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High species turnover and low intraspecific trait variation in endemic and non-endemic plant species assemblages on an oceanic island

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Abstract

Questions: Both species turnover and intraspecific trait variation can affect plant assemblage dynamics along environmental gradients. Here, we asked how community assemblage patterns in relation to species turnover and intraspecific variation differ between endemic and non-endemic species. We hypothesized that endemic species show lower intraspecific variation than non-endemic species because they tend to have high rates of in situ speciation, whereas non-endemic species are expected to have a larger gene pool and higher phenotypic plasticity.

Location: La Palma, Canary Islands.

Methods: We established 44 sampling sites along a directional gradient of precipitation, heat load, soil nitrogen, phosphorus and pH. Along this gradient, we estimated species abundances and measured three traits (plant height, leaf area and leaf thickness) on perennial endemic and non-endemic plant species. In total, we recorded traits for 1,223 plant individuals of 43 species. Subsequently, we calculated community-weighted mean traits to measure the relative contribution of species turnover, intraspecific variation and their covariation along the analysed gradient.

Results: The contribution of intraspecific variation to total variation was similar in endemic and non-endemic assemblages. For plant height, intraspecific variation explained roughly as much variation as species turnover. For leaf area and leaf thickness, intraspecific variation explained almost no variation. Species turnover effects mainly drove trait responses along the environmental gradient, but intraspecific variation was important for responses in leaf area to precipitation.

Conclusions: Despite their distinct evolutionary history, endemic and non-endemic plant assemblages show similar patterns in species turnover and intraspecific variation. Our results indicate that species turnover is the main component of trait variation in the underlying study system. However, intraspecific variation can increase individual species' fitness in response to precipitation. Overall, our study challenges

the theory that intraspecific trait variation is more important for the establishment of non-endemic species compared with endemic species.

KEYWORDS
intraspecific variation, oceanic islands, precipitation, soil acidity, soil nutrients, species turnover, succulent scrub, traits

1 | INTRODUCTION

Oceanic islands harbour a morphologically unique and endemic-rich flora that is often of high conservation concern (Fernández-Palacios et al., 2021). Multiple studies have analysed the trait diversity (i.e. the extent of trait variation in a species assemblage) of oceanic island floras to determine their responses to abiotic conditions and stressors (Ottaviani et al., 2020; Schrader et al., 2021; Whittaker et al., 2014). However, intraspecific trait variation has not yet been analysed thoroughly, even though it can have important implications for the fitness and survival of species (Des Roches et al., 2018), especially under changing environmental conditions (Björklund et al., 2009; Norberg et al., 2001). Assessing trait variation of endemic species might show isolation-driven adaptations to local environmental conditions resulting from their evolutionary history.

Trait variation occurs both as species turnover and intraspecific variation (de Bello et al., 2011; Lepš et al., 2011). Here, we refer to trait variation due to changes in species composition and abundance as species turnover and to trait variation due to within-species differences as intraspecific variation. Previous studies have found that species turnover is usually higher than intraspecific variation across terrestrial plant assemblages because it is a focal parameter of species coexistence due to differing degrees of trait and niche overlap between species (de Bello et al., 2011; Messier et al., 2010; Violle et al., 2012). However, other studies have shown that intraspecific variation can be as extreme as trait variation between species in plant assemblages (Albert et al., 2010). Hence, it remains unanswered to what extent species turnover and intraspecific variation contribute to total trait variation.

Oceanic islands are valuable to analyse trait variation because they harbour both endemic and non-endemic species. Endemic species have undergone an isolated evolution on islands through anagenetic or cladogenetic speciation (Stuessy et al., 2006). In situ speciation often results in specific adaptations to local environmental conditions (Burns, 2019; Carlquist, 1974), possibly leading to high trait variation between species. Non-endemic species are either native and have colonized from the mainland by natural means or were (un-)intentionally introduced by humans. Because of their larger genetic pool and successful establishment in novel environments, non-endemic species are expected to have high phenotypic plasticity (i.e. trait variation for a given genotype in different environments; Alexander et al., 2011; Davidson et al.,

2011), yielding substantial intraspecific variation (Bradshaw, 1965). Hence, we expect non-endemic species to show higher intraspecific variation, whereas we expect endemic species to show higher species turnover owing to local adaptations resulting from in situ speciation.

