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RESEARCH ARTICLE

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Effects of climate change on the distribution of plant species and plant functional strategies on the Canary Islands

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Abstract

Aim: Oceanic islands possess unique floras with high proportions of endemic species. Island floras are expected to be severely affected by changing climatic conditions as species on islands have limited distribution ranges and small population sizes and face the constraints of insularity to track their climatic niches. We aimed to assess how ongoing climate change affects the range sizes of oceanic island plants, identifying species of particular conservation concern.

Location: Canary Islands, Spain.

Methods: We combined species occurrence data from single-island endemic, archipelago endemic and nonendemic native plant species of the Canary Islands with data on current and future climatic conditions. Bayesian Additive Regression Trees were

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used to assess the effect of climate change on species distributions; 71% ($n = 502$ species) of the native Canary Island species had models deemed good enough. To further assess how climate change affects plant functional strategies, we collected data on woodiness and succulence.

Results: Single-island endemic species were projected to lose a greater proportion of their climatically suitable area ($\tilde{x} = -0.36$) than archipelago endemics ($\tilde{x} = -0.28$) or nonendemic native species ($\tilde{x} = -0.26$), especially on Lanzarote and Fuerteventura, which are expected to experience less annual precipitation in the future. Moreover, herbaceous single-island endemics were projected to gain less and lose more climatically suitable area than insular woody single-island endemics. By contrast, we found that succulent single-island endemics and nonendemic natives gain more and lose less climatically suitable area.

Main Conclusions: While all native species are of conservation importance, we emphasise single-island endemic species not characterised by functional strategies associated with water use efficiency. Our results are particularly critical for other oceanic island floras that are not constituted by such a vast diversity of insular woody species as the Canary Islands.

KEYWORDS
climate change, climatic niche, endemism, functional strategies, oceanic island flora, potential habitat, range shift

1 | INTRODUCTION

Oceanic islands are nature's laboratories often having unique floras and faunas, owing to their ontogeny, remoteness and evolutionary potential (Whittaker et al., 2017; Whittaker & Fernández-Palacios, 2007). However, oceanic island biodiversity is considered to be disproportionately threatened by causes directly or indirectly related to human activities (Fernández-Palacios, Kreft, et al., 2021; Macinnis-Ng et al., 2021; Tershy et al., 2015; Veron et al., 2019), particularly climate change (Fernández-Palacios, Kreft, et al., 2021). To date, climate change research on land has mainly focussed on continents, even though changing temperature and precipitation patterns on oceanic islands will have particular relevance for island biota (Harter et al., 2015). Given the disproportionately large contribution of islands to global biodiversity (Fernández-Palacios, Kreft, et al., 2021; Kier et al., 2009), the implications of climate change for oceanic island biodiversity are globally important.

The United Nations Intergovernmental Panel on Climate Change (IPCC) states that global surface temperatures will rise, leading to severe alterations in precipitation patterns in the 21st century (IPCC, 2021). These climatic changes could have severe impacts on oceanic island floras (Harter et al., 2015). Most island species can only retreat to potential refuge habitats within their island, or neighbouring islands, if they are within reach (Gillespie et al., 2008). In addition, oceanic islands are restricted in area, which limits the range size of endemic species. A limited range is often associated with small population sizes and higher vulnerability of species to environmental changes, natural hazards and demographic stochasticity (Barton & Fortunel, 2023; Lande, 1993). Many island endemic species are already under pressure from habitat loss, intensification of land use and the introduction of invasive alien species. Consequently, many island species are listed as threatened on the IUCN Red List (www.iucnredlist.org; Romeiras et al., 2016). Furthermore, according to 21st century climate change scenarios, ongoing climate change will exacerbate the threat levels for island plants (Fortini et al., 2013; Gillespie et al., 2008). However, climatic alterations and their consequences on an entire archipelago's diversity and floristic composition (e.g. species richness, endemism and functional strategies) have not yet been assessed.

Under changing climatic conditions, species populations need to track their climatic niche (Chen et al., 2011; Lenoir & Svenning, 2015) or adapt to the novel climatic conditions for survival (Bradshaw & Holzapfel, 2006; Hoffmann & Sgrò, 2011). The tracking of climatic niches requires that climatically suitable habitat is still available within the dispersal range of a species (Zanatta et al., 2020; Zurell et al., 2016). However, many island species are bound to their islands and have narrow climatic niches (Fernández-Palacios, Otto, et al., 2021), which can increase the risk of extinction under changing environmental conditions (Fortini et al., 2013; Thuiller et al., 2005). For example, species assemblages in high-elevation areas on oceanic islands are disproportionately rich in endemic species (Steinbauer et al., 2016) and alpine plants on islands have been found to be particularly vulnerable to both changing precipitation patterns (Marrero-Gómez et al., 2007; Sperling et al., 2004) and increasing temperatures (Giambelluca et al., 2008). Moreover, species occurring in arid areas may be particularly threatened, despite water conservation strategies and drought adaptations, because arid areas may experience greater aridification than humid areas (Huang et al., 2017), and aridification can have critical effects on biodiversity (Cartereau et al., 2023; Shi et al., 2021). In addition, islands have a higher proportion of keystone species than mainland regions, and their shift in space or possible extinction may dramatically affect entire ecosystems (Olano et al., 2017). Hence, understanding the effects of climate change on the potential distribution of island plants is vital for informing conservation efforts for endemic and native floras.

Insular woodiness is a key syndrome in island endemic plants (Burns, 2019; Carlquist, 1974; Lens, Davin, et al., 2013) and describes the evolutionary transition from herbaceous to woody species on islands. There are several hypotheses regarding the origin of insular woodiness, but one particularly well-supported hypothesis suggests that insular woodiness may be induced by drought stress, which requires better protection of root-to-shoot water transport against hydraulic dysfunction (Dória et al., 2018; Hooft van Huysduynen et al., 2021; Lens, Tixier, et al., 2013; Zizka et al., 2022). Therefore, insular woody species may be better protected from increasing drought frequencies under future climatic conditions, giving them a more prominent role than herbaceous and noninsular woody species in island floras. However, owing to dispersal limitations, long generation times and longevity of many woody plant species, a time lag in the response of woody plants to climate change is expected (Kissling et al., 2010). Therefore, it is unclear whether insular woody species have advantages or disadvantages under future climatic conditions.

