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RESEARCH ARTICLE

Primary succession and plant functional traits on an oceanic island

Rüdiger Otto[1] | **Francisco Cabrera Rodríguez**[1] | **Julian Schrader**[2] | **Natalia Sierra Cornejo**[1] | **Martha Paola Barajas Barbosa**[3,4] | **Holger Kreft**[5,6,7] | **Dagmar Hanz**[8] | **Severin D. H. Irl**[8] | **Amanda Ratier Backes**[3,9] | **José María Fernández-Palacios**[10]

[1]Departamento de Botánica, Ecología y Fisiología Vegetal, Universidad de La Laguna (ULL), La Laguna, Spain; [2]School of Natural Sciences, Macquarie University, Sydney, New South Wales, Australia; [3]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany; [4]Department of Computer Science, Martin Luther University Halle-Wittenberg, Halle, Germany; [5]Biodiversity, Macroecology and Biogeography, University of Göttingen, Göttingen, Germany; [6]Centre of Biodiversity and Sustainable Land use (CBL), University of Göttingen, Göttingen, Germany; [7]Campus Institute Data Science (CIDAS), University of Göttingen, Göttingen, Germany; [8]Biogeography and Biodiversity Lab, Institute of Physical Geography, Goethe-University Frankfurt, Frankfurt am Main, Germany; [9]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, Germany and [10]Island Ecology and Biogeography Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUETSPC), Universidad de La Laguna (ULL), La Laguna, Spain

Correspondence
Rüdiger Otto
Email: rudiotto@ull.edu.es

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Abstract

1. The discipline of functional island biogeography and studies on plant ecological strategies shaping island assemblages have emerged only recently. Due to volcanic activity, primary succession is an important natural process driving ecosystem dynamics on oceanic islands. However, our knowledge about plant functional traits in explaining the mechanism of ecological succession on these islands characterized by impoverished and disharmonic, but endemic-rich floras, is limited.
2. We investigated the distribution of plants with respect to nine functional traits related to resource use, reproduction, and growth as well as their overall functional diversity during primary succession using a chronosequence on 10 lava flows of La Palma, Canary Islands. We analysed changes of single traits with age using community-weighted trait means and applied ordination techniques to evaluate changes in trait composition. Based on ecological succession theory, we tested several hypotheses for changes of functional traits along the successional gradient. We also analysed the role of endemic and introduced plants in structuring successional communities.
3. Both the single-trait and trait compositional approach revealed that the composition of plants displaying core traits related to leaf economics and dispersal ability shifted with substrate age showing a change from acquisitive to conservative traits and from anemochory to zoochory along the gradient. These shifts were entirely driven by endemic shrubs, while other growth forms contributed to the increase in species and functional richness with lava age but little to vegetation structure. Introduced species were almost absent in successional trajectories.

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Functional dispersion increased whereas trait turnover was constant and low during succession.

4. *Synthesis*. Our island system reflects a directional succession governed by the selection of functional traits related to environmental conditions and acquisitive-conservative strategies as well as to dispersal capacity in early stages followed by a gradual modification of the environment and an expansion of the niche space linked to functional divergence in later stages. Major changes in functional traits occurred five hundred years after the eruptions indicating that primary succession in this dry environment is very slow. The dominance of endemic shrubs and the lack of introduced plants at all successional stages highlight the importance of evolutionary processes in shaping species ecological strategies linked to disturbances like volcanism on this oceanic archipelago.

KEYWORDS

chronosequence, endemism, functional diversity, lava flows, oceanic island, primary succession, vascular plants

1 | INTRODUCTION

Primary succession is the temporal process of ecosystem recovery on newly created or exposed substrate with little biological remnants (i.e. lacking soil and organisms) after an extreme disturbance (Prach & Walker, 2019; Walker & del Moral, 2003). On young oceanic islands with high volcanic activity, primary succession is one of the most important natural processes and an important determinant of ecosystem dynamics and the distribution of plant life (Whittaker et al., 2023). However, our knowledge about the drivers of primary succession is mostly based on continental studies in the context of deglaciation, dune systems and volcanism (Grishin et al., 1996; Prach & Walker, 2019), whereas this topic has generally received much less attention on islands (but see Cutler et al., 2008; del Moral & Poli Marchese, 2010; Elias & Dias, 2009; Kitayama et al., 1995; Vitousek et al., 1987).

Plant functional traits are crucial in characterizing ecological strategies and developing mechanistic models predicting the response of ecosystems to disturbances (Chang & Turner, 2019; Grime, 2002). Functional trait approaches have only recently been introduced in island biogeography as a framework to understand how functional traits are influenced by biogeographical and evolutionary processes in interaction with the dynamic abiotic environment in an island context (Barajas Barbosa et al., 2023; Barton & Fortunel, 2023; Ottavani et al., 2020; Schrader, 2020; Schrader, Westoby, et al., 2021; Schrader, Wright, et al., 2021).