Across environmental gradients, plant traits can change because of species turnover and intraspecific variation (Ackerly, 2003; Cornwell & Ackerly, 2009). Most studies state that species turnover is the main driver of trait characteristics along gradients because abiotic conditions select species with adequate traits to survive in a given environment (Keddy, 1992; Kraft et al., 2015; Weiher et al., 1998). For example, dry and high-irradiation environments select species with water-efficient and temperature-regulative traits, such as smaller plant height, smaller leaf area and thicker leaves (Moles et al., 2009; Poorter et al., 2009; Wright et al., 2017). Soil nutrient availability (notably nitrogen and phosphorus) can further affect plant trait values because of species turnover (Aerts & Chapin, 2000; Cadotte et al., 2011; Ordoñez et al., 2009). Nutrient-deficient soils lead to a shift from species associated with rapid resource acquisition to species associated with resource conservation (Aerts & Chapin, 2000; Díaz et al., 2004; Ordoñez et al., 2009). Furthermore, soil acidification can affect trait values due to species turnover because low pH requires plants species that efficiently acquire micronutrients or phosphorus from soils (Lambers et al., 2008). Yet, most studies have ignored the role of intraspecific variation, even though it can also be important in driving trait characteristics along gradients (Lepš et al., 2011). Simultaneously analysing how the relative contribution of species turnover and intraspecific variation change along climatic and soil gradients might help to redefine our understanding of community assemblage mechanisms.

In this study, we analyse species turnover and intraspecific variation in essential plant traits in endemic and non-endemic assemblages on the oceanic island of La Palma (Canary Islands, Spain). First, we hypothesize that trait variation mostly depends on species turnover rather than intraspecific variation in endemic assemblages compared with non-endemic assemblages. Second, we hypothesize that species turnover and intraspecific variation decrease with decreasing resource availability through selective filtering in plant species assemblages. However, it is not yet clear how the relative contributions of species turnover and intraspecific variation change along environmental gradients.

2 | METHODS

2.1 | Study site and plot selection

We conducted our study on La Palma (Canary Islands, Spain) from March to April 2018. La Palma is an oceanic island located in the Atlantic Ocean, ca. 500 km off the coast of northwestern Africa. The island is characterized by northeasterly trade winds giving rise to a humid windward and a dry leeward side (Garzón-Machado et al., 2014). This rainfall pattern can even be observed in the inframediterranean thermotype along the island's coast (hereafter referred to as coastal succulent scrub), where the ombrotypes range from arid in the southwest to upper-dry in the northeast (Garzón-Machado et al., 2014). La Palma is a volcanic island made of basaltic rock. It can be divided geologically into the older northern part (ca. 2.0 Ma), where volcanic activity has ceased and erosive processes dominate, and the younger southern part, where subaerial volcanic ontogeny is ongoing (0.54 Ma to 2021; Ancochea et al., 1994; Carracedo et al., 2001). The most common vegetation assemblage of the coastal succulent scrub, the Tabaibal-Cardonal vegetation, is characterized by focal species such as *Kleinia neriifolia*, different *Euphorbia* and *Echium* ssp. (del Arco Aguilar et al., 2010). *Opuntia* and *Agave* ssp. are successful invaders within the Tabaibal-Cardonal vegetation as they are adapted to arid–dry conditions (del Arco Aguilar et al., 2010). The Tabaibal-Cardonal vegetation represents a circum-insular ecosystem, in which the temperature is relatively constant and the species pool is endemic-rich.

We selected 44 study plots along the entire coastal succulent scrub at an elevation of ca. 100–200 m a.s.l. with a minimum distance of 700 m (Figure 1). At each point, we selected a 7 m × 7 m plot by haphazardly throwing an object to determine the centre, on the condition that there was minimal evidence of human disturbance. Areas affected by recent volcanic eruptions, on which vegetation is poorly developed, were not taken into consideration. The study area covered strong variation in both climate and soil (Table 1). Hence, our study system is ideal for comparison of these factors and their influence on trait variation between species assemblages.

2.2 | Vegetation survey and plant trait measurements

We estimated the percentage coverage of every perennial plant individual visually in each plot to quantify species composition. For each perennial species within a plot, five individuals were chosen for trait sampling, if available. We measured three essential "soft" (i.e. easy to measure, sensu Hodgson et al., 1999) morphological traits of perennial plant species that capture the essence of plant form and function. Overall, we recorded trait information for 1,223 individual plants of 43 species (27 endemic species and 16 non-endemic species; see Appendix S1, Table S1.1).

To determine maximum plant height, we measured the orthogonal distance from the upper boundary of the main photosynthetic tissues of plants to ground level (Pérez-Harguindeguy et al., 2013). We estimated leaf area based on measurements of maximum leaf length and maximum leaf width using digital callipers. For simple-leaved species, we measured three young but fully developed (i.e. current growing season) and undamaged leaves (excluding petiole because it is of less importance for light interception compared with the leaf blade) per individual. For compound-leaved species, we measured one leaflet of three different leaves per individual. Subsequently, we averaged the three leaf measurements for each individual. We determined leaf length as the maximum distance from the base to the tip of the leaf and leaf width as the maximum distance from one side of the leaf to the other. Assuming an oval-shaped leaf, we approximated leaf area as the product of (leaf length × width × π)/2. For stem-photosynthesizing succulents (*Opuntia dillenii*, *Opuntia maxima* and *Euphorbia canariensis*), a leaf length of zero was determined. Leaf thickness was measured with digital callipers at an intermediate position between the tip and the base of the leaf, avoiding major veins. We measured leaf thickness on the same three leaves per individual we measured leaf area. We averaged the three measurements for each individual and determined a leaf thickness of zero for stem-photosynthesizing succulents (*O. dillenii*, *O. maxima* and *E. canariensis*).