Succulent plants are drought tolerant because they store water to sustain their metabolism when hygric stress occurs (Griffiths & Males, 2017). Additionally, succulence is accompanied by a crassulacean acid metabolism (CAM) photosynthetic pathway in some clades, leading to higher water use efficiency due to a shift in CO_2 fixation from day to night (Griffiths & Males, 2017). Hence, succulent species could have an advantage over nonsucculent species if hot and dry climatic conditions increase because of anthropogenic climate change. However, previous studies have been ambiguous regarding the resilience of succulent species to climate change; they have shown a high susceptibility of succulents to drought intensity (Midgley & Thuiller, 2007; Young et al., 2016), no effect (Thuiller et al., 2006; Schmiedel et al., 2012) or a lesser impact than for nonsucculent species (Hoffman et al., 2009). Nonetheless, as arid environments are predicted to expand due to ongoing climate change (Seneviratne et al., 2012; Zscheischler et al., 2018), succulent species may be able to track their climatic niche, while nonsucculent species may lose climatically suitable habitat. In any case, the role of succulence in the response of oceanic island floras to changing climatic conditions is yet to be assessed.

In this study, we aim to assess how much potentially climatically suitable area will be lost or gained for endemic and nonendemic native seed-plant species of the Canary Islands, and their associated plant functional strategies, under different climate change scenarios. We divided the endemic species group into single-island endemics and archipelago endemics (see Hanz et al., 2022) to test the following three hypotheses: (1) Single-island endemics are the most susceptible to changing climatic conditions, as they may have narrower climatic niches and smaller range sizes than other species and limited potential for range shifts. (2) High-elevation and arid areas have greater loss of potentially climatically suitable area than lower-elevation and humid areas across all floristic groups. The loss of climatically suitable area might be driven by difficulties for species to track their climatic requirements, particularly under distinct environmental pressures. (3) Herbaceous, noninsular woody and nonsucculent species will experience greater climate change-related reductions in potentially climatically suitable areas than insular woody and succulent species. This is because we expect increases in temperature and decreases in precipitation across the Canary Islands—conditions that are less favourable for these plant functional strategies.

2 | METHODS

2.1 | Study area

The Canary Islands span an age gradient from the easternmost island of Fuerteventura (21 Ma) to the westernmost island of El Hierro (1.1 Ma; Carracedo et al., 2002; Florencio et al., 2021). The old, eastern islands of Lanzarote and Fuerteventura are eroded and relatively flat (highest peak = 807 m a.s.l.), whereas the western isles are steeper and more rugged, reaching a maximum elevation on Tenerife (3718 m a.s.l., Mt. Teide). The Canary Islands are characterised by a Subtropical-Mediterranean climate regime (del Arco Aguilar et al., 2010). The average temperature decreases gradually from the inframediterranean zone (mean annual temperature (MAT): 18–22°C), through the thermo- and mesomediterranean zone (MAT: 11–18°C) up to the supra- and oromediterranean zone (MAT: 3.5–11°C; del Arco Aguilar et al., 2010). NE trade winds influence the western and central islands, and rain shadow effects cause water availability to differ between windward and leeward slopes. Annual rainfall is 50–500 mm in the lower parts, 300–800 mm in the mid-elevation areas (with maxima up to 1400 mm in the cloud zone) and 500–600 mm in the upper parts (Patiño et al., 2023). Leeward slopes are generally drier, with a more continuous climatic gradient from the coast to the summit.

The archipelago represents an appropriate study system for analysing climate change-induced shifts in suitable areas of endemic and nonendemic native plant species because it offers diverse environmental conditions and a large proportion of endemic species throughout different zonal ecosystems (del Arco Aguilar & Rodríguez-Delgado, 2018). It can be roughly divided into the following zonal belts (from coast to summit): succulent scrub, thermophilous forest and woodland, evergreen laurel forest (only on the windward side), pine woodland, summit broom scrub and the Teide violet community (del Arco Aguilar & Rodríguez-Delgado, 2018). Water stress and adaptation to arid conditions are important determinants of species distribution in the low- and high-elevation ecosystems of the archipelago (del Arco Aguilar et al., 2010), whereas mid-elevation ecosystems strongly depend on the trade wind layer and constantly humid conditions with limited temperature variation (García-Santos et al., 2004). The native flora of the Canary Islands has a dominant Mediterranean influence, but the laurel forest is considered rich in Tertiary relictual palaeoendemics (del Arco Aguilar & Rodríguez-Delgado, 2018; but see Kondraskov et al., 2015). Currently, the Canary Island vascular flora encompasses approximately 2400 species, of which roughly 60% are considered native and 42% endemic (Beierkuhnlein et al., 2021).

2.2 | Plant occurrence data

We used occurrence data from the Banco de Datos de Biodiversidad de Canarias, an open-access database, for single-island endemic (SIE; $n=325$), archipelago endemic (AE; $n=234$) and definitely nonendemic native (NEN; $n=149$) extant seed-plant species (excluding subspecies), in a raster of 500 × 500 m grid cells covering the Canary Islands (https://www.biodiversidadcanarias.es/biota/) [accessed 14/03/2022]. The database includes all species listed in the checklist of the Banco de Datos de Biodiversidad de Canarias, across 31,628 grid cell assemblages. Species range in occurrence from 1 to 4466 cells. We only retrieved occurrences for which a species has been certainly observed or collected (precision level 1 of four levels). The Banco de Datos de Biodiversidad de Canarias provides presence-only information that is spatially biased by sampling effort (Hortal et al., 2007). However, the sampling bias of SIEs, AEs and NENs is less than for species overall because studies incorporated into the database involved focus on, and extensive sampling of, endemic and nonendemic native species (https://www.biodiversidadcanarias.es/biota/documentos). We considered a species (pseudo-)absent if it was not recorded at a site, although we recognise that there is debate as to whether this truly represents absences.

We excluded 153 species with fewer than 10 database occurrences (97 SIEs, 25 AEs and 31 NENs) from the analysis, since model fits and evaluation with few data may be unreliable (Collart & Guisan, 2023; Jiménez-Valverde, 2020; Proosdij et al., 2016). However, we acknowledge that range-restricted species are often particularly threatened by climate change (Ohlemüller et al., 2008) and that our models are, to some extent, biased against small-ranged SIEs and nonsucculent herbs within AEs and NENs (see Appendix S1). Furthermore, we restricted the frequent species to 500 random occurrences to avoid sampling bias (seven AEs and six NENs). We excluded the frequently cultivated *Phoenix canariensis* from the dataset because its occurrence was overrepresented in the database ($n=4446$ occurrences) and the current species distribution does not reflect its climatic niche. A list of the number of occurrences of all species is provided in the Appendix S2.

