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# Climate controls plant life-form patterns on a high-elevation oceanic island

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**Abstract**

**Aim:** Plant life-forms characterize key morphological strategies that enable large-scale comparisons of plant communities. This study applies Raunkiaer's plant life-form concept that was developed for temperate climate to a subtropical island flora, in parts, dominated by summer aridity. We quantify how plant life-form patterns as well as patterns of important plant functional traits (PFTs) relate to important climate and topographic characteristics.

**Location:** La Palma, Canary Islands.

**Taxon:** Flora of La Palma.

**Methods:** We assigned each native plant species a plant life-form, that is, phanerophyte, chamaephyte, hemicryptophyte, geophyte and therophyte, as well as PFTs (succulence and N-fixer). We used stacked species distribution models to assess occurrence probability for each species using the Atlantis database (500 m × 500 m grid). We related richness and percentage values for each plant life-form and PFT to climate and topography.

**Results:** Plant life-forms and PFTs showed a clear pattern within geographic but also climate space, while topography had a minor effect. Phanerophytes mainly contributed to the flora in humid areas. Chamaephytes and hemicryptophytes most strongly contributed to the summit scrub flora and, to some degree, also to the arid coastal regions. Geophytes and therophytes were mainly found in dry coastal regions. N-fixers contributed mainly to warm-arid and cool-arid regions, while succulent species were mainly found in arid coastal regions.

**Main conclusions:** Raunkiaer's plant life-form concept can be comprehensively transferred to a subtropical island flora by adapting to local unfavourable growing conditions, that is, aridity. Using the strong environmental gradients offered by our study island, we identify substantial climate-driven variation in patterns of plant life-forms and PFTs that might be used for large-scale comparisons in macroecological studies. The growth strategies reflected in Raunkiaer's plant life-forms suggest differences in species establishment and coexistence dynamics within different parts of the island's climate space.

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## KEYWORDS

climate, gradient, island, N-fixer, plant functional traits, plant life-forms, Raunkiær, succulence

## 1 | INTRODUCTION

Plant life-forms are an established ecological approach to classify plant species based on their environmental demands. They help understand environmental and ecological characteristics of ecosystems (Klimes, 2003). Particularly, plant–climate interactions based on the location of reproductive organs in relation to the soil surface giving insights how plants can withstand and recover from disturbance and stress are well represented (Lavorel & Garnier, 2002; Raunkiær, Fausbøll, Gilvert-Carter, & Tansley, 1934). Classification of plant species into functional groups (e.g. life-form types) provides the advantage of global comparability of research results despite regional differences in species taxonomy (Diaz, Cabido, Zak, Carretero, & Aranibar, 1999; Diaz et al., 2016). Indeed, a plant life-form approach for areas of high taxonomic distinctness due to endemism such as islands seems particularly promising to allow standardized inter-island comparisons with a functional island biogeographic perspective.

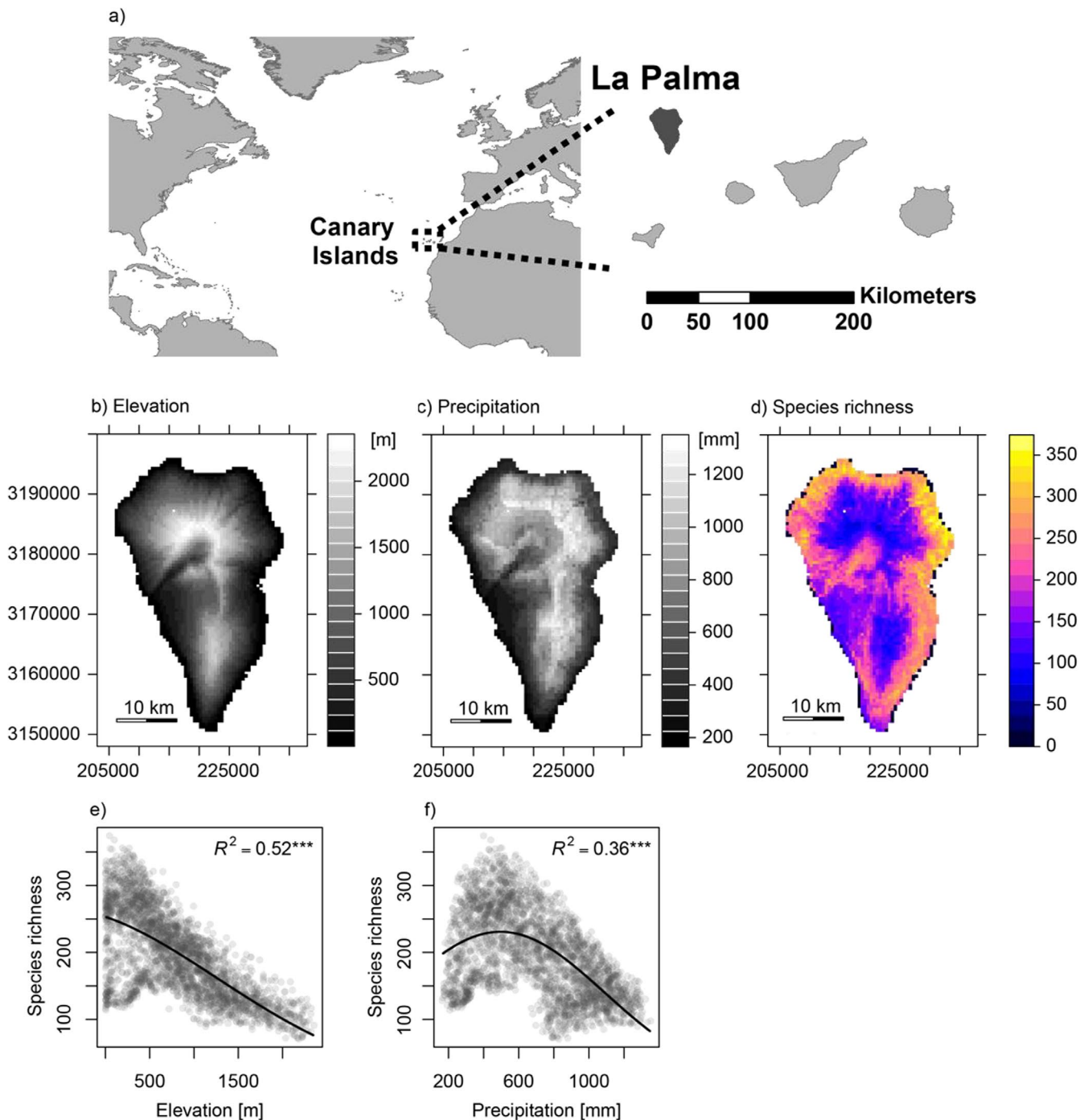
Due to its compelling simplicity, the life-form classification system of Raunkiær et al. (1934) is the most used plant classification concept in the world (Klimes, 2003; Leuschner & Ellenberg, 2017). It is based on key survival strategies of plants, most importantly the height of the renewable buds of plants relative to the soil surface layer during unfavourable seasons. Raunkiær's classification system was thus developed for temperate seasonal climates where winter frosts end the growing season (Ewel & Bigelow, 1996; Mueller-Dombois & Ellenberg, 1974). Despite some additional refinements of his classification system (e.g. Cain, 1950; Ellenberg & Mueller-Dombois, 1967; Ewel & Bigelow, 1996; Mueller-Dombois & Ellenberg, 1974), five basic classes for terrestrial plants are still in wide use (phanerophytes, chamaephytes, hemicryptophytes, geophytes and therophytes). Because of the sole focus on regenerative buds during the unfavourable season, a reduced usability in warmer climates (e.g. subtropics or tropics) seems obvious. However, other seasonally occurring unfavourable conditions such as drought or heat can likewise restrict plant growth (Bello-Rodríguez et al., 2019). Taxonomy independent classifications for plant strategies in ecosystems are particularly useful for large-scale comparisons and for answering evolutionary questions related to species functioning (like convergent evolution; Chave et al., 2009; Diaz et al., 2016; Lavorel & Garnier, 2002; Reich, 2014; Wright et al., 2004).