2.3 | Climate and soil variables

Interpolated data for mean annual temperature and annual precipitation were obtained from Irl et al. (2020). We used mean annual temperature (range: 18.4–21.0°C) to analyse a possible effect of potential direct incident radiation on trait variation. Hence, we calculated the heat load index after McCune and Keon (2002) using the *spatialEco* package in R (Evans, 2021). The heat load index assumes that a slope with the afternoon sun shining on it will have a higher maximum temperature than an equivalent slope with the morning sun shining on it.

To measure soil nitrogen and phosphorus content, we collected one soil sample for each plot. Each sample consisted of a homogenized mixture of five subsamples collected in each corner and at the centre of the plot (from ca. 10 cm depth). The samples were passed through a 2-mm sieve and air-dried for 3 days. Soil pH was measured using a glass electrode in a soil/$CaCl_2$ ratio of 1:2. We determined total N and C by dry combustion using a LECO TruSpec N auto analyser and a LECO RC-412, respectively (LECO Corporation). Phosphorus was determined following the CAL-Method described by Schüller (1969). We excluded soil carbon from the analyses because almost all plots had a carbon content of ca. 0%.

We ln-transformed nitrogen and phosphorus values to approximate normality, and subsequently centred and scaled all environmental variables, yielding estimates in *SD* units. After standardization, we calculated correlation coefficients (Pearson's *r*) between the environmental variables (Appendix S2, Table S2.1).
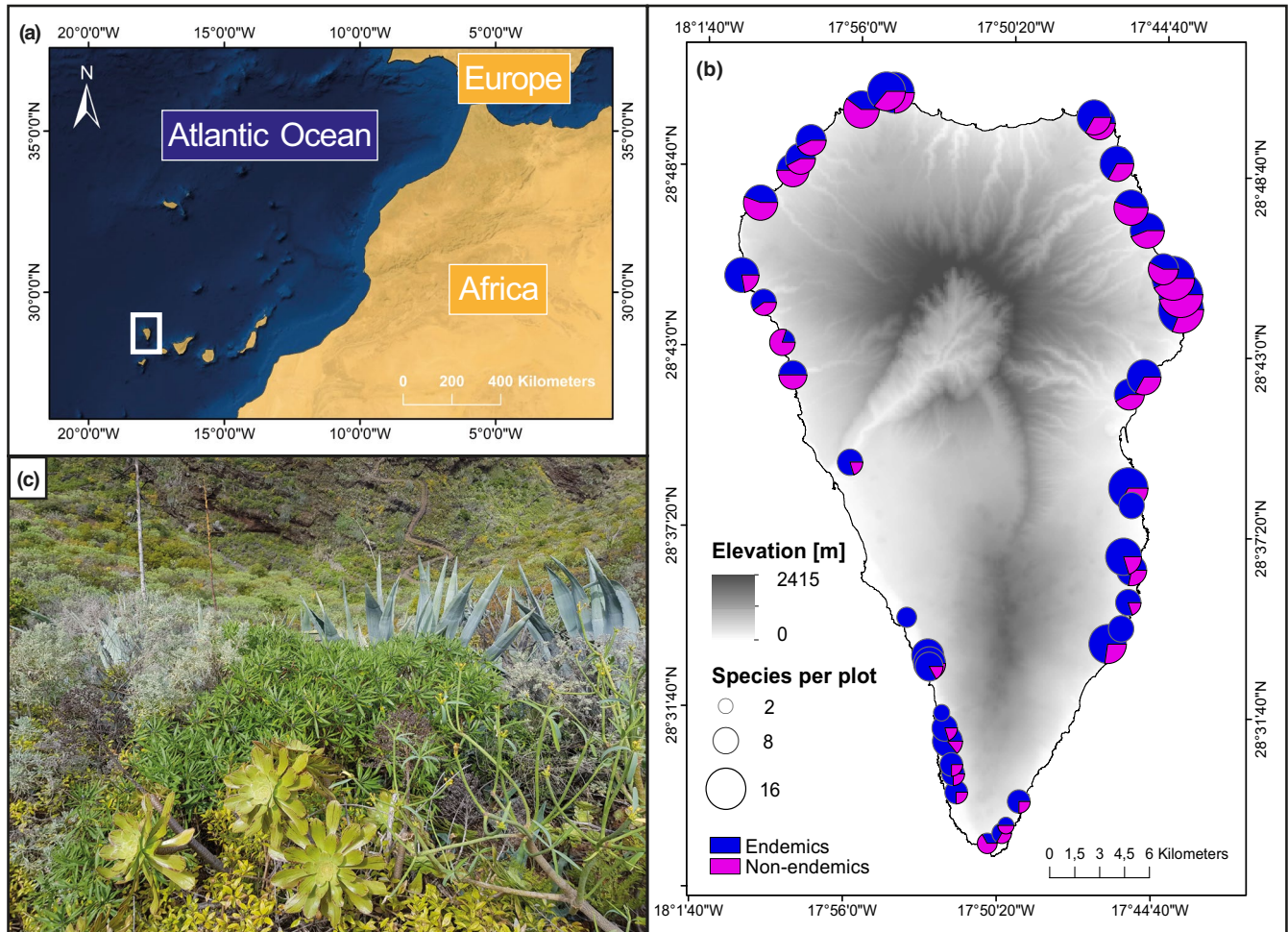
FIGURE 1 (a) La Palma is the most northwestern island of the Canary Islands archipelago (white rectangle). (b) Map of study sites, circles correspond to vegetation survey plots where trait data was collected (circle size = the number of species sampled in each plot; *n* = 44). The proportion of sampled endemic (blue) and non-endemic (purple) species is given for each plot. All plots were sampled at an elevation of approximately 100–200 m a.s.l. (c) Typical vegetation assemblage of the Tabaibal-Cardonal consisting of endemic species (here: *Aeonium arboreum*, *Euphorbia lamarckii*, *Rubia fruticosa*) and non-endemic species (here: *Agave americana*, *Globularia salicina*, *Schizogyne sericea*)

