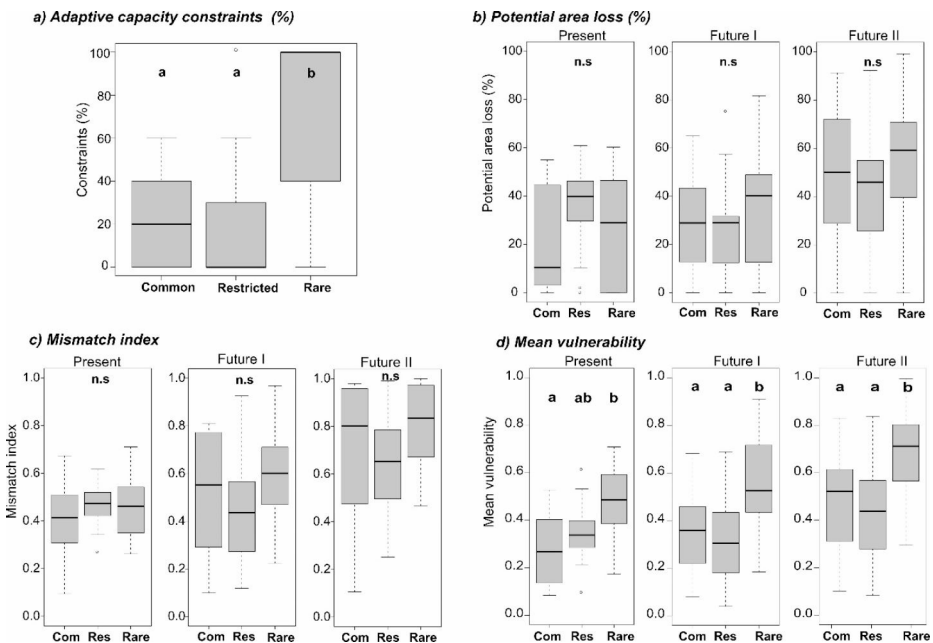
	Vulnerability index						Risk (%)		
	Low	Intermediate	High	Very high	Critical	Very critical	Low	High	Critical
<b>Common</b>									
Present	11	11	4	0	0	0	84.62	15.38	0.00
F I	8	11	6	1	0	0	73.08	26.92	0.00
F II	5	5	9	6	1	0	38.46	57.69	3.85
<b>Restricted</b>									
Present	3	9	2	1	0	0	80.00	20.00	0.00
F I	5	6	2	2	0	0	73.33	26.67	0.00
F II	3	4	4	2	2	0	46.67	40.00	13.33
<b>Rare</b>									
Present	3	4	10	4	1	0	31.82	63.64	4.55
F I	1	4	7	4	5	1	22.73	50.00	27.27
F II	0	1	8	3	5	5	4.55	50.00	45.45
<b>La Palma</b>									
Present	2	15	10	3	0	0	56.67	43.33	0.00
F I	8	10	6	4	1	1	60.00	33.33	6.67
F II	5	7	9	3	5	1	40.00	40.00	20.00
<b>Tenerife</b>									
Present	15	9	6	2	1	0	72.73	24.24	3.03
F I	6	11	9	3	4	0	51.52	36.36	12.12
F II	3	3	12	8	3	4	18.18	60.61	21.21
<b>All species</b>									
Present	17	24	16	5	1	0	65.08	33.33	1.59
F I	14	22	13	9	4	1	57.14	34.92	7.94
F II	9	10	19	12	8	5	30.16	49.21	20.63

risk. Critical risk at present was found only for rare species (4.5%). Examining the changes through the present studied period (1990–2019) to FI (2041–2060) and FII (2061–2080), it is noteworthy that for common species the high risk in FI may soon be near twice as much as today (26.9%), increasing up to 26.6% for restricted species (Table 1). For rare species, an increase in critical risk (27.2%) was projected for the near FI, indicating a higher priority for management of many species in this group, which in FII show 45.4% of species at critical risk.