Here we expand Raunkiær's life-form concept to assemblages on oceanic islands, which are considered model systems for understanding the evolution of species, often called 'nature's test tubes' where ecological patterns can be observed in independently repeated evolutionary settings on different islands (Losos & Ricklefs, 2009; Whittaker, Fernández-Palacios, Matthews, Borregaard, & Triantis, 2017). Island taxa often show island-specific adaptations such as secondary island woodiness, that is, the evolution of woody life-forms on islands from predominantly herbaceous lineages

(Burns, 2019; Carlquist, 1974; Darwin, 1859). On the Canary Islands, for example, secondary island woodiness appears in more than 50% of endemic species including prominent genera such as *Aeonium*, *Argyranthemum*, *Crambe*, *Echium* and *Sonchus* (Lens, Davin, Smets, & del Arco, 2013). Furthermore, oceanic islands are ideal study systems to answer ecological as well as evolutionary questions as they often represent climatic 'mini-continents' with steep environmental gradients (Darwin, 1859; Irl et al., 2015) along which systematic changes in the survival strategy of plant and thus the life-form spectrum can best be quantified and tested (Hoffmann et al., 2019; Klimes, 2003; Pavon, Hernandez-Trejo, & Rico-Gray, 2000). Spatial climatic heterogeneity is amplified by the influence of trade winds in many tropical and subtropical islands, which leads to an asymmetric distribution of precipitation (Garzón-Machado, Otto, & Aguilar, 2014). The large environmental heterogeneity of islands on a relatively small scale has the advantage of a clearly definable extent of the study area, ideally without external influences (but see Ibanez et al., 2019). Furthermore, results of the study are also valuable for larger spatial scales (e.g. for continents) because the investigated responses of life-forms to climatic parameters can be easily transferred.

Examining individual functional traits offers an alternative view to plant life-forms that are an interacting aggregation of individual traits and functions (Diaz et al., 2016). Thereby, we refer to functional traits as 'any morphological, physiological or phenological feature measurable at the individual level' that links functional traits to the performance and fitness of individuals (Violle et al., 2007). In addition, functional traits are also linked with ecosystem functioning and stability (Bruehlheide et al., 2018; Diaz & Cabido, 2001; Diaz et al., 2016). Plant functional traits strongly respond to climatic conditions and change along environmental gradients (Bruehlheide et al., 2018; Cornwell & Ackerly, 2009; de Bello, Leps, & Sebastià, 2005; Diaz, Cabido, & Casanoves, 1998; Swenson et al., 2012). On the subtropical, and partly arid, Canary Islands, plant functional traits expressing drought tolerance and water use efficiency are particularly important, leading to an interspecific competitive advantage. Such traits are well expressed in plants that are able to internally store water for extended time periods to survive hygric stress (hereafter referred to as *succulents*, Ellenberg, 1981) and nitrogen fixers that can fix atmospheric nitrogen and have an increased water use efficiency under hygric stress as a result of their metabolism (hereafter referred to N-fixers, Reich et al., 2001). The evolution of traits associated with succulence and nitrogen fixing are thus remarkable adaptations to harsh environmental conditions, enabling these species to occupy environmental niches that are not accessible otherwise (Swenson et al., 2012).