TABLE 1 Mean, standard deviation and range of environmental variables included in regression analyses

Variable	Unit	Mean	Standard deviation	Min	Max
Annual precipitation	mm	377.13	92.22	202.90	572.65
Heat load index		0.76	0.18	0.43	1.0
Soil nitrogen	%	23.47	15.33	0.70	95.00
Soil phosphorus	mg/100 g	6.02	19.37	0.30	202.56
Soil pH		6.21	0.79	4.44	7.85
Species richness (total)		9	3.46	2	16

2.4 | Total variation, species turnover and intraspecific variation

To assess the contribution of species turnover and intraspecific variation to total variation in traits, we calculated community-weighted mean trait values for endemic and non-endemic species assemblages in each plot (because of the small number of non-endemic species in our study system and our focus on endemic species, we did not further differentiate between native and non-native species assemblages). To assess the relevance of species turnover and intraspecific trait variation on community-weighted mean traits, we calculated specific and fixed averages (Lepš et al., 2011). Specific averages were calculated from the plot-specific trait values per species:

$$\text{Specific average} = \sum_{i=1}^{S} p_i x_{i\_plot},$$

where p_i is the relative abundance of the *i*th species based on the cover in the plot, S is the number of species and x_{i_plot} is the specific trait value of the *i*th species for the specific plot in which it was sampled. Fixed averages were calculated with trait values averaged over all plots within the gradient for each species. Fixed averages are therefore plot-independent, meaning that one species has one mean trait value regardless of the plot in which it is found. Subsequently, we calculated intraspecific variation as the difference between specific averages and fixed averages.

2.5 | Statistical analyses

To summarize variation in plant species composition, we used Non-Metric Multidimensional Scaling (NMDS; Minchin, 1987). NMDS ordination was obtained using the "metaMDS" function in the R package *vegan* (Oksanen et al., 2020) using Bray–Curtis dissimilarity on the matrix of species abundances across sites. To further examine the effects of the environmental gradients on plant species composition, we used vector fitting, as implemented in the "envfit" function (R package *vegan*; Oksanen et al., 2020).

We performed partitioning of trait variation among plots to quantify how much variability can be accounted for by species turnover or intraspecific variability alone. The method is based on a sum of squares decomposition (De Bello et al., 2011; Lepš et al., 2011) and was calculated using the "decompCTRE" function in the R package *cati* (Taudiere & Violle, 2015). This function fits an ANOVA to each component (i.e. total variation, species turnover and intraspecific variation) and takes the total sum of squares as a measure of the total variability for the respective component. The decomposition of sum of squares can also be applied across ANOVAs to calculate their covariation. If the covariation between species turnover and intraspecific variation is positive, both effects reinforce each other. If the covariation between species turnover and intraspecific variation is negative, both effects oppose each other (e.g. when effects of large-leaved species are decreased by small-leaved individuals). Before analyses, we normalized leaf area and leaf thickness using an ln-transformation.