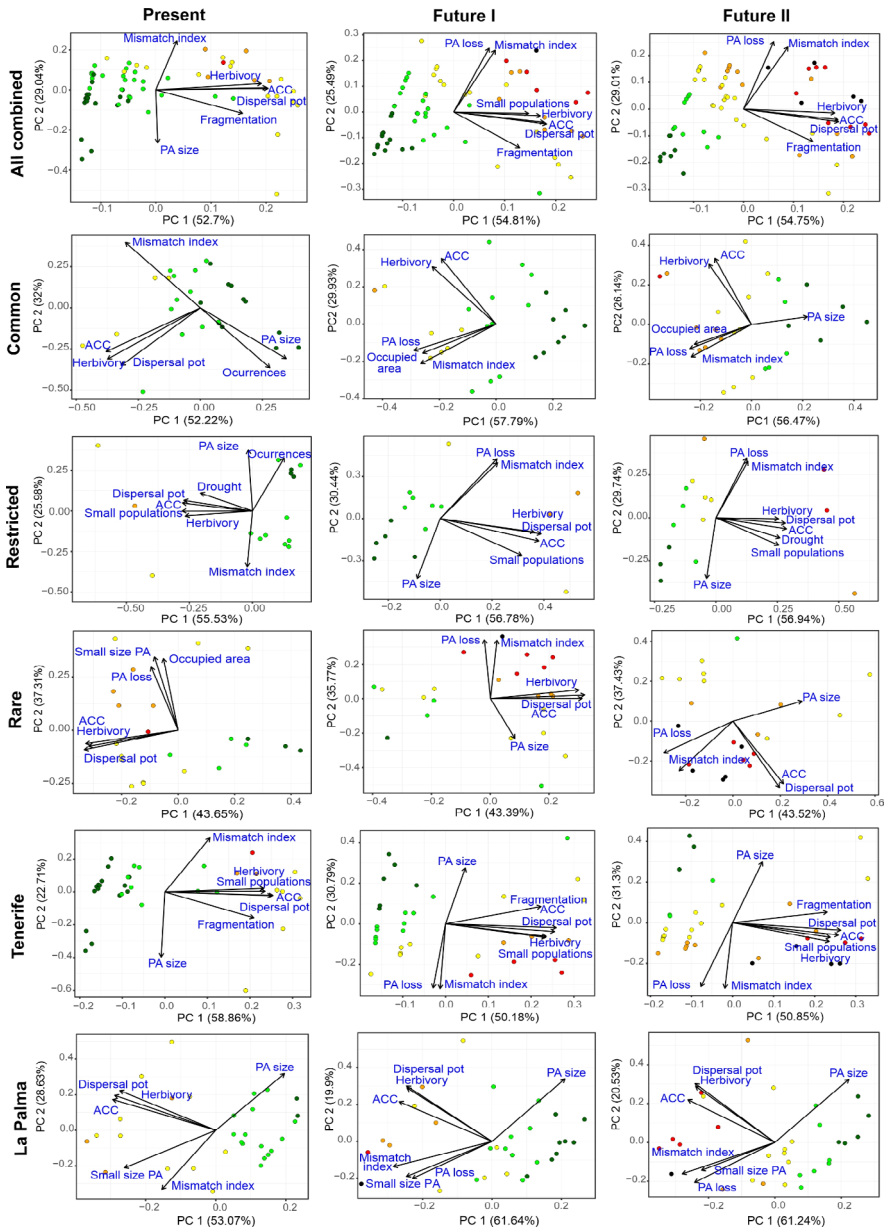
Rare species show significantly higher vulnerability index than common and restricted species (Present, Kruskal-Wallis test,  $\chi^2_2=16.40$ ,  $p<0.0001$ ; future I:  $\chi^2_2=17.50$ ,  $p<0.0001$  and future II:  $\chi^2_2=14.98$ ,  $p<0.001$ ) (Fig. 2d). However, to estimate the vulnerability index focusing on the drivers considered (PA loss, mismatch index and ACC), the adaptive constraints are the only significant driver explaining the vulnerability difference for rare species ( $\chi^2_2=22.23$ ;  $p<0.00001$ , Fig. 2a). Mismatch index and PA shows no significant differences between rarity groups ( $p>0.05$ ).