The aim of this study is to apply Raunkiær's life-form concept within the context of the emerging field of functional island biogeography to the entire flora of the island of La Palma (Canary Islands). Plant life-form strategies should reflect the strong



**FIGURE 1** Map of (a) location of the Canary Islands and La Palma, (b) elevation, (c) mean annual precipitation and (d) plant species richness. (e) and (f) show the relationship between plant species richness and elevation as well as precipitation respectively. Coordinates in (b)–(d) are given in UTM 28N projection [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

elevation-temperature gradient (~2,400 m) as well as precipitation differences between the windward and leeward side of the island (c. 200–1,500 mm/a). Topographic variables influence island plant diversity on large scales (comparisons between islands, Kreft, Jetz, Mutke, Kier, & Barthlott, 2008), where they likely reflect habitat diversity and climatic gradients. Here we analyse plant life-form patterns on very high spatial scales within islands. We expect this variability to be better reflected by climate than to small-scale

topography (slope, aspect). We thus expect (a) the percentage of woody plants (phanerophytes and chamaephytes) to increase with the amount of rainfall reflecting a global tendency of tree diversity with increasing moisture conditions (Bhattarai & Vetaas, 2003). (b) The percentages of phanerophytes and chamaephytes will increase with elevation (Vazquez & Givnish, 1998) resulting from an adaptation to colder climates including frost. Non-woody plant species are likely to have a heterogeneous spatial distribution because they can

strongly depend on local parameters, for example soil type and canopy cover (Bhattarai & Vetaas, 2003). Therefore, we expect (c) that the percentage of hemicryptophytes, geophytes and therophytes is unrelated to elevation and precipitation. N-fixers, in contrast have crucial adaptation mechanisms (e.g. nitrogen fixation, high morphological and physiological diversity) that allow them to cope better with harsh environmental conditions than other plant life-forms. Therefore, they are expected (d) to be more important in lower and higher altitudes where thermal and hygric stress limits plant growth of other life-forms (Haffner, 2011). Succulent plants are known to have the ability to store water and use it in times of dry periods (Willert, 1992). Because of their water use efficiency, we expect to find (e) succulent plants in arid regions of the island in the lower elevations because succulents are likely to be outcompeted when climatic conditions improve (Otto, Fernandez-Palacios, & Krusi, 2001; Vendramini et al., 2002).

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

La Palma (28°26' to 28°51'N and 18°00' to 17°43'W) is the most northwestern island of the Canary Islands archipelago located in the Atlantic Ocean at the western continental margin of Northern Africa. The island is of volcanic origin and has its highest summit (the Roque de los Muchachos) at 2,426 m within a total island area of only 708 km<sup>2</sup>. On a landscape scale, La Palma shows great topographic and climatic variability (Irl et al., 2015). Due to the longitudinal positioned mountain chain, clouds are blocked in the trade wind zone and therefore cloudbanks can form (Garzón-Machado et al., 2014). Thus, a higher amount of annual precipitation can be observed in the northeastern part of the island with about 1,500 mm and in the southwestern part with about 200 mm (Figure 1). Mean annual temperature ranges from 21°C in coastal regions down to 9°C at the summit (Irl et al., 2015). In winter months, occasional snow falls in the summit region (Kunkel, 1993) and frost events down to 1,500 m a.s.l. are possible (Hohenester & Welss, 1993). High solar radiation occurs at high elevations that causes high potential evapotranspiration, especially in the summer months (Garzón-Machado et al., 2014). The climatic heterogeneity of the island leads to a spatially explicit distribution of plant species richness that is strongly influenced by elevation and precipitation (Figure 1; Steinbauer et al., 2017). The distribution of vegetation zones is directly reflected in the heterogeneous climatic conditions of the island (del Arco-Aguilar, Gonzalez-Gonzalez, Garzón-Machado, & Pizarro-Hernandez, 2010; Garzón-Machado et al., 2014).

### 2.2 | Life-form classification and environmental data

The classification system of Raunkjær is one of the most frequently used in ecology (Ellenberg & Mueller-Dombois, 1967; Ewel &

Bigelow, 1996; Mueller-Dombois & Ellenberg, 1974). As the system is based on the height of reproductive organs, it needs modifications to fit for island taxa and subtropical climate conditions. Species in the subtropics often show adaptations to unfavourable conditions like aridity, many of which are not covered by the standard Raunkjær approach. Moreover, Raunkjær neglected the growth phase during favourable conditions (Mueller-Dombois & Ellenberg, 1974). We therefore modified the concept allowing the classification of all species into five main plant life-forms (Figure 2). The adapted approach classifies species according to their growth strategy. It is expected that the selected distinguishing species characteristics have an effect on the presence/absence of certain plant life-form types along environmental gradients (Klimes, 2003; Lavorel & Garnier, 2002). Especially, phanerophytes and chamaephytes can show a high variation with precipitation (Bhattarai & Vetaas, 2003), whereas herbs such as hemicryptophytes, geophytes and therophytes are considered to be driven by the interplay of climatic factors with their local environmental components (e.g. canopy cover, disturbance regime) as well as topographic conditions such as slope and aspect (Vazquez & Givnish, 1998).

All native species occurring on the Canary Islands were classified into the modified plant life-form concept based on extensive available literature for all vascular plants (Guittonneau & Huon, 1983; Hohenester & Welss, 1993; Jäger & Rothmaler, 2013; Lauber & Wagner, 2012; Schönfelder & Schönfelder, 2002, 2012), for nitrogen fixing plants (Du Puy et al., 2002; Haffner, 2011; Lock, 1989) and for succulents (Jacobsen, 1974; Kunkel & Kunkel, 1978; Lodé, 2010; Schönfelder & Schönfelder, 2012). Here we define succulence as the ability of plant organs (stems, roots and leaves) to store water in their tissues and can be therefore identified as thickened or fleshy. Additionally, they have to have the ability to use stored water during dry conditions. Because of this definition, the degree of succulence is not essential (Jacobsen, 1974; Willert, 1992). As a consequence, even slightly succulent plants like *Rumex lunaria* are considered as succulent species (Schönfelder & Schönfelder, 2012). Non-native species were not considered in this study.