During ecological succession, plant strategies usually follow two main gradients of specialization (but see also unifying concepts, Laughlin, 2024); the first representing the plant resource economy related to water, light and nutrient acquisition, and the second is linked to dispersal and reproductive capacity (Westoby et al., 2002). An acquisitive strategy is typical for ruderal or pioneer plants (Grime, 2002) which show fast growth, high values of specific leaf area (SLA), leaf area and leaf nitrogen (N) and low values of leaf C:N and leaf carbon (C) and leaf dry matter (LDMC). A conservative strategy is related in turn to the opposite trend and is found for slow-growing late-successional plants. SLA reflects photosynthetic capacity as well as to leaf longevity (Cornelissen et al., 2003) and represents a cost-benefit trade-off in leaf carbon economy.

In succession studies of glacier forelands, Caccianiga et al. (2006) found a decrease of SLA and leaf N with terrain age. Chang and HilleRisLambers (2019) also reported a temporal decrease in SLA in plants established after the Mount St. Helens eruption. On Tenerife, higher SLA and leaf nutrients, but lower leaf C and C:N ratio were reported for disturbed roadside communities compared to more natural vegetation types (Ratier Backes et al., 2023) supporting the idea that acquisitive plant strategies are favoured after disturbance. However, nutrient and, especially, N availability in early primary succession on volcanic substrate is usually low (Cabrera Rodríguez, Otto, & Fernández-Palacios, 2022; Gallardo et al., 2020; Vitousek et al., 1993) due to the lack of soil and, consequently, leaf N of plants growing in these nutrient-poor environments might be reduced as reported for *Metrosideros polymorpha*, a native tree abundant on young lava flows on Hawaii (Matson, 1990). Hence, primary succession in volcanic environments usually represents a productivity gradient linked to soil development and fertility. Additionally, plant functional traits have been shown to vary along climatic gradients on continents and on islands (Ratier Backes et al., 2023; Westoby & Wright, 2006). In this context, a conservative trait strategy was related to drought-tolerant species (Pavanetto et al., 2024).

Commonly, strong dispersal filtering has been reported where anemochorous species with small, vagile seeds dominated in open stressful micro-environments while endozoochorous fleshy-fruited species with heavier seeds corresponded with later successional stages formed by closed shrub and forest communities (Fuller & del Moral, 2003; Greinwald et al., 2021; Korablev et al., 2020; Walker &

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del Moral, 2003). On Krakatau Island, this trend has been explained by positive feedback at later successional stages in which an increasing number of fruiting shrubs and trees attract greater numbers of visiting birds and flying foxes, the primary dispersers, which drop more seeds, introducing further endozoochorous species (Whittaker et al., 1989). Generally, seed size is related to life-history strategies, where small seeds are often associated with high colonization rates due to their dispersal ability, while large seeds are linked to better establishment and competitive abilities due to maternal investment of resources (Moles & Westoby, 2004).

Furthermore, functional diversity measures such as functional dispersion or beta diversity have been applied to evaluate temporal trends in community assemblage during primary succession such as trait convergence or divergence which depend on the importance of ecological filters (dispersal limitations, abiotic environment and biotic interactions) among different successional stages (Callaway & Walker, 1997). Trait convergence due to dispersal and abiotic filtering is expected to prevail in early successional communities on exposed mineral substrate with harsh environments whereas trait divergence due to biotic interactions such as competition or facilitation dominates in mid- to late-successional stages where environmental conditions are less restrictive (Grime, 2006). In general, an increase of functional richness related to species richness has been described during primary succession (Greinwald et al., 2021).

Several studies on the Canary Islands focused on functional trait space and the distribution of traits along environmental gradients (Cutts et al., 2023; Hanz, Beloiu, et al., 2022; Hanz, Cutts, et al., 2022; Ratier Backes et al., 2023), but the relationships of endemism reflecting evolutionary processes, functional plant traits and disturbance have rarely been assessed (Irl et al., 2021). Recent studies on the Canary Islands reported an overall high proportion of shrubs in the endemic flora of Tenerife (Barajas Barbosa et al., 2023), and a dominance of endemic ruderal shrubs in secondary succession which serve as “vaccine species” increasing the resilience of native plant communities to invasion by introduced species which only dominate at highly disturbed sites (Arévalo et al., 2005; Fernández-Palacios et al., 2023; Otto et al., 2006, 2014). Therefore, the analysis of the role, through their functional traits, of endemics, non-endemic natives and introduced plants in community assembly during primary succession might provide new insights in evolutionary processes related to plant strategies.