When Principal Component Analysis was applied to all species (Fig. 3), the most important driver (PCA1) explaining vulnerability was ACC (PCA1) followed by potential dispersal ability, herbivore damage index and fragmentation; while PA size (present scenario), mismatch (along all three scenarios) and PA loss and (future I and II) index were significant along axis 2 (PCA2) (see also Table S2, supplementary material). This pattern of drivers (PCA1) occurs in all three scenarios.

For common species, vulnerability is mainly explained by the same drivers explaining the general patterns mentioned before, although mismatch index and number of occur-



**Fig. 2** Rarity index groups and drivers considered in the species vulnerability index: **a)** adaptive capacity constraints **b)** Potential area loss, **c)** mismatch index between different scenarios, and **d)** vulnerability index obtained for each scenario (present, future I and future II). Com=common, Res=restricted. Lower-case letters show significant differences between the rarity groups



**Fig. 3** Principal Component Analyses for all species combined, rarity groups and islands along all three scenarios (present, future I and future II). Variables are indicated by arrows. Points represent species and colors the vulnerability category (dark green = low, green = intermediate, yellow = high, orange = very high, red = critical, black = very critical). P.A. size (=area (ha) of the potential area). P.A. loss (= % potential area loss), mismatch (=mismatch index), constraints (ACC) (%). Rarity approaches: occurrences (=number of occurrence cells), occupied area (=PA occupied (%)). Significant individual A.C.C. includes: fragmentation, small P.A. (P.A. occupy less than 5% of the island area), habitat specificity, herbivory (herbivore damage index), small populations, drought and dispersal pot. (=potential dispersal ability)

rence cells were highly significant while no correlations were found for fragmentation. For restricted species vulnerability is highly significantly correlated also with ACC, herbivory index and potential dispersal, but drought is significant for restricted species at present and FII scenarios and small populations in all three scenarios. It is interesting that the  $n^{\circ}$  of occurrence cells only was a significant ( $p < 0.001$ ) driver of vulnerability for common and restricted species at present and the percentage of occupied area ( $p < 0.0001$ ) for common species in both future scenarios (see table S2 supplementary material). For rare species, dispersal potential was the most generalized adaptive constraint, while herbivory damage index was only highly significant ( $p < 0.0001$ ) in the present and future I scenarios.).

When La Palma and Tenerife were analysed separately, we found clearer differences between islands in the present scenario, compared to futures I and II. Percentage of ACC, small populations, species dispersal capacity, herbivore damage index and fragmentation were the most important drivers (PCA1) ( $p < 0.0001$ ) throughout the whole period assessed for Tenerife. For La Palma, mismatch index and PA loss and PA size were also highly significant in futures I and II on both islands. Among the individual constraints considered, herbivore damage and potential dispersal were significant ( $p < 0.0001$ ) on both islands along all three scenarios.

Herbivore damage represented a constraint for 66% of the species (S3), being highly significant for all rarity groups and both islands in all scenarios, except for future II for rare species (Fig. 3). Potential dispersal ability was a constraint for 36.5% of the species and highly significant for both islands and all rarity groups, except for common species in the future scenarios. Contrastingly, small populations (33.3%) were significant for restricted species and for Tenerife. Island area < 5% (25.4% of the species) was significant on La Palma (all three scenarios), while fragmentation (19.0%) on Tenerife (all three scenarios) Drought was only significant for restricted species (17.5%).