2.3 | Plant functional strategies

We collected data on insular woodiness and succulence, which are relevant for species' responses to changing climatic conditions. As insular woodiness can be challenging to distinguish from noninsular woodiness (ancestral and derived woodiness) and herbaceousness, we mostly referred to literature sources from extensive studies on the woodiness of Canary Island plants (Hooft van Huysduynen et al., 2021; Lens, Davin, et al., 2013; Zizka et al., 2022). We defined plants as succulent if they displayed thickened leaves or fleshy stems. The thickness or fleshiness of plant organs indicates their ability to store water in their tissue (including moderately succulent species such as *Rumex lunaria*). We retrieved information on succulence from Muer et al. (2016) and taxonomic monographs, which have been shown to be reliable sources of trait data (Cutts et al., 2021).

2.4 | Climate data

We implemented species distribution models focussing on 19 climatic variables with potentially direct or indirect impact on species occurrences (Xu & Hutchinson, 2013). Climate data were retrieved from Patiño et al. (2023), who generated bioclimatic variables based on a bias-corrected downscaling from 30-arc-second to 100 m resolution of climatological data (1979–2013) from CHELSA V1.2 (Karger et al., 2017, 2018), using observations from meteorological stations (Patiño et al., 2023). Specifically, these data comprise mean, maximum and minimum daily near-surface air temperatures and precipitation. Bias correction was applied to the 30-arc-second resolution and the subsequent downscaling was achieved by applying an atmospheric lapse rate correction following the approach described in Karger et al. (2017). High-resolution climate data for the future (2071–2100) were generated by a Delta change anomaly interpolation (Karger et al., 2023). This computed and downscaled the anomalies between present and future monthly climatic maps at 30-arc-second resolution, resulting from a downscaling of Global Circulation Models (GCMs) from the 6th phase of the Climate Model Intercomparison Project (CMIP6) using the CHELSA CMIP6 module (https://gitlabext.wsl.ch/karger/chelsa_cmip6; Karger et al., 2023). The anomalies were then downscaled using B-spline interpolation to 30-arc-seconds and applied to present maps at 100 m (Patiño et al., 2023).

We used three Shared Socioeconomic Pathways (SSPs) to represent a wide range of future socioeconomic conditions: from sustainable development and equality (SSP1 or 'sustainability'), a world of resurgent nationalism (SSP3 or 'regional rivalry'), and rapid and unconstrained growth in economics and energy use (SSP5 or 'fossil-fuelled development'; Gidden et al., 2019). Five Global Circulation Models (GCMs; including GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-LR, MRI-ESM2-0, UKESM1-0-LL) from the Impact Model Intercomparison Project (ISIMIP) were considered for this study (Lange, 2019; Lange & Büchner, 2021). All the climatic maps were then aggregated for this study to a resolution of 500 m to match the occurrence data resolution in R, using the 'raster' package (Hijmans, 2019). Hence, we analysed an ensemble of 15 different future potential distributions of spermatophytes native to the Canary Islands for 2071–2100. Differences between projected future (ensemble means from five GCMs under SSP3) and current MAT and annual precipitation are mapped in Figure 1b,c (see also Appendix S1 for mean differences per island).

2.5 | Modelling

We used Bayesian additive regression trees (BARTs) implemented with the R package 'embarcadero' (Carlson, 2020) to model the current and future distribution of plant species. BART is a method defined by a prior probability distribution and the likelihood of returning occurrence predictions that quantify the uncertainty around the projections (Carlson, 2020). BARTs have proven to be statistically powerful, excellent in performance and robust to changes in parameter choices (Baquero et al., 2021; Carlson et al., 2022; Dansereau et al., 2022; Pinto-Ledezma & Cavender-Bares, 2021). Before modelling a species' distribution, we randomly sampled pseudo-absences across the study area. We tested the same number of pseudo-absences as unique presences (*n* pseudo-absences = *n* occurrences), avoiding spatial overlap with the presence data (Descombes et al., 2022). To identify the main subset of predictors, we ran an automated variable selection implemented in the R package 'embarcadero', following the recommendations of Chipman et al. (2012). The variables with the lowest average model root mean square error (RMSE) and, therefore, the highest accuracy, were selected (Carlson et al., 2022). The BART algorithm is insensitive to multicollinearity and can simultaneously model several predictors (Chipman et al., 2012). We ran final models separately for each species with the reduced variable set using default BART model settings (200 trees, 1000 posterior draws with a burn-in of 100 draws) and hyperparameters (power = 2.0, base = 0.95). For SIEs, we conducted each model under the assumption of full dispersal (i.e. dispersal across all islands of the archipelago is possible) and again assuming limited dispersal (i.e. dispersal is only possible within the islands with current occurrences).

To evaluate our models, we first fitted our models to 10 random subsets of 70% of the data and validated them against the remaining 30% of data. As we had many species with few occurrences in our dataset, which can lead to imperfect performance measurements (Collart & Guisan, 2023), we then pooled the suitability values of the hold-out data across replicates (Collart et al., 2021) to compute the Area Under the receiver operating characteristic Curve (AUC) and the Boyce index, which is used for presence-only data (Hirzel et al., 2006), using the R package 'ecospat' (Broennimann et al., 2022; Di Cola et al., 2017). The final variable sets, AUC and Boyce index for each species are provided in the Appendix S2.

We used baseline and projected distributions for a total of 554 species, including 228 SIEs, 209 AEs and 117 NENs. The five most frequent climatic variables with the highest importance were precipitation seasonality (bio 15), precipitation of wettest quarter (bio 16), precipitation of wettest month (bio 13), annual precipitation (bio 12) and precipitation of driest quarter (bio 17). Species-specific