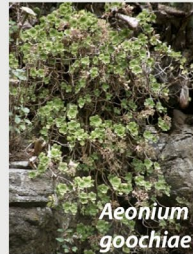
### 2.3 | Plant species data and species distribution modelling

Information on the spatial occurrence of vascular plant species was available from the Banco de Datos de Biodiversidad (Atlantis 3.1 at [www.biodiversidadcanarias.es](http://www.biodiversidadcanarias.es)), a long-term governmental initiative to assemble and complete all known distribution records of species on the Canary Islands (see Steinbauer, Field, Fernandez-Palacios, et al., 2016 for discussion of data quality). Occurrence records are reported in a resolution of a 500 m × 500 m grid size (3,063 grid cells covering the island of La Palma, mean number of occupied grid cells per species was 976). The data are presence-only information with much better coverage for endemic species than for native non-endemics (Steinbauer, Field, Fernandez-Palacios, et al., 2016). Life-form type distribution was analysed after interpolating species



**(a) Plant life forms****Phanerophyte**

Woody plants &gt;50 cm

**Chamaephyte**Woody plants  
<50 cm**Hemicryptophyte**Biennial and perennial plants with a  
periodic shoot reduction. The remnant  
shoot system is near ground height**Geophyte**Biennial and perennial plants which  
underlie a periodic reduction of the  
whole shoot system. The surviving  
storage organs are located in the soil**Therophyte**Annual plants whose shoot and root  
system dies after completion of its life  
cycle within one year (including seed  
production)**(b) Plant functional traits****Succulence**Plants possessing water storage organs,  
e.g. in leaves and/or stem**N-fixer**Plants with the ability to fix atmospheric  
nitrogen

**FIGURE 2** Modified classification of plant life-forms based on Raunkjær et al. (1934) (a) and plant functional traits (b) on the island of La Palma. Plant life-forms are phanerophytes, chamaephytes, hemicryptophytes, geophytes and therophytes. In addition, two main plant functional traits were classified, that is, succulence and N-fixers [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

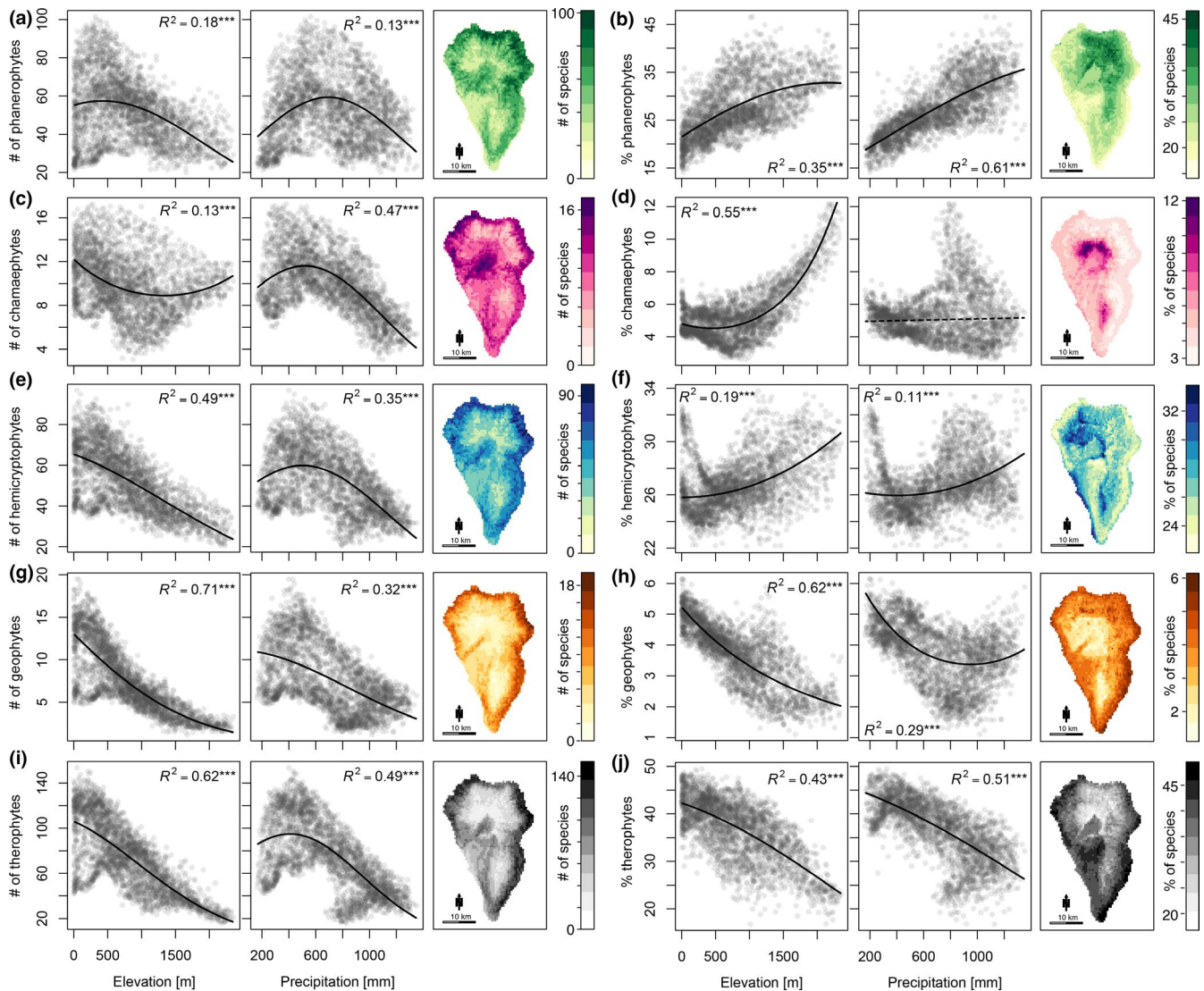
occurrence using stacked species distribution models (S-SDMs; Calabrese, Certain, Kraan, & Dormann, 2014; Distler, Schuetz, Velásquez-Tibatá, & Langham, 2015; Grenié, Violle, & Munoz, 2020). We thus stacked individual species distribution models for each species to calculate probability-based richness for different life-forms (Grenié et al., 2020). This spatial interpolation is conceptually similar to gap-filling methodology frequently applied in macroecological studies including trait imputation that are accepted tools for reducing sampling bias (Penone et al., 2014). This partly corrects for spatial sampling biases. SDMs were implemented using generalized linear models with automated variable selection using small sample size-corrected Akaike information criterion.