Here, we investigate the distribution of plants with respect to nine functional traits related to resource use, dispersion and growth as well as functional diversity metrics during primary succession using a chronosequence on 10 lava flows ranging in age between 40 and over 15,000 years in the lowlands of the southern part of La Palma Island. We formulate the following three hypotheses for our island system:

> **Hypothesis 1.** Plant strategies shift from ruderal strategists in early-stage pioneer communities to competitive strategists at late-successional stages. (1a) Community-weighted trait means (CWMs) change from acquisitive to conservative strategies (decreasing SLA and LA, increasing LDMC, N, C and specific stem density SSD) with increasing lava age except for leaf N (increase or no trend) due to low soil fertility conditions on young lava flows. (1b) Dispersal strategies and seed characteristics shift from anemochory to endozoochory and from small to large and heavy-seeded plants along the chronosequence.

> **Hypothesis 2.** Endemic shrubs dominate in abundance at all successional stages reflecting their evolutionary adaptation to this disturbance type, while introduced species are less important in terms of taxonomic richness and abundance. We expect a moderate increase of the contribution of introduced species in late-successional stages due to improved soil conditions and possible small-scale anthropogenic disturbances such as extensive grazing in the past on the oldest lava flows but without altering the dominance of endemic shrubs and, hence, impacting on the functioning of this ecosystem.

> **Hypothesis 3.** Strong environmental and dispersal filtering during successional stages leads to a shift from trait convergence to divergence within the coastal scrub with increasing terrain age.

2 | METHODS

2.1 | Study site

La Palma is the northwestern-most island of the Canarian archipelago situated about 400 km off the north-western coast of Africa (Figure 1). It is the second highest island of the archipelago, with a maximum elevation of 2426 m a.s.l., covering an area of 708 km^2. The island is characterized by a geologically older northern part (1.8 Ma) and a very active young southern part (<0.15 Ma), known as Cumbre Vieja (Carracedo et al., 2001), where eight (years AD 1480, 1585, 1646, 1677, 1712, 1949, 1971 and 2021) of the 16 historical eruptions in the Canary Islands have occurred producing lava flows running from the flanks of Cumbre Vieja (up to 2000 m a.s.l.) toward both the eastern and western coasts.

The main vegetation types on La Palma are determined by the island's high elevation and its interaction with the predominant humid north-eastern trade winds. Hence, there are steep climatic gradients distinguished by a humid eastern windward side and a drier western leeward side of the island. Our chronosequence study was carried out in the lowlands of Cumbre Vieja characterized by a subtropical semi-arid climate with mild temperature (18–21°C mean annual temperature) and low rainfall (150–500 mm mean annual precipitation), mostly occurring in winter. The vegetation was classified as coastal sub-desert scrub and is formed by endemic succulent shrubby spurges (genus *Euphorbia*) and other xerophytic shrubs, which potentially occurs from sea level up to 350 m a.s.l. (del Arco Aguilar et al., 2010).

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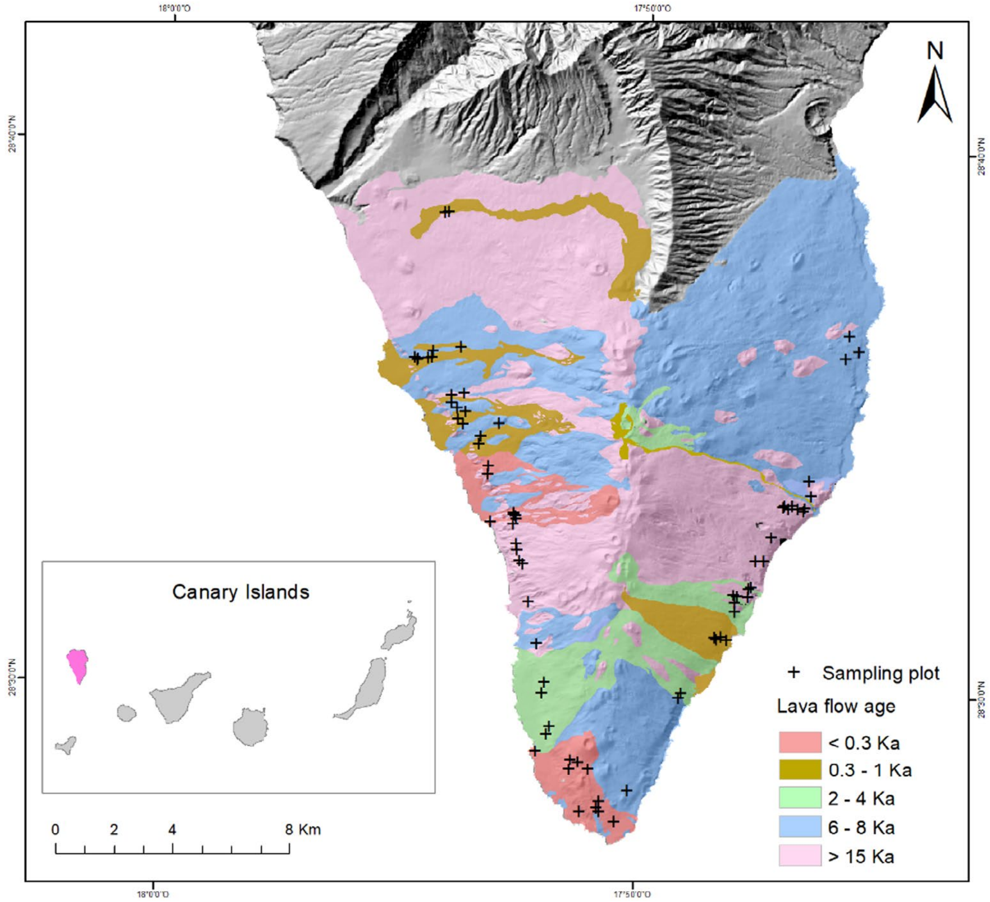