We further assessed responses in trait variation to climate, soil and species richness because changes in trait values can be driven by species turnover alone, by intraspecific variation alone or by both species turnover and intraspecific variation. We built multiple linear regression models for each plant trait, considering the specific averages (which include the effect of both species turnover and intraspecific variation) and fixed averages as the response variables, and the environmental variables (annual precipitation, heat load index, soil nitrogen, soil phosphorus, soil pH and species richness) as explanatory variables. We tested all models for quadratic relationships ($y \approx x + x^2$) because trait characteristics do not necessarily change linearly along environmental gradients. We first ran an initial full model for each trait (including all five environmental variables) and subsequently checked for spatial autocorrelation

using Moran's *I* statistic. We could not detect spatial autocorrelation in any of the multiple regression models. Subsequently, we chose a model selection procedure, based on minimizing the AICc (Burnham & Anderson, 2002). We performed AICc model selection using the function "dredge" in the R package *MuMIn* (Bartoń, 2020) to obtain the overall best model. All analyses were performed using R (version 4.1.1, R Core Team, R Foundation for Statistical Computing, Vienna, AT).

3 | RESULTS

3.1 | Species richness and species composition

Total species richness in the 44 plots ranged from 2 to 16, with an average of 9. Proportion of endemic species in assemblages ranged from 20% to 100%, with an average of 67%. Species composition varied across the analysed plots on La Palma. Species composition was significantly correlated with precipitation ($r^2 = 0.71$, $p < 0.001$), heat load index ($r^2 = 0.42$, $p < 0.001$), soil nitrogen ($r^2 = 0.17$, $p = 0.025$) and soil pH ($r^2 = 0.44$, $p < 0.001$). Soil phosphorus had no significant effect on species composition ($r^2 = 0.01$, $p = 0.910$; Figure 2).
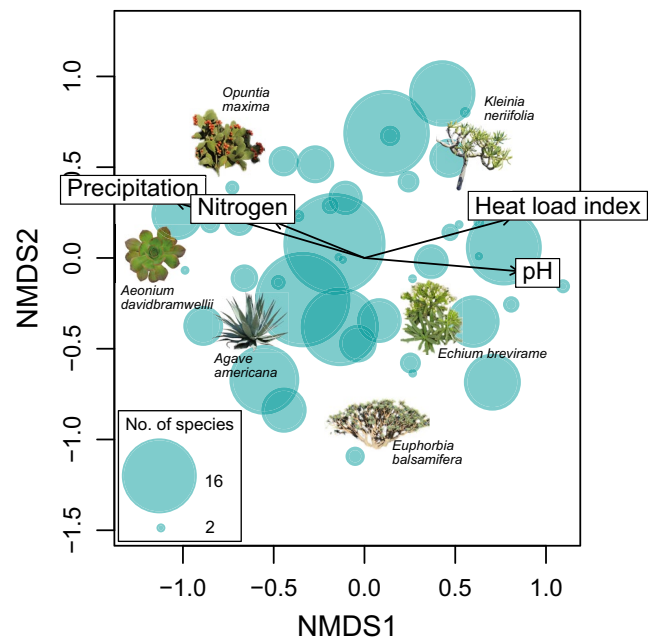

FIGURE 2 Non-Metric Multidimensional Scaling (NMDS) ordination of plant species assemblages in 44 plots in the coastal succulent scrub on La Palma, Canary Islands. Circle sizes illustrate total species richness in each plot. A Bray–Curtis similarity index on coverage data was used. Arrows represent the environmental variables that correlated significantly with the ordination ($p < 0.05$). The stress value was 0.16. Plant icons display the position of characteristic endemic (*Aeonium davidbramwellii*, *Echium brevirame*, *Euphorbia balsamifera*) and non-endemic (*Agave americana*, *Opuntia maxima*, *Kleinia neriifolia*) plant species

3.2 | Contribution of species turnover and intraspecific variation

The contribution of species turnover and intraspecific variation to total variation showed only minor discrepancies between endemic and non-endemic assemblages (Figure 3; see Appendix S2, Table S2.2). Species turnover accounted for most variation across almost all traits in endemic (plant height, 46%; leaf area, 98%; leaf thickness, 81%) and non-endemic assemblages (plant height, 33%; leaf area, 81%; leaf thickness, 89%). For plant height, intraspecific variation accounted for 31% of explained variation in endemic assemblages and 41% of explained variation in non-endemic assemblages. For leaf area and leaf thickness, intraspecific variation accounted for 18% and 28% of explained variation in endemic assemblages, and 7% and 6% of explained variation in non-endemic assemblages, respectively. We found positive covariation between species turnover and intraspecific variation for plant height in endemic assemblages, and for plant height, leaf area and leaf thickness in non-endemic assemblages. This indicates that plots dominated by species with high values for those traits also held individuals with comparatively high trait values for their species. Conversely, we found negative covariation between species turnover and intraspecific variation for leaf area and leaf thickness in endemic assemblages. This indicates that plots dominated by endemic species with high values for leaf area and leaf thickness held individuals with comparatively low trait values for their species.