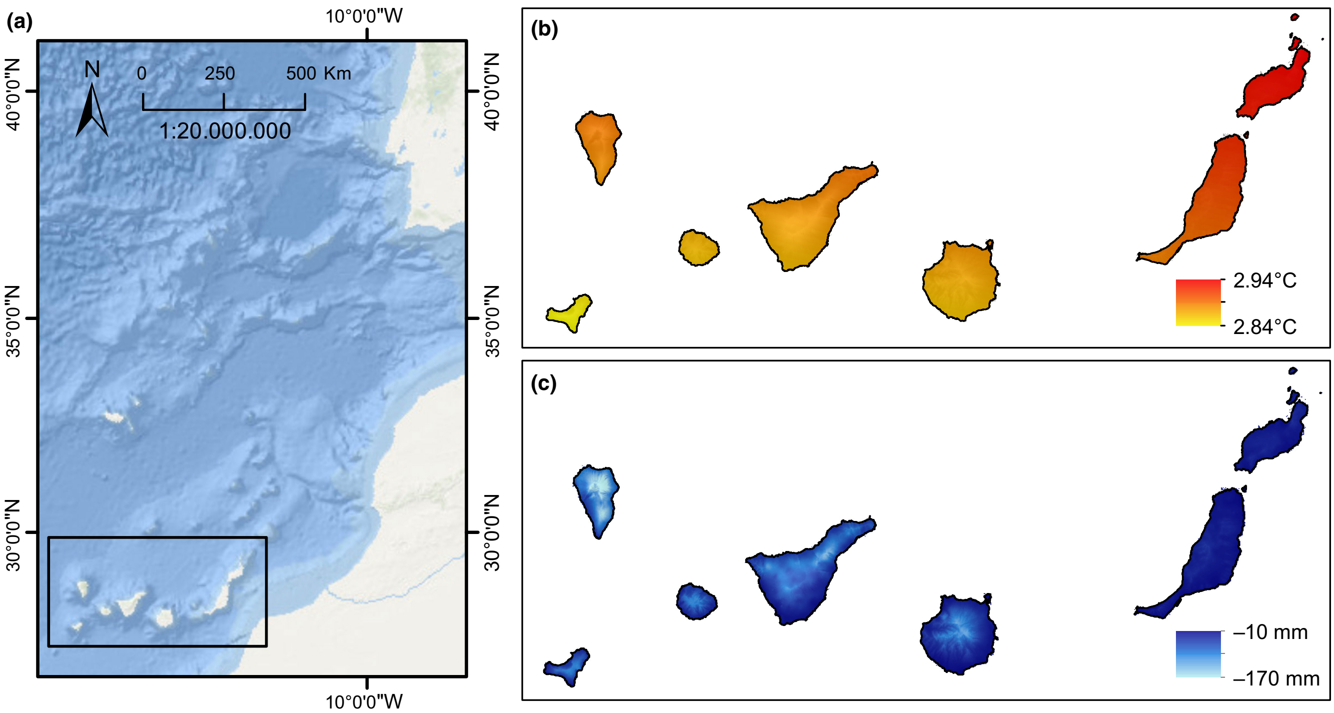

FIGURE 1 (a) Location of the Canary Islands (Spain); (b) 2071–2100 mean annual near-surface air temperature; and (c) mean annual precipitation anomalies from the 1979 to 2013 reference period. Data shown are for an ensemble of five GCMs (including GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-LR, MRI-ESM2-0, UKESM1-0-LL). Basemap source: Esri, Garmin, GEBCO, NOAA, NGDC and other contributors.

probabilities of occurrences were averaged across GCMs and for each SSP scenario, resulting in three different climate change scenarios. Subsequently, we converted the projected probabilities of occurrence for the current and future distributions into a binary outcome according to the threshold that maximises the True Skill Statistic (maxTSS) for each species (Allouche et al., 2006; Liu et al., 2013). Species for which models performed poorly (AUC < 0.7, Boyce < 0.4 or maxTSS < 0.4) were not included in the analyses (i.e. 26 SIEs, 15 AEs, 11 NENs), which left a total of 502 species. After the exclusion of species for which models performed poorly, the quality of models ranged from an AUC of 1.00 to 0.72 (mean 0.94 ± 0.05) and Boyce index of 0.4 to 1.00 (mean 0.82 ± 0.17), indicating an overall good model performance (Hirzel et al., 2006; Lantz, 2019; see Appendix S1). The ODMAP protocol of our analysis (Zurell et al., 2020) and a methodological flowchart are available in the Appendix S3.

2.6 | Statistical analyses

We quantified the gain and loss in a suitable climatic area between the current and future periods by summing the binarised numbers of gained and lost presences for each species, respectively. We then divided the gains and losses by the total number of occupied grid cells to obtain proportional gains and losses per species. We performed Kruskal–Wallis tests to test whether the relative difference in the area of potential climatic niche was significantly different between and within floristic groups. We further performed Kruskal–Wallis and Mann–Whitney *U*-tests to analyse whether the change in potentially climatically suitable area differed between herbaceous, noninsular woody and insular woody species, and between nonsucculent and succulent species within each floristic group. If necessary, post-hoc testing was performed using a Dunnett's test with Bonferroni adjustment for multiple comparisons. We repeated the analysis for each of the three SSP scenarios. All analyses were performed in R 4.1.1 (R Core Team, 2021).

3 | RESULTS

3.1 | Change in potentially climatically suitable area between and within floristic groups

Overall, we found significantly smaller gains and greater losses in potentially climatically suitable area for SIEs than for AEs under climate change scenario SSP1 (Dunnett's test – gain: SIE – AE, $p = .020$; Dunnett's test – loss: SIE – AE, $p = .031$; Figure 2). NENs gained significantly more potentially climatically suitable area than SIEs under SSP1 and SSP5 (Dunnett's test – SSP1: SIE – NEN, $p < .001$; Dunnett's test – SSP5: SIE – NEN, $p = .021$). SIEs had the overall highest loss in climatically suitable area (SSP1: mean ± standard deviation = −0.25 ± 0.2, median = −0.22; SSP3: −0.38 ± 0.3, −0.36; SSP5: −0.40 ± 0.3, −0.38). Moreover, the loss of potentially climatically suitable area increased with the intensity of climate change scenarios in SIEs (Kruskal–Wallis test: $\chi^2 = 9.93$, $p = .015$) and AEs (Kruskal–Wallis test: $\chi^2 = 17.68$, $p < .001$). A total loss in potentially climatically suitable area was predicted for 25 species, including 10 SIEs (*Aeonium lancerottense*, *Argyranthemum maderense*, *Carduus bourgeaui*, *Cheirolophus satarataensis*, *Convolvulus lopezsocasii*, *Dactylis metlesicsii*, *Echium lancerottense*, *Erigeron calderae*, *Helichrysum monogynum*, *Senecio bollei*), 11 AEs (*Aeonium balsamiferum*, *Aichryson tortuosum*, *Androcymbium psammophilum*, *Asteriscus intermedius*, *Bupleurum handiense*, *Crepis canariensis*, *Limonium bourgeaui*, *Limonium puberulum*, *Polycarpaea divaricata*, *Reichardia famarae*, *Sideritis pumila*) and four NENs (*Caralluma burchardii*, *Carex paniculata*, *Lolium saxatile*, *Sonchus pinnatifidus*) under at least one of the climate scenarios (e.g. see Figure 3a for the Lanzarote and Fuerteventura endemic *Ferula lancerotensis*). One of the highest gains was predicted for the Tenerife endemic *Sideritis cretica* (+400% or +104 grid cells under climate scenario SSP5; Figure 3b). The results considering island-bound climatic niches of SIEs were qualitatively similar to those considering the archipelago-wide climatic niche (see Appendix S4). There was a significantly greater gain in potentially climatically suitable area for AEs and NENs than in dispersal-limited SIEs under SSP1, SSP3 and SSP5 (Dunnett's test SIE – AE, $p < .001$; SIE – NEN, $p < .001$). The results for limited dispersal models are provided in the Appendix S4.