Potential explanatory variables were aspect, slope, mean annual temperature and precipitation as well as mean monthly temperature and precipitation for January, April, July and October representing climatic conditions during the four seasons. Although similar explanatory variables are used for the stacked species distribution models as well as the subsequent analyses, the danger of circular reasoning is minimal; Within the S-SDMs, every species differs in its relationship with the environmental variables, while the subsequent analyses of life-form distribution are based on the integrated signal across all species. For a further test of robustness, we repeated all analyses with non-interpolated occurrence data finding qualitatively similar relationships (see Appendices S3 and S4). Explanatory variables entered the SDMs as first and second order polynomial ( $y \sim x + x^2$ ) to

allow for nonlinear relationship. Resulting from the model complexity, species with less than 25 occurrence values were excluded to prevent overfitting. Models were trained using occurrence records of plant species from all seven Canary Islands, but did not allow species occurrence on islands where species are naturally absent. For each species, a probability of occurrence in each 500 m × 500 m grid cell is assigned by the SDM. This probability was directly used to calculate community means in life-form type (probability-based richness, see Grenié et al., 2020). For example, a species with an occurrence probability of 20% is weighed by 0.2 when quantifying the number of species of a specific life-form type in the focal grid cell. Climatic variables applied in the SDM were interpolated from climate station data ( $N = 155$  temperature,  $N = 305$  precipitation) provided by Agencia Estatal de Meteorología based on topography and including rain shadow effects (calculated based on topography assuming a main wind direction of 20° corresponding to the main trade wind direction).

## 2.4 | Statistical analysis

The relation of life-form type distribution with elevation, precipitation slope and aspect (northness and eastness) was analysed by means of generalized linear models. A Poisson error distribution was used for the overall number of species associated with a specific



**FIGURE 3** Relationship between both elevation and precipitation with the number and percentage of different plant life-forms on the island of La Palma. The maps show the spatial pattern of the respective indices. Asterisks \*\*\* indicate a  $p$ -value  $< 0.001$  [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

life-form per grid cell, while binomial error distributions were used for the percentage of species equipped with a specific life-form in relation to the overall number of species present in that grid cell. Models were implemented as unimodal relationships ( $y \sim x + x^2$ ) and the quadratic term dropped based on AICc using the R *step* function for model optimization. As a goodness-of-fit measure, pseudo- $R^2$  were calculated using R package *MODeVA* version 1.3.2 (Barbosa, Brown, Jimenez-Valverde, & Real, 2016) following the approaches suggested by Guisan and Zimmermann (2000). As elevation and precipitation were much better explanatory variables for plant life from distribution and plant functional trait distribution than slope, northness and eastness, we only show results including elevation and precipitation in the main paper, while the results for slope, northness and eastness can be found in Appendices S1 and S2.

Spatial patterns in life-form type distribution were visualized using R packages *RASTER* version 2.8-4 (Hijmans, 2018). All analyses were performed in R version 3.3.2.

## 3 | RESULTS

### 3.1 | Plant life-form distribution

We assigned plant life-forms and plant functional traits to all 584 plant species native to the island of La Palma. Of these 142 (24%) were phanerophytes, 31 (5%) chamaephytes, 164 (28%) hemicryptophytes, 30 (5%) geophytes and 213 (36%) therophytes. Two hydrophytes were excluded from the analyses. Of all species, 72 (12%) were succulents and 58 (10%) N-fixers.

All relationships presented in this section were highly significant with  $p < .001$ . This should not be over-interpreted, as significance in the relationships is facilitated by the high spatial resolution (500 m  $\times$  500 m) resulting in a high number of grid cells ( $N = 3,063$ ). Pseudo- $R^2$  values (hereafter  $R^2$ ) are depicted in the individual graphs reported in Figure 3 and range from  $R^2 = 0.11$  to 0.71.



Plant life-forms were assumed to follow climate-driven spatial pattern, although different plant life-forms showed different reactions. The number of phanerophytes showed a hump-shaped distribution both with elevation and precipitation, although the relationship with elevation was substantially right-skewed (Figures 3a and 4a). This led to a spatial pattern that showed highest values at low elevations in the northeastern zone of the island. Percentage of phanerophytes increased with elevation and precipitation (Figure 3b). Topographic variables had little effect on life-form distribution, although phanerophytes are an exception. Their number and percentage increased with the steepness of the slope (Appendix S1). This spatial pattern highlights the high contribution of trees and large shrubs to the humid laurel forest found at steep mid elevations on the northeastern side, where they contributed around 40% of species to the respective plant communities.

The number of chamaephytes showed a weak U-shaped distribution with elevation, whereas it showed a hump with precipitation (Figures 3c and 4b). This led to a heterogeneous distribution with low values in laurel forest and high values on northern coasts and the Caldera de Taburiente complex in the centre of the island. Percentage of chamaephytes showed a strong positive relationship with elevation but a non-significant relationship with precipitation (Figure 3d).

The number of hemicryptophytes decreased with elevation and showed a right-skewed hump with precipitation (Figures 3e and 4c). The resulting spatial pattern revealed hot spots of the number of hemicryptophytes at low elevations, mainly in the north and east, and cold spots at high elevations. The percentage of hemicryptophytes increased with elevation and precipitation (Figure 3f). The spatial distribution revealed that hot spots were located at mid to high elevations, in some parts contributing more than 30% of species to the respective plant communities.

The number of geophytes decreased with elevation and precipitation (Figures 3g and 4d). Thus, hot spots of the number of geophytes were found at low elevations (mainly on the northern to eastern side), while the cold spots were located at high elevations. We found a similar relationship of elevation and precipitation with % geophytes (Figure 3h). However, geophytes only contributed a maximum of around 4% of species to the respective plant communities.