3.3 | Variation in traits along environmental gradients

For plant height, specific averages increased significantly with increasing precipitation, and both specific and fixed averages increased with heat load index (Figure 4a). Also, fixed averages of plant height had a significant unimodal relationship with soil phosphorus (Figure 4a). For leaf area, specific averages increased significantly with increasing precipitation (Figure 4b). Both specific and fixed averages of leaf area had a significant U-shaped relationship with heat load index and increased significantly with soil phosphorus (Figure 4b). For leaf thickness, specific and fixed averages increased significantly with heat load index and had a significant U-shaped relationship with soil nitrogen (Figure 4c). The explained variation in the multiple regression models analysing specific averages was 27% for plant height, 51% for leaf area and 44% for leaf thickness. The explained variation in the multiple regression models analysing fixed averages was 18% for plant height, 41% for leaf area and 49% for leaf thickness (Appendix S2, Table S2.3).

Specific and fixed average relationships of endemic and non-endemic assemblages with environmental variables were overall similar to those of entire assemblages. Adversely, fixed averages of leaf area decreased with species richness in endemic assemblages and specific averages of leaf area increased with species richness in non-endemic assemblages. Coefficient estimates and adjusted R^2-values are given in the Supporting Information (Appendix S2, Figure S2.1–2, Table S2.3).

4 | DISCUSSION

Our study tests whether trait variation in endemic and non-endemic plant assemblages is related to species turnover (differences in species composition) and intraspecific variation, and what drives plant trait variation along multiple environmental gradients in the coastal succulent scrub of the island of La Palma. In contrast to our first hypothesis, we found that trait variation mostly relates to species turnover rather than intraspecific variation in both endemic and non-endemic assemblages. Following our second hypothesis, our study shows that total plant trait variation generally decreased with
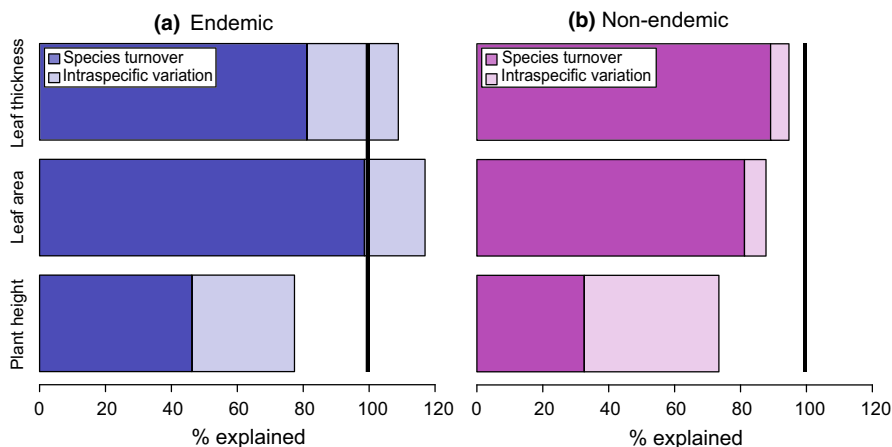