3.2 | Inter-island comparison of change in climatically suitable area

The median proportional gain and loss in potentially climatically suitable area was different for each island of the Canary Islands archipelago (Figure 4). Under each climate change scenario, SIEs gained the least, and lost the most, potentially climatically suitable area on Fuerteventura (SSP1: median gain = 0/median loss = −0.62; SSP3: 0/−0.75; SSP5: 0.005/−0.62) and Lanzarote (SSP1: 0/−0.49; SSP3: 0/−0.79; SSP5: 0/−0.89). Moreover, on Fuerteventura and Lanzarote, AEs had the highest median losses of climatically suitable area, whereas NENs had the highest median gains on Lanzarote. On Lanzarote, in particular, there was a greater loss in species richness in SIEs and AEs in the *Famara* cliff but a gain in NEN species richness in flatter areas (Figure 5). The mean proportional loss increased with the increasing severity of climate change scenarios across all islands and floristic groups.

3.3 | Effect of woodiness and succulence on change in potentially climatically suitable area

We compared 156 herbaceous species (SIE = 42; AE = 72; NEN = 42) to 160 noninsular woody species (SIE = 46; AE = 59; NEN = 55) and 166 insular woody species (SIE = 103; AE = 57, NEN = 5). The origin of woodiness could not be identified for 20 species. There was a significantly lower gain and higher loss in potentially climatically suitable area in herbaceous than in insular woody SIEs under SSP3 (Dunnett's test – gain: $p = .030$; Dunnett's test – loss: $p = .030$, Figure 6a). Moreover, we compared 381 nonsucculent species (SIE = 158;

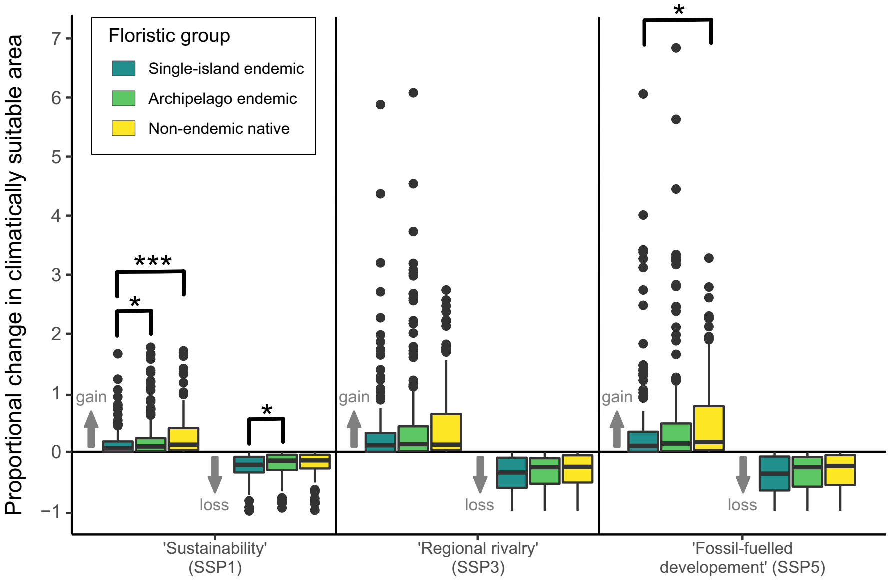

FIGURE 2 Proportional gain and loss in climatically suitable area by 2100 in single-island endemic ($n=202$), archipelago endemic ($n=194$) and nonendemic native plant species ($n=106$) on the Canary Islands, using three different climate change scenarios (SSP1, SSP3 and SSP5). SSP1 describes a world with strong economic growth via sustainability, SSP3 describes a future with high inequality between countries and SSP5 describes a world with strong economic growth via fossil fuel pathways. Single-island endemics have significantly lower gains and higher losses of potentially climatically suitable area than archipelago endemics under SSP1. Moreover, single-island endemics have significantly lower gains of climatically suitable area than nonendemic natives under climate change scenarios SSP1 and SSP5. Asterisks denote statistical significance (*$p \le .05$, **$p \le .01$, ***$p \le .001$).

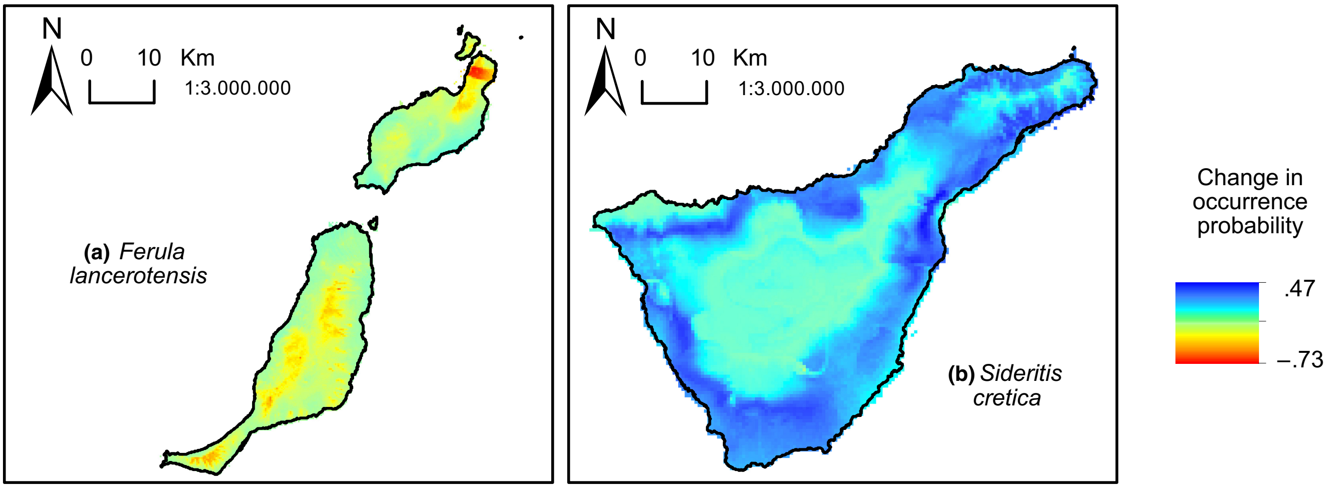

FIGURE 3 Example maps showing the differences in potentially climatically suitable area between projected future climate (2071–2100; mean of five GCMs under SSP3) and current climate (1979–2013) for two (opposing) example species: (a) *Ferula lancerotensis* (Lanzarote and Fuerteventura endemic) and (b) *Sideritis cretica* (Tenerife endemic). Blue tones represent gains, and red tones represent losses in potentially climatically suitable area.