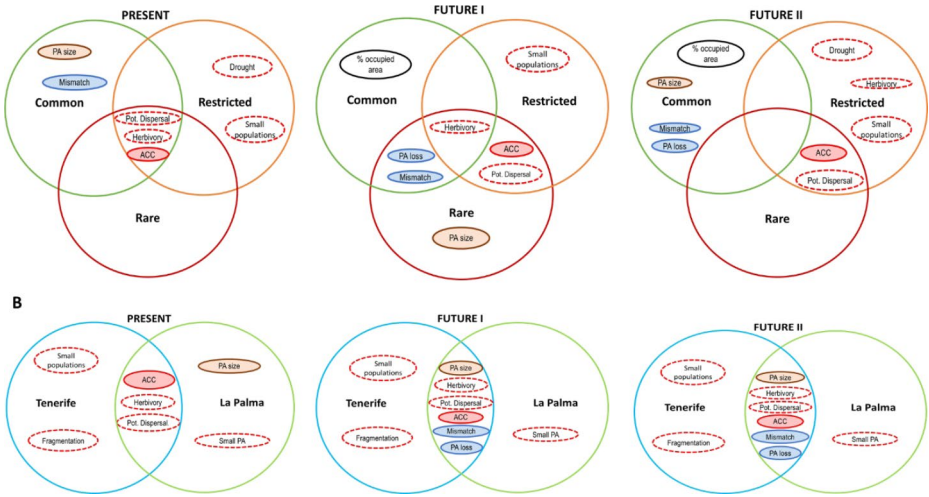
The PA size of the species showed a significant negative Spearman correlation with species vulnerability ( $p < 0.0001$ ) throughout our assessment periods, but no correlation was found with the percentage area occupied ( $p > 0.05$ ). In fact, rare species showed no significant differences from common species in PA size ( $p > 0.05$ ). Potential area size was negatively correlated with drivers directly related to climate change: PA loss ( $p < 0.0001$ ) and mismatch index ( $p < 0.0001$ ), and with the mismatch of the number of occurrence cells ( $p < 0.0001$ ).

## Discussion

Despite the restricted vulnerability evaluation method used here, since it depends on three components, our assessment revealed that the flora of alpine ecosystems in the Canary Islands is at significant risk due to climate change. According to the vulnerability index applied here, even at present 33.3% of the species are at risk (high vulnerability index), and this percentage will increase to 35% in the high-risk category in 2040–2060 (future I) and to 49% in 2061–2080 (future II), including also the critical category (8% in FI and 20.6 in F2). Species vulnerability depends on a balance between the PA size and the ACC of the species. These two drivers vary according to the rarity group under assessment. The specific drivers associated with global warming (PA loss and mismatch index) were no high significant drivers ( $p < 0.0001$ ) explaining species vulnerability at present (only MI for common

species), although their significance increased in the future scenarios for both islands and for common species, including PA loss (Fig. 4). The ACC hindering the species responses was an important driver in all scenarios on both islands and for all rarity groups at present and for rare and restricted species in the future scenarios (Fig. 4). Rare species showed significantly higher vulnerability than common and restricted species. However, this difference is not due to a stronger significant effect of climate change drivers, but rather to the current state of the populations and their threats. The vulnerability pattern during all three scenarios was different on the two islands (Fig. 4). While on La Palma it was notably differentiated by the influence of the small PA size, on Tenerife was by fragmentation and small populations. Tenerife, where the alpine ecosystem occupies a larger zone, shows a delay in climate change impact compared to La Palma, resulting in lower vulnerability at present (intermediate on Tenerife with an index of 0.31 and high on La Palma, 0.44). However, this vulnerability will probably increase according to the future scenarios, due to shrinkage in potential area attributable to island topography and in the mismatch of the currently suitable areas for plants to survive.

In this study we are working with very small areas (mean PA size for all species was 14,996 ha at present, 11,690 ha in future I and 9,237 in future II). The PA size of the species showed a significant negative correlation with species vulnerability throughout our assessment periods, but no with the percentage of occupied area. In fact, rare species showed no significant differences from common species in PA size, which along with their significant higher percentage of constraints points to anthropogenic rarity. Thus, constraints are limiting the area of the realized niches within the potential areas (Gaston 2003; Svening and Skov 2004) and the effectivity of species dispersal capacity, an important trait in their



**Fig. 4** Conceptual summary of the main drivers obtained in the PCA ( $p < 0.0001$ , see table S2) explaining vulnerability in the rarity groups of 63 endemic vascular plant species distinguished (common, restricted and rare species); a) in three scenarios: present, future I, and future II. b), on the islands Tenerife and La Palma. Shared drivers are situated in the intersect area between circles. Brown: PA size (ha). Blue: drivers related to climate change (mismatch=mismatch index, and PA loss=% area lost from potential area). Red: percentage of adaptive capacity constraints (ACC). Dashed red: Significant individual adaptive capacity constraints, i.e., small PA (potential area occupies less than 5% of the island area), herbivory (=herbivore damage), small populations, drought, Pot. dispersal (=potential dispersal ability). White: % occupied area=% of the PA occupied)