FIGURE 3 Decomposition of total variation in plant height, leaf area and leaf thickness for (a) endemic ($n = 44$) and (b) non-endemic ($n = 41$) assemblages. Dark areas on the bars correspond to species turnover and light areas to intraspecific variation effects. Vertical black lines denote total variation. The space between the end of the bar and the black line corresponds to the effect of covariation; if the line is to the right the bar, the covariation is positive, whereas if the line crosses the bar, the covariation is negative
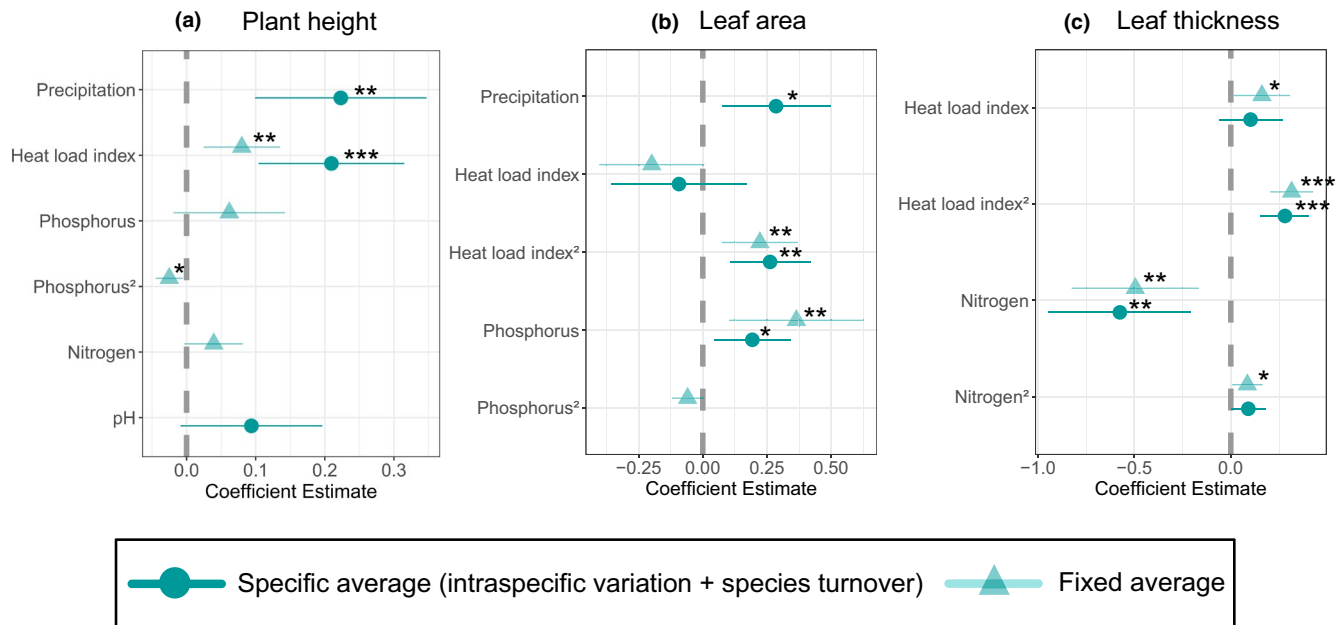
FIGURE 4 Multiple regression models of precipitation, heat load index, soil nitrogen, soil phosphorus and soil pH on specific averages and fixed averages of (a) plant height, (b) leaf area and (c) leaf thickness in entire plant assemblages ($n = 44$) across the coastal succulent scrub of La Palma, Canary Islands. Circles denote the specific averages (species turnover and intraspecific variation); triangles denote fixed averages only. Standardized estimates are provided for each predictor. Error bars represent confidence intervals of the coefficient estimates. Asterisks denote statistical significance (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$)

decreasing resource availability, mostly due to species turnover effects. The importance of intraspecific variation in driving trait responses depended on the environmental factor considered. Despite their distinct evolutionary history, trait variation for endemic and non-endemic assemblages on oceanic islands may be driven by similar mechanisms across strong climatic and edaphic gradients.

4.1 | Similar contribution of species turnover and intraspecific variation

In most cases, species turnover was the main contributor to trait variation in both endemic and non-endemic plant assemblages on La Palma. However, we expected higher intraspecific variation in non-endemic species because of a larger gene pool and higher phenotypic plasticity. Indeed, we recorded few, but consistently occurring invasive species (*Agave americana*, *Opuntia dillenii*, *Opuntia maxima*) across the coastal succulent scrub, known to be plastic in their traits and diverse in their genetic composition (Alexander et al., 2011; Davidson et al., 2011). We expected high species turnover in endemic assemblages because species that have developed on the Canary Islands through adaptive radiation, such as species from the genera *Aeonium* and *Echium*, are known to have high morphological variation between species (Böhle et al., 1996; Jorgensen & Olesen, 2001; Liu, 1989). Even though trait variation was driven primarily by species turnover, our results show that intraspecific variation in plant height made a relatively high contribution to total trait variation both in endemic and non-endemic assemblages. These results concur with previous studies showing that intraspecific variation has

a relevant role in total trait variation in plant height (Gross et al., 2013; Jung et al., 2010; Lepš et al., 2011). By contrast, leaf area and leaf thickness are less plastic and hence less variable within species (Roche et al., 2004; Wilson et al., 1999). However, we acknowledge that trait responses can be variable because they are dependent on functional trade-offs driven by biotic interactions (Callaway et al., 2003) and the abiotic environment (Ackerly, 2003). Hence, the here observed species turnover effect in plant assemblages might be biased by our trait choice and the studied environment.

Intraspecific variation contributed to trait variation not only directly, but also through covariation with species turnover effects. Positive covariation occurred in traits of endemic and non-endemic assemblages, which is consistent with the expectation that species turnover and intraspecific trait responses should be in the same direction to increase individual plant fitness (Cornwell & Ackerly, 2009). However, we also found that intraspecific variation decreases total variation through negative covariation with species turnover in leaf area and leaf thickness of endemic assemblages. This indicates that within some individual plant species, trait characteristics showed opposing responses in comparison with responses among species trait characteristics (Kichenin et al., 2013; Weemstra et al., 2021). This response of species might be driven by trait divergence as a consequence of a reduction in niche overlap and heterospecific competition (Ackerly et al., 2006; Schluter, 2000), which seems to be more pronounced in endemic than non-endemic species. This distinct pattern seems reasonable because endemic species are often associated with minor competitive ability due to their evolution in less-competitive environments (Fernández-Palacios et al., 2021). Our results indicate that endemic and non-endemic assemblages underlie

similar mechanisms shaping trait variation but might respond differently to competition because of their distinct evolutionary history.