AE = 144; NEN = 79) with 121 succulent species (SIE = 44; AE = 50; NEN = 27). Nonsucculent species showed a significantly lower gain and higher loss in potentially climatically suitable area than succulent species in SIEs and NENs under SSP3 (Mann–Whitney *U* test: gain – SIE, $p=.008$; loss – SIE, $p=.008$; gain – NEN, $p<.001$; loss – NEN, $p=.009$; Figure 6b). The results for climate change scenarios SSP1 and SSP5 and dispersal-limited SIEs were qualitatively similar and can be found in the Appendices S4 and S5.

4 | DISCUSSION

In this study, we investigated the effect of climate change on the potentially climatically suitable area of plant species native to the Canary Islands, an archipelago renowned for its exceptional plant endemism (Cai et al., 2022; Fernández-Palacios & Whittaker, 2008). As hypothesised, we found that single-island endemic species that currently occur in predominantly arid regions would have the highest

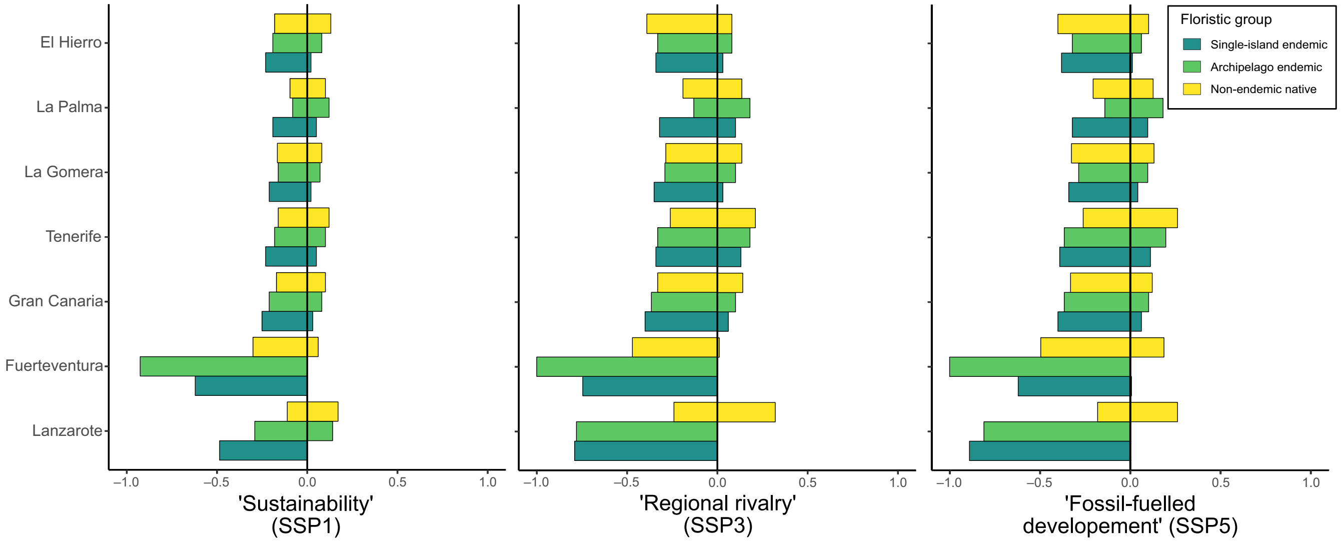

FIGURE 4 Median proportional gain and loss in potentially climatically suitable area for each floristic group on all seven islands of the Canary Islands by 2100. The change was calculated under three different climate change scenarios (SSP1, SSP3, SSP5).