response to climate change (Estrada et al. 2015). These results are clearly related to the high degree of anthropogenic disturbance of the alpine ecosystem on both islands (Rodríguez-Delgado & Elena-Roselló, 2006; Garzón et al. 2010; Irl et al. 2012). Human impacts are significantly more intense on islands than in mainland areas (Kier et al. 2009), which might explain the large potential areas of rare species. Mostly due to invasive herbivores, many rare species occupy only a small area within their potential area. Consequently, their ecological requirements are unknown, since reduced populations do not always show the true ecological requirements of the species. Sometimes, they are even preserved in areas where they are doomed to extinction, because the climatic conditions there are not the most suitable for them (Marrero-Gómez et al. 2007). For these species, experimental translocations, close monitoring and modelling are essential to estimate the potential area necessary to manage them in the face of climate change (Bellis et al. 2021).

Potential area size was negatively correlated with drivers directly related to climate change, PA loss and mismatch index, and with the mismatch of the number of occurrence cells. Therefore, we should expect that vulnerability of common species (those occupying a greater proportion of the potential area), would be more dependent on the drivers directly related to climate change. However, PA size prevents establishing this relationship, since the common species are also highly vulnerable in very small habitats that are disappearing with global warming. Small habitat size is itself a notable risk (Enquist et al. 2019; Horváth et al. 2019), and vulnerability of the studied alpine ecosystem is probably underestimated due to habitat loss. Moreover, the characteristic isolation of insular alpine ecosystems, islands within islands (Fernández-Palacios et al. 2014) makes them more vulnerable because of limitations to spatial processes to migration (Rybicki and Hanski 2013; Horváth et al. 2019).

The emerging picture is that species with large ranges may have small populations, and that there are common species with small potential areas. Thus, two types of rarity are combined in the species of this alpine ecosystem: habitat rarity (dependent on PA size) and species rarity, mostly related to stressor factors (ACC). This appears to reduce the ecological significance of PA to climate change and highlights the importance of identifying and understanding the drivers that most constrain the realized niche. In fact, the widely established close relationship between rarity and extinction risk (e.g., Schwartz et al. 2006) has been long questioned because of the existence of natural rarity in small habitats (Gaston 1994; Martín 2009). Indeed, the use of the IUCN absolute presence thresholds to evaluate the risk species face has been discouraged on small oceanic islands (Martín et al. 2009; González-Mancebo et al. 2012), since it can lead to overestimating the threat in smaller habitats. Nevertheless, current climate change has arrived as a factor that increases the risk level of small populations, whether the rarity is due to natural or anthropogenic causes. Thus, small natural habitats may be also at risk even for common species, because climatic stability is particularly essential to species survival in small areas and populations (Morueta-Holme et al. 2013). This is of special concern regarding geographically isolated habitats subjected to sustained stress over time, as occurs on oceanic islands with undergoing introduced herbivore damage (Caujapé-Castells et al. 2010).

Although rare species show significantly higher vulnerability index than common and restricted species, these latter two groups include species at high risk at present and even critical in the future. Common species may play an important role in ecosystem functioning and their decline can even lead towards ecosystem collapse, as recently detected for *Spartocytisus supranubius* on Tenerife (Cubas et al. 2022). Although common species may have

a greater evolutive potential under the pressure of abiotic and biotic changes, the rapidity of current climate change may cancel advantages for this species group, depending on the constraints to their adaptability and loss of their potential areas. Other common species at high risk at present on La Palma include *Arrhenatherum calderae*, the dominant member of Poaceae currently present in this ecosystem, *Genista benehoavensis* and *Echium gentianoides*. The latter two are threatened species managed for the last 30 years by the Caldera de Taburiente National Park. They now occupy respectively 89.15% and 83.03% of their potential area, which however is currently very small (4708 ha and 6109 ha respectively). The near future also holds high risk for some common species on Tenerife: *A. calderae*, *Argyranthemum teneriffae*, *Descurainia bourgeauana*, *Nepeta teydea* and *Tolpis webbii*. Some of these species are currently in expansion: *A. teneriffae*, *T. webbii* and *A. calderae* (Martin et al. 2021), which suggests a delay in their reaching high risk in the alpine zone of this island. A greater area and elevation (more than 1000 m higher than La Palma) mean without doubt more time to extend their survival of climate change in this zone. Although some species are already starting to retreat in southern areas, such as *D. bourgeauana*, *N. teydea* or *S. supranubius* (Martin et al. 2020, 2021, Cubas et al. 2022).