The number of therophytes decreased with elevation and showed a strongly right-skewed relationship with precipitation (Figures 3i and 4e).

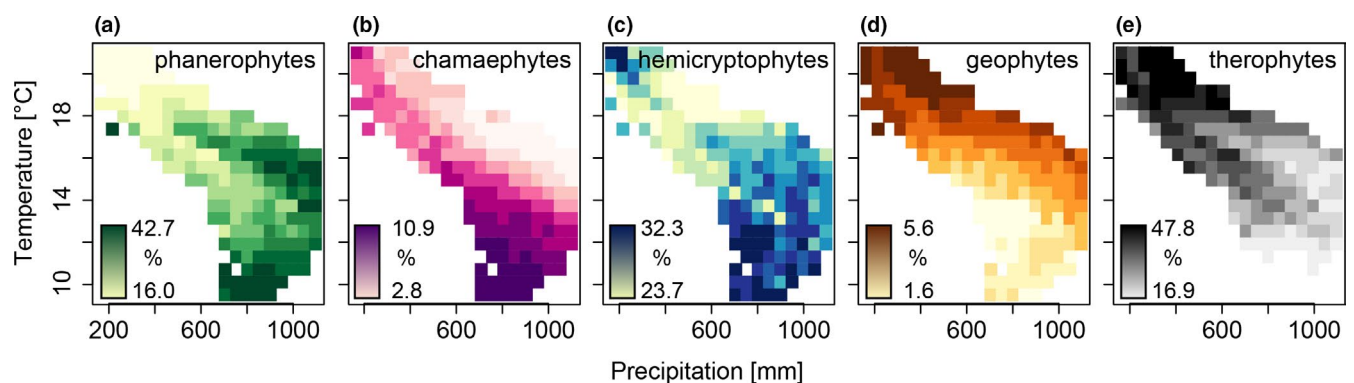
As a result, we found the highest number of therophytes at low elevations. Similarly, the percentage of therophytes decreased strongly both with elevation and precipitation (Figure 3j) and also slope (Appendix S1). Hot spots of % therophytes were found on flat ground at low to mid elevations. In some parts, therophytes contributed up to 45% of species, indicating the importance of this plant life-form for low and mid elevation systems that are often subject to current or historic human land use.

### 3.2 | Plant functional traits: Succulence and N-fixers

In order to assess the influence of climate on the spatial distribution of the two plant functional traits, succulence and N-fixers, we correlated absolute and relative values against elevation (as a proxy for temperature) and precipitation. All relationships presented in this section were strongly significant with  $p < 0.001$ .  $R^2$  values are depicted in the individual graphs and range from Pseudo- $R^2 = 0.21$  to 0.77. The number of N-fixers decreased with elevation, while it showed a unimodal distribution with precipitation (Figure 5d). The number of N-fixers peaked at low elevations on the northern and eastern side of the island. Lowest values were found at high elevations, at mid elevations within the influence of the NE-trade winds and on the arid leeward coast. The percentage of N-fixers slightly increased with elevation, whereas it showed a hump-shaped relationship with precipitation (Figure 5e). Values of % N-fixers were highest at mid and high elevations on the western side of the island. Mid elevation on the northern to eastern side and the western coast showed lowest values.

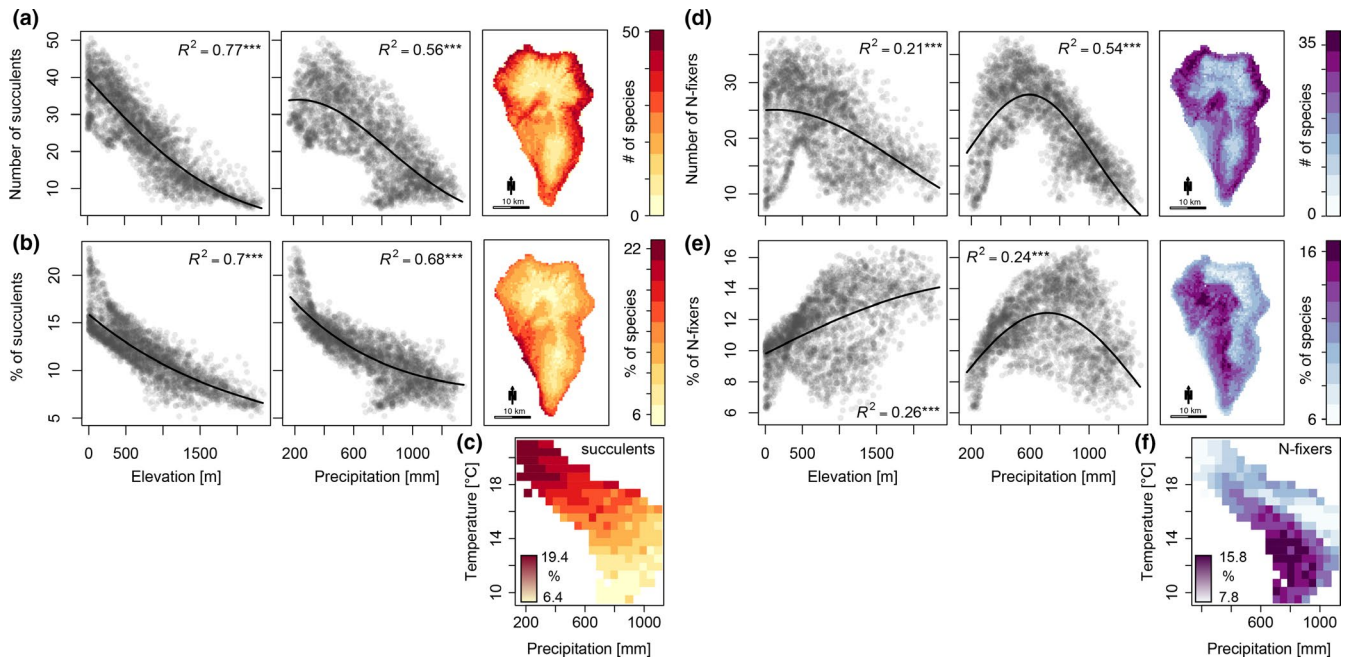
Both elevation and precipitation had a negative effect on the number of succulents (Figure 5a) as well as on % succulents (Figure 5b). The number of succulents was highest in coastal regions and had their lowest values at high elevations. The spatial distribution of % succulents was analogous to the number of succulents, although the hot spot of % succulents was shifted to the arid western coast, where more than 20% of species were succulents.