4.2 | Strong environmental filtering of trait characteristics due to species turnover

Specific and fixed averages showed similar responses to climatic and edaphic variables across all traits. This overlap indicates that species turnover is the most important contributor to total trait variation across the analysed gradients. However, intraspecific variation tended to play a substantial role in trait responses of endemic and non-endemic assemblages to precipitation. This result may reflect a wide variation in precipitation against more stable heat load and soil conditions. Most of the precipitation on La Palma falls between October and April, with extensive drought periods in summer (Garzón-Machado et al., 2014). Environmental variation, such as precipitation seasonality, can promote adaptive phenotypic plasticity for plants to increase their fitness (Ghalambor et al., 2007). Previous studies corroborate our results because they found that plant height and leaf area are highly responsive to precipitation within species and contribute strongly to total trait variation (Gross et al., 2013; Jung et al., 2014; but see Siefert et al., 2014).

Fixed averages generally decreased with decreasing resource availability allocated by climate and soil. This result indicates that trait-mediated environmental filtering mainly occurred by changes in species composition of plant assemblages. Dry, highly irradiated and infertile environments can result in low trait values because plant species need to possess adequate traits to survive in such environments (Keddy, 1992; Kraft et al., 2015; Weiher et al., 1998). However, we found that plant height increased with heat load index, especially in endemic assemblages. This pattern could indicate that heat stress for plant height is less pronounced due to high isothermality (Moles et al., 2009) in the succulent scrub on the Canary Islands. Large and thin leaves generally have a low water stress tolerance, whereas species with small and thick leaves are better suited for arid environments (Moles et al., 2009; Poorter et al., 2009; Wright et al., 2017). In fact, the invasive species *O. dillenii* and *O. maxima*, as well as the endemic *Euphorbia canariensis*, are striking examples of convergent evolution and have analogously developed ephemeral leaves in which photosynthetic activities have been replaced by cladodes or photosynthesizing stems, respectively. Those species also use CAM photosynthesis, an adaptation of plants to increase water-use efficiency under arid conditions (Cushman, 2001). Moreover, trait averages responded mostly nonlinearly to soil nutrient availability. Nutrient-poor soils promote a shift from acquisitive to conservative strategies in species (Díaz et al., 2004; Ordoñez et al., 2009). Hence, species in nutrient-poor sites display small but thick leaves, which in theory translates into greater investment in leaf construction (but see Cutts et al., 2021). However, this pattern is less clear for plant height, possibly because of the prevalent limitation of nitrogen in young soils (Lambers et al., 2008). Surprisingly, soil acidity decreased leaf area in only endemic

assemblages, even though it can limit nutrient uptake and therefore restrict growth (Gujas et al., 2012). This pattern could be explained by the relatively narrow range of soil pH values captured in our study.

Interestingly, fixed averages of leaf area decreased with increasing species richness in endemic assemblages, but increased in non-endemic assemblages. This indicates that small-leaved endemic species and large-leaved non-endemic species are more prominent in species-rich assemblages. Large-leaved species can outcompete other species because of light interception to lower vegetation layers (Parkhurst & Loucks, 1972). Hence, our results indicate that non-endemic species might have a competitive advantage over endemic species in comparatively species-rich assemblages owing to the dominance of large-leaved species.

4.3 | Conclusions

Disproving our first hypothesis, we found that species turnover accounted for a considerable part of the total variation in plant height, leaf area and leaf thickness in endemic and non-endemic plant species assemblages. Hence, our results challenge the theory that intraspecific trait variation is important for the proliferation of non-endemic species. Concurring with our second hypothesis, we found that species turnover and intraspecific variation generally increased with resource availability. Moreover, we were able to show for the first time that intraspecific variation is more important than species turnover in response to limiting environmental factors, such as precipitation in an arid ecosystem. We conclude that non-endemic plant species can establish successfully in coastal environments despite low levels of intraspecific trait variation. However, plant species can establish higher intraspecific trait variation in response to seasonal environments, which could have important implications during a time of global change.

AUTHOR CONTRIBUTIONS

D.M.H., M.B., R.W., C.B. and S.D.H.I. conceived the research idea. D.M.H., M.B. and R.W. collected the data. D.H. performed statistical analyses and wrote the paper. All authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT
All environmental and morphological data are available in the Supporting Information (see Appendix S3, Table S3.1) and were

submitted to the TRY Plant Trait Database (www.try-db.org) on 8 July 2021.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. List of endemic and non-endemic species.
Appendix S2. Variation in traits of entire, endemic, and non-endemic plant assemblages.
Appendix S3. Environmental and morphological trait data.

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