Rare species with large PA size included some with a high dispersal potential, but highly threatened, like *Cicer canariense* (Tenerife and La Palma). This small legume can grow from 445 to 2000 m in elevation, is also quite drought tolerant and regenerates quickly but is highly palatable for invasive herbivores. Its potential area is 21,290 ha with 12% occupied on La Palma, 50,741 ha on Tenerife (1% occupied). 61% of the species we classified as rare occupy a maximum 5% of their potential area and are threatened on their native island, while those that occupy more are expanding currently, such as *Cheirolophus teydis* on Tenerife, or threatened species with new populations resulting from National Parks management. Knowledge is greatly lacking about the fundamental and realized niches of these species, even though some are well studied. However, there are also species whose rarity derives from their small PA size, as for instance *Viola palmensis* (64% of 1784 ha occupied, in 46 occurrence cells).

Climate change is affecting plant communities and ecosystems around the world. Managing communities so that they can resist requires specific measures with precise methods for assessing vulnerability. Such supportive aids can prioritize actions within the framework of comprehensive management. Our results indicate that conservation management nowadays must be widely distributed among all native species, and not only focus on threatened or restricted ones. Drivers of vulnerability vary strongly between species, and therefore understanding and including them in climate change vulnerability assessments is essential for efficient allocation of finite management resources (Beever et al. 2015). Our results highlight the need for urgent management of rare and restricted species, to gauge the possibilities of enlarging their realized niches to enhance and prolong their adaptive capacity (Thurman et al. 2022). In other words, to reduce the constraints on the adaptability of these species through the removal or mitigation of threats, and to strengthen and better understand the realized niche by means of experimental translocations. Common species also need management since they are inhabiting habitats that are already disappearing around the summits of the islands, so management must be addressed to preserve them in the best possible conditions. Notably, removal or effective control of invasive herbivores will help to achieve this, since they are the strongest constraint on all the groups analyzed. This study



emphasizes the need to further assess the climate change vulnerability of species and the drivers of their responses, to achieve better management of these unique ecosystems.

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**Author contributions** J.M.G.M. designed the study and wrote the manuscript; V.B.R. collected the data; J.M.G.M., J.C. and J.P.D. analysed the data; J.L.M.E., A.B.B., A.P. and M.A. improved the original manuscript and contributed to the evaluation of the species. All authors gave final approval for publication.

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**Data Availability** Supplementary material includes the main data obtained for each species.

## Declarations

**Competing interests** The authors declare no competing interests.

**Ethical approval** Not applicable for both human and/ or animal studies.

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## Authors and Affiliations

Juana María González Mancebo<sup>1</sup> · Víctor Bello-Rodríguez<sup>1</sup> · Jonay Cubas<sup>1</sup> · Jesús Parada-Díaz<sup>1</sup> · Ángel Bañares-Baudet<sup>4</sup> · Ángel Palomares<sup>2</sup> · José Luís Martín-Esquivel<sup>3</sup> · Marcelino J. del Arco<sup>1</sup>

✉ Juana María González Mancebo  
jglezm@ull.edu.es

<sup>1</sup> Plant Conservation and Biogeography Research Group, Departamento de Botánica, Ecología y Fisiología Vegetal, Universidad de La Laguna, Avda. Francisco Sánchez s/n, 38200 Apdo 456. La Laguna, Tenerife, Islas Canarias, España

<sup>2</sup> Caldera de Taburiente National Park, El Paso, La Palma 38750, Spain

<sup>3</sup> Teide National Park, La Orotava, Tenerife, Islas Canarias 38300, España

<sup>4</sup> Departamento de Botánica, Ecología y Fisiología Vegetal, Universidad de La Laguna, La Laguna, España