Topographic variables had only a very minor influence on both the number and percentage of succulent and N-fixing plant species (see Appendix S2).



**FIGURE 4** Plant life-form distribution of all life-forms (phanerophytes, chamaephytes, hemicryptophytes, geophytes and therophytes) in % of all species plotted in climate space (mean annual temperature versus. mean annual precipitation on the island of La Palma) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]





**FIGURE 5** Relationship between both elevation and precipitation with (a) number of succulents, (b) % succulents, (d) number of N-fixers and (e) % N-fixers on the island of La Palma. The maps show the spatial pattern of the respective indices. Figures (c) and (f) display the distribution of the respective plant functional trait in climate space. Asterisks \*\*\* indicate a  $p$ -value < 0.001 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

## 4 | DISCUSSION

Our study comprehensively transfers Raunkjær's plant life-form concept to a subtropical insular flora and a functional island biogeographic context by adapting it to local unfavourable growing conditions, that is, seasonal drought and aridity. Furthermore, we identify a clear spatial structure within geographic but also climate space of plant life-forms and plant functional traits on the mountainous and climatically heterogeneous island of La Palma. Interestingly, climate explained plant life-form distribution as well as plant functional trait distribution much better than topography. Different plant life-forms and plant functional traits react in differing, often opposing ways to thermal and moisture gradients. However, beside climatic factors, evolutionary drivers as well as anthropogenic disturbances (especially fire and introduced herbivores) likely modulate the overall pattern for certain plant life-forms and plant functional traits.

### 4.1 | Climate drives distribution of woody life-forms

Woody species, especially the large group of phanerophytes, show a strong relationship to climate. Thereby, it becomes clear that the importance of woody species decreases with temperature but increases with precipitation. Indeed, within the perpetually humid and mild evergreen laurel forest laurophyllous trees (e.g. *Laurus novocanariensis*, *Morella faya*, *Ocotea foetens*, *Ilex canariensis*, *Persea indica*, *Apollonias barbujana*, *Picconia excelsa* and others) and large shrubs (*Gesnouinia arborea*, *Bencomia caudata*, *Bystropogon canariensis*, etc.) comprise a substantial proportion of species diversity (del Arco-Aguilar et al., 2010). Under such favourable growing conditions with very little seasonality

in temperature and precipitation (Weigel et al., 2018), short-lived species such as therophytes and low stature species (geophytes and hemicryptophytes but also dwarf shrub chamaephytes) are outcompeted by tall-growing woody species (trees, large shrubs) that produce a dense and dark canopy (Delgado et al., 2007). Merely as a result of their large structures, phanerophytes have a competitive advantage over other plant life-forms, indicating a climate-driven selection of tall-growing plant life-forms under humid and mild conditions.

In the cool but arid high elevation summit scrub, large shrubs with a hemispheric growth form (e.g. *Adenocarpus viscosus* subsp. *spartioides*, *Genista benehoavensis*, *Teline stenopetala*, *Spartocytisus supranubius* or *Chamaecytisus proliferus* subsp. *proliferus*, *Echium gentianoides*) dominate the vegetation. As trees are more closely coupled to atmospheric processes (especially low temperatures and high winds speeds at high elevations) and cannot profit from latent heat coming from the high solar radiation warming the soil, the growth form 'tree' reaches its elevational limit at lower elevations than shrubs or other low stature species, forming the widely studied alpine tree line (Körner, 2012). On the Canary Islands, alpine tree line is reached at around 2,000 m a.s.l. and is modulated by local climatic processes such as aridity or the mass elevation effect (Irl et al., 2016). Thus, at high elevations a highly specialized endemic shrubby flora has developed (Steinbauer et al., 2017) possessing many species that are often entirely restricted to this system (Irl et al., 2017). Indeed, the summit scrub is an evolutionary very active system as its high degree of (neo-)endemism indicates (Merckx et al., 2015; Steinbauer, Field, Grytnes, et al., 2016). This suggests that the life-forms dominating in this system strongly reflect a climate-speciation coupling in the sense that the current pattern of plant life-forms is directly shaped by in situ climate conditions leading to the evolution and persistence of certain life-forms.





#### 4.2 | Modulation of the non-woody plant life-form distribution

Interestingly, hemicryptophytes and therophytes show a strongly opposing pattern. The relative contribution of hemicryptophytes increases with increasing precipitation and decreasing temperature, while it is vice versa for therophytes. Two non-mutually exclusive explanations are likely: (a) On the arid leeward side of the island, where therophytes are more important, inter-annual precipitation variability is high, making precipitation events much less predictable (Jiang et al., 2017). In unpredictable environments it is advantageous to be short-lived (such as therophytes) in order to take advantage of specific precipitation events and then survive long periods of unfavourable conditions as a seed. Nevertheless, in the driest and most arid regions of the island, the share of perennial hemicryptophytes increase again, likely because perennial hemicryptophytes might have effective perennial structures below the ground to survive water-limited periods. (b) *Pinus canariensis* forests cover large areas of the leeward part of the island, especially at mid elevations, that are particularly prone to reoccurring wildfires (Molina-Terrén, Fry, Grillo, Cardil, & Stephens, 2016). This archipelago endemic pine species has up to 30 cm long needles, a thick bark and the unique ability to resprout from epicormics shoots from all above-ground organs—all remarkable features that either promote fire or enable the tree to survive fire events (Climent et al., 2004). For understorey vegetation, it makes sense to be adapted to reoccurring fire events, and being a short-lived therophyte might be a good strategy. Therophytes can take advantage of the low competition and high resource availability of post-fire conditions to complete their life cycle before other, more competitive life-forms emerge (Arévalo, Fernández-Palacios, Jiménez, & Gil, 2001). One has to note though that this system is also strongly affected by browsing damage caused by introduced herbivores (Cubas et al., 2019), which might additionally alter plant life-form patterns. In sum, we probably see a modulation of the generally climate-driven plant life-form pattern by local influences such as disturbances in the case of hemicryptophytes and therophytes.