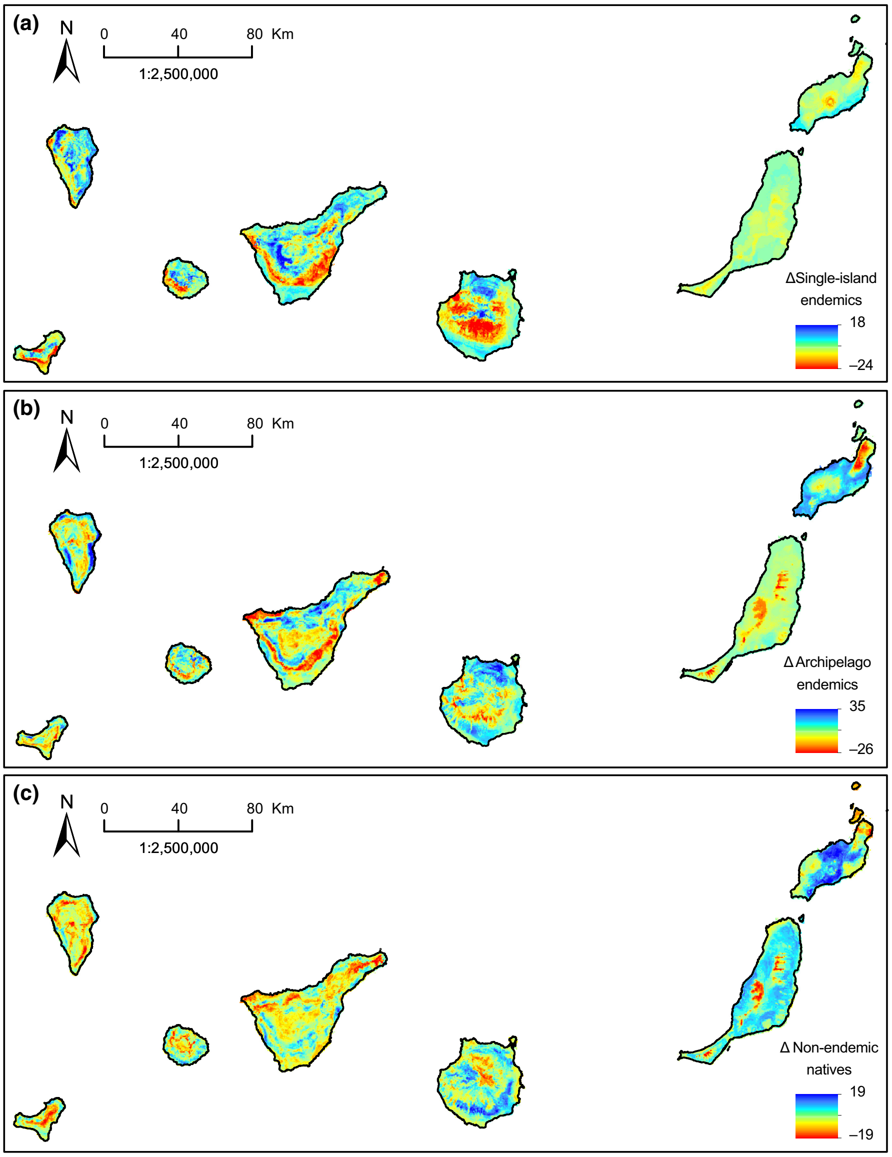

FIGURE 5 Maps displaying differences in species richness between projected future climate (2071–2100; mean of five GCMs under SSP3) and current climate (1979–2013) for (a) single-island endemics, (b) archipelago endemics and (c) nonendemic natives. Blue tones represent gains, and red tones represent losses in species richness.

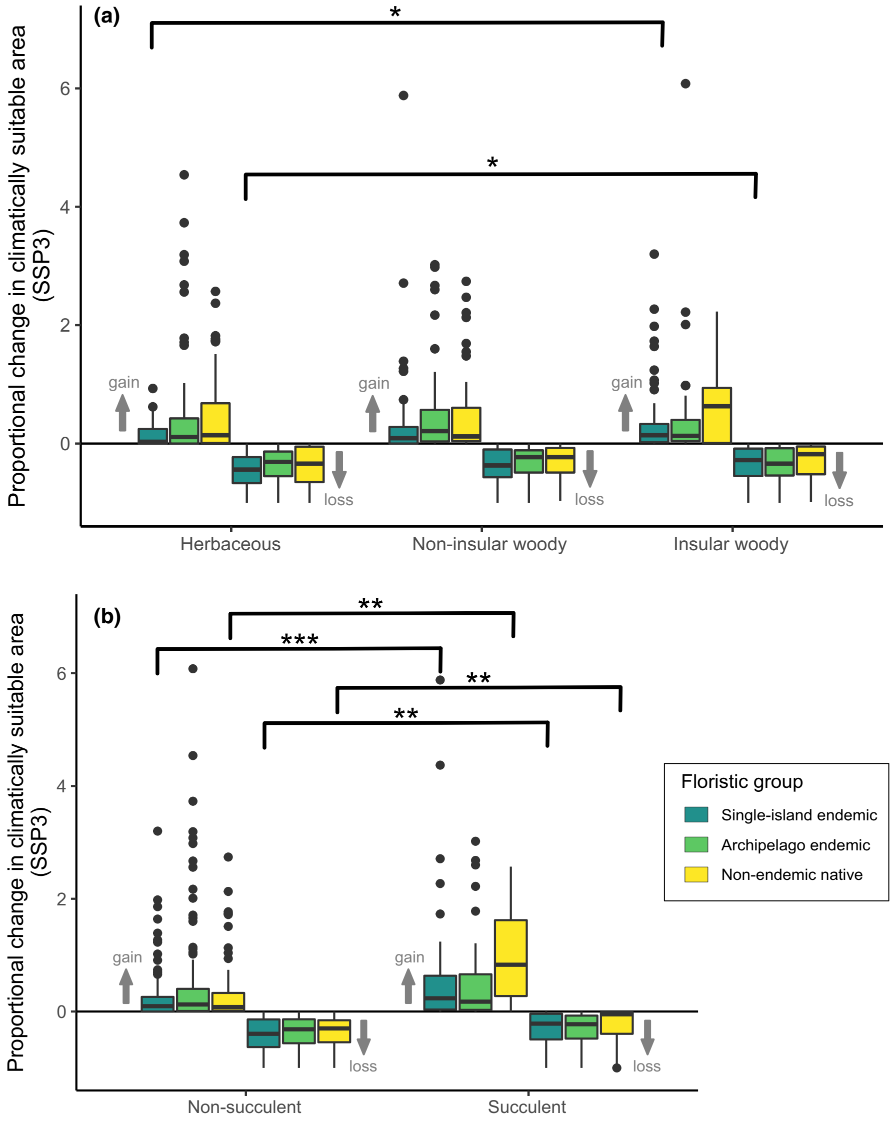

FIGURE 6 Proportional gain and loss in potentially climatically suitable area (SSP3) for single-island endemic (*n* = 202), archipelago endemic (*n* = 194) and nonendemic native species (*n* = 106) on the Canary Islands when accounting for different functional strategies. (a) Herbaceous species have significantly lower gains and higher losses of climatically suitable area than insular woody species in single-island endemics. (b) Nonsucculent species have significantly lower gains and higher losses of climatically suitable area than succulent species in single-island endemics and nonendemic natives. Asterisks denote statistical significance ($*p \leq .05$, $**p \leq .01$, $***p \leq .001$).

losses of climatically suitable area. Functional strategies can mediate whether a plant is vulnerable to climate change (Andrew et al., 2022; Butt & Gallagher, 2018; Dudley et al., 2019). Indeed, our models suggest that species characterised by woodiness or succulence will be less negatively affected by climate change. Nevertheless, climate change is a substantial threat to most plant species native to the Canary Islands, and species vulnerable to environmental and demographic stochasticity, or species characterised by specific functional strategies, are exceedingly threatened.

4.1 | Single-island endemics are most susceptible to changing climatic conditions

We found that single-island endemic species are more vulnerable than nonendemic native species under a mild climate change scenario on the Canary Islands, possibly because of their small climatic niche. The loss in climatically suitable area indicates that species on islands will have limited opportunities to escape unfavourable climatic conditions and may be unable to track their climatic niches (Harter et al., 2015), which is further aggravated by the species' inherently small ranges and population sizes. The climate is predicted to become warmer and drier on the Canary Islands by 2100, under all three analysed climatic scenarios. In particular, precipitation seems to play an essential role for native Canary Island species, as the five most critical climatic variables across all species were related to precipitation rather than temperature. In general, the increase in temperature and decrease in precipitation were more severe under scenarios SSP3 and SSP5 than under SSP1. This indicates that a socioeconomic pathway favouring sustainability and equality might prevent many species from oceanic island floras from losing their climatic niche.