#### 4.3 | Only minor influence of topography on plant life-forms and plant functional types

Topography only has a subordinate influence on plant life-form distribution and plant functional traits compared to climate. Nevertheless, we see a shift in importance from therophytes to phanerophytes with increasing slope steepness. This likely reflects suitability for human land use, with flatter areas being more suitable for land use than steeper slopes. Thereby, short-lived (herbaceous) therophytes are much better adapted to disturbance regimes associated with human land use, while long-lived (woody) phanerophytes thrive better in more natural settings that are not disturbed by high intensity land use (Moser et al., 2015).

#### 4.4 | Strong coupling of plant functional traits and climate

N-fixers show a complex pattern driven by a nonlinear interaction of temperature and precipitation. They occur mainly at mid elevations on the dry leeward side of the island and at high elevations above the trade wind inversion. At high elevations, N-fixer shrubs dominate the vegetation (e.g. *Adenocarpus viscosus* subsp. *spartioides*, *Spartocytisus supranubius*, *Genista benehoavensis*, *Chamaecytisus proliiferus* subsp. *proliiferus*, *Teline stenopetala*) with *A. viscosus* subsp. *spartioides* being by far the most abundant as a result of introduced herbivore browsing (Irl et al., 2012, 2014). The high elevation summit scrub is climatically cool but arid (del Arco-Aguilar et al., 2010). Thus, plant species, such as N-fixing legumes, that possess traits associated with high water use efficiency will have a competitive advantage (Reich et al., 2001). At mid elevations, N-fixers are an important species group in the undergrowth of the *Pinus canariensis* forest (e.g. *Lotus* spp., *C. proliiferus* subsp. *proliiferus*, *Adenocarpus foliolosus*, *Cicer canariensis* and near the tree line also *S. supranubius*). This might result from the fact that the leeward pine forest is (a) relatively dry supporting species with high water use efficiency (Reich et al., 2001), and (b) the pine forest is prone to frequent reoccurring fire events (Molina-Terrén et al., 2016). Similar to therophytes, fast growing N-fixers can profit from low competition and high resource post-fire conditions, as can be seen with the endemic herbaceous N-fixer *Lotus campylocladus* subsp. *hillebrandii* that covers large areas of the pine forest floor only a few months after a fire event, turning it bright yellow (pers. obs.).

As expected, succulents are favoured at low elevations, especially on the dry leeward coast of the island. Indeed, these results are consistent with Ellenberg (1981) who found that succulents dominate at regular amounts of annual precipitation between 100 and 200 mm—approximately the average annual precipitation at the leeward coast of La Palma (Irl et al., 2015). Besides being able to store water internally, succulents have a higher water use efficiency than other plant functional types because many are CAM plants (e.g. many species from the Crassulacean family; Mort, Solits, Soltis, Santos-Guerra, & Francisco-Ortega, 2007). At high elevations regular winter frost and ice storms likely regulate the distribution of succulents, while at high precipitation, for example, in the perpetually humid laurel forest, being succulent does not result in a competitive advantage over other functional traits as storing water is uneconomical if water is abundantly available (Teeri, Stowe, & Murawski, 1978). Thus, succulence on La Palma has a clearly defined climatic niche restricting it to low and dry elevations.

## 5 | CONCLUSION

Using the strong environmental gradients offered by the climatic 'mini-continent' of La Palma, we identify strong variation in plant life-forms and plant functional traits. The strong patterns in life-forms underline the importance to acknowledge within-island

differences in theory of island biogeography. Treating an island as a single unit does not account for the fact that different parts within that island differ considerably in their connectivity to surrounding landmasses and thus in their species source pool and isolation (Steinbauer, 2017). The growth strategies reflected in Raunkiaer's plant life-forms suggest differences in species establishment and coexistence dynamics within different parts of the island's climate space. The within-island differences have considerable consequences for the processes of colonization and extinction that should reflect the here identified within-island patterns. Our study showed that topographic variables were of subordinate importance for plant life-forms and plant functional traits on La Palma, although they have been shown to be important in other (island) contexts (Stein, Gerstner, & Kreft, 2014) together with further aspects of topography such as geology or habitat diversity (Keppel, Gillespie, Ormerod, & Fricker, 2016; Otto et al., 2016). In addition, important ecological relationships such as the species-area relationship can vary among plant growth forms on small islands (Schrader et al., 2020).

The strong plant life-form-climate relationship as well as the plant functional trait-climate relationship suggest that climate change—that will substantially alter island climatic conditions in the near future (Harter et al., 2015)—will affect the future distribution of plant life-forms and plant functional traits. How this might relate to ecosystem stability and functioning as well as ecosystem services warrants further research on this topic. Overall, we show that the concepts of plant life-forms and plant functional traits are relatively easily adapted to a new flora unrelated to the original intentions of the concepts. By applying both concepts to island floras that are often quite unique as a result of the high endemism, inter-island as well as inter-archipelago comparisons become feasible and potentially very interesting for future island biogeographical studies, especially in the context of the emerging field of functional island biogeography.

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## DATA AVAILABILITY STATEMENT

Data collected for this manuscript is accessible in DRYAD online repository (Irl et al., 2020) <https://doi.org/10.5061/dryad.0rxwdbx1>

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**BIOSKETCH**

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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