4.2 | Arid and high-elevation areas are disproportionately affected by climate change

The inter-island comparison indicates that endemic species on older and less elevated islands, that is, Lanzarote and Fuerteventura, will experience an above-average loss of climatically suitable area. These two islands already have water scarcity and predominantly arid climatic conditions (del Arco Aguilar et al., 2010), in which many species already experience physiological limitations due to drought stress. Species occurring on the topographically complex *Famara* cliff (Lanzarote) or *Jandía* massif (Fuerteventura) are predicted to be especially vulnerable. For example, the archipelago endemic *Ferula lancerotensis* occurs on these two hills and is predicted to lose almost its entire suitable climatic niche on the Canary Islands by 2100. *Ferula lancerotensis* depends on moist conditions and lower insolation on the windward slopes of the Famara and Jandía hills (Scholz & Reyes-Betancort, 2013). However, temperature is predicted to increase, whereas precipitation is predicted to decrease in these areas, likely making the climatic conditions unsuitable for many native species in the future.

Not only are species from the inframediterranean zone disproportionately affected by climate change; but species that occur in the supra- and oromediterranean zone (>2.000 m) may also be particularly vulnerable to changing climatic conditions, for example, *Viola cheiranthifolia* (Tenerife endemic) and *Echium gentianoides* (La Palma endemic). By contrast, species that currently occur across mid-elevations, for example, the lower *Teno* massif (peak at 1.345 m), may be able to increase their range size. For example, the potentially climatically suitable area for *Sideritis cretica* is projected to increase disproportionately in the future. These results indicate that upward range shifts might compensate for lost habitats where possible, but an upward shift to the highest elevational areas (e.g. Teide or Roque de los Muchachos) might not be possible. Disproportionate temperature increases at high elevations (Expósito et al., 2015; Krushelnycky et al., 2016; Sperling et al., 2004), water stress and area reduction with elevation can restrict upslope migration, making high-elevation species highly vulnerable to climate change (Costion et al., 2015; Dullinger et al., 2012; Rumpf et al., 2018; Steinbauer et al., 2018). Although floristic groups across all islands might lose climatically suitable area on average, we identified the Famara and Jandía hills, the summit broom scrub of Tenerife and La Palma and the Teide violet community (Tenerife) as the regions in which plant species are most vulnerable to climate change in the 21st century.

4.3 | Insular woody and succulent species face lower climate change-related reductions

We found that insular woody species may gain more and lose less climatically suitable area than herbaceous species, among the single-island endemics. This finding can be linked to the theory that palaeodrought is a major driver of insular woodiness in Canary Island lineages (Hooft van Huysduynen et al., 2021; Lens, Davin, et al., 2013; Zizka et al., 2022). As there is evidence that in-situ wood development coincides with palaeoclimatic aridification (Hooft van Huysduynen et al., 2021), insular woody endemic species may be better adapted to drought than perennial herbaceous endemic species. Indeed, insular woody species are less sensitive to drought-induced gas embolisms than related herbaceous species (Dória et al., 2018; Lens, Tixier, et al., 2013). Hence, insular woody endemics could have an advantage given the predicted decrease in precipitation and expansion of dry habitats on the Canary Islands. Insular woody genera include *Aeonium*, *Argyranthemum*, *Cheirolophus*, *Crambe*, *Echium*, *Limonium*, *Lotus*, *Micromeria*, *Sideritis* and *Sonchus* (Lens, Davin, et al., 2013). However, the evolution of insular woodiness may also be driven by lower past climate change velocity in precipitation on oceanic islands (Carlquist, 1974; Zizka et al., 2022) favouring an increase in plant longevity (Givnish, 2010; Smith & Donoghue, 2008). Therefore, adaptation to stable climates and long generation times could pose a possible conflict with rapid climate change-induced range shifts in insular woody species.

Our results suggest that succulent species are more likely to gain climatically suitable area by 2100 than nonsucculent species, among single-island endemics and nonendemic natives. Succulent plants may have an advantage over nonsucculent plants under more arid conditions because of their ability to store water and their water-efficient metabolism (Griffiths & Males, 2017; Vendramini et al., 2002). For example, *Euphorbia canariensis*, a keystone species in the succulent scrub, is predicted to increase its suitable climatic area by 78% under climate change scenario SSP3. Hence, succulence seems to be an effective strategy in the face of climate change, especially in native plants with preadaptations to arid conditions (e.g. the 'dragon tree' *Dracaena draco* subsp. *draco*., but see a predicted decrease in the climatic area for *Dracaena draco* subsp. *caboverdeana* on Cabo Verde; Varela et al., 2022).

4.4 | Study limitations

Although our models provide robust predictions for the change in potentially climatically suitable area of species native to the Canary Islands, we must address the fact that our models did not include biotic factors, such as species interactions or dispersal. In particular, interspecific competition with succulent invasive species, such as *Opuntia* and *Agave*, may be favoured and accelerated by climate change (Arévalo et al., 2017). In addition to habitat destruction, grazing by introduced herbivores poses a massive threat to many native species on the Canary Islands. A poignant example is the Jandía peninsula, Fuerteventura, where feral cattle are found in high numbers most of the year (Scholz & Reyes-Betancort, 2013). Moreover, in high-elevation areas, climate change-induced high rabbit densities are already threatening the persistence of native plant species (Cubas et al., 2018), as well as in most other ecosystems of the archipelago (Cubas et al., 2019). Therefore, additional threats, such as invasive species, habitat loss and resource overexploitation (Fernández-Palacios, Kreft, et al., 2021; Morente-López et al., 2023), strongly influence whether species can shift their range to climatically suitable areas in the future. Additionally, we acknowledge that we analysed the native species' realised niches and not their fundamental niches. Hence, our results may underestimate the climatic niches of these species.

5 | CONCLUSION

Although climate change is recognised as a growing threat to the outstanding biodiversity of oceanic islands (Harter et al., 2015; Macinnis-Ng et al., 2021; Veron et al., 2019), the impact of climate change on the functional strategies of island floras is less clear. We found that endemic species in aridity-dominated environments are particularly threatened by future decreases in precipitation. However, insular woody and succulent species may have an advantage in a climate that is warmer and drier than today on the Canary Islands. Indeed, the Canary Islands are a hotspot of insular woody species and succulent plants (Barajas-Barbosa et al., 2022; Irl et al., 2020; Zizka et al., 2022), which suggests that a large proportion of the Canary Islands flora could be able to cope with the predicted climatic changes. Nonetheless, with ongoing climate change, a net loss of species with unique functions seems inevitable, leading to functional homogenisation and impoverishment, and a possible deterioration of ecosystem stability.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13750.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study can be found in the Dryad data repository at https://doi.org/10.5061/dryad.cc2fqz6b4. The coordinates of the location records used in this study can be found in Zenodo at https://doi.org/10.5281/zenodo.7993090.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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