FIGURE 1 Location of sampling plots and age of the lava flows on La Palma Island (simplified after Carracedo et al., 2001). The most recent lava flow (Tajogaite, 2021) is not mapped.

2.2 | Experimental design

Our study follows the chronosequence approach (space-for-time substitution, Pickett, 1989), a widely used method to study primary succession, especially when long-term permanent plots are lacking and/or very long periods (hundreds, thousands of years) are of interest (Walker et al., 2010). Since La Palma is the volcanically most active island of the archipelago and most eruptions are precisely dated (Carracedo et al., 2001), it represents a perfect setting to study primary succession.

Within the potential area of the *Euphorbia* scrub, we established a chronosequence on 10 recent and historical lava flows, dividing the substrate into the following decreasing age classes (>15 Ka, 6–8 Ka, 2–4 Ka, 1480, 1585, 1646, 1677, 1712, 1949 and 1971) (Figure 1). We applied a stratified random selection process installing five plots of 20 m × 20 m for each lava age class on both windward and leeward slopes where possible (only two plots in case of the lava flow from 1480 due to human disturbances; Cabrera Rodríguez, Otto, & Fernández-Palacios, 2022). We avoided placing plots at the edges of lava flow (at least 20 m distance) to prevent spill over from other habitats, areas with difficult access as well as human-disturbed patches. We also excluded pyroclastic deposits to make samples comparable. In total, we established 72 plots (15 age classes), 30 at the windward (SE slope), 32 at the leeward (SW slope) and 10 in the southern part of La Palma.

We recorded all vascular plants within each plot and measured abundance with the line intercept method (Canfield, 1941) for all perennial species, whereas the abundance of annuals was visually estimated. The method consists in recording the intercept distance of the canopies of each species by a number (here five) of parallel tapes within the plot and calculating its proportion to the overall tape length. Furthermore, we measured the height and two diameters (widest and perpendicular) of shrub individuals. Taxonomy and biogeographical status (introduced, non-endemic native and endemic species) followed the most recent vascular plants checklist (Beierkuhnlein et al., 2021). Sampling was conducted from February to May of 2011, the best season to record annual plants.

2.3 | Environmental variables

Our topographical variables included plot elevation, slope, aspect and geographic coordinates and were taken in the field or extracted using a geographic information system (ArcGIS 9.3, 2008; Cabrera Rodríguez, Otto, & Fernández-Palacios, 2022). We interpolated climatic variables (mean annual temperature and annual precipitation)

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and topographic variables (slope and aspect) using statistical models (Garzón-Machado et al., 2013). The following soil chemical variables were studied and obtained by randomly taking five soil samples to a depth of 5–25 cm depending on soil development and a minimum of 1 kg at each plot: soil pH, soil organic matter (SOM), phosphorus (P), nitrogen $\left(NH_4^+\right)$ and exchangeable cations (K^+, Na^+, Ca^{2+}, Mg^{2+}) (for details see Cabrera Rodríguez, Otto, & Fernández-Palacios, 2022).

2.4 | Trait sampling

We compiled data for nine plant traits of 110 vascular plants (40 endemic, 53 non-endemic native and 17 introduced species) of the total species pool of 169 species recorded in the survey of primary succession along the established chronosequence (Cabrera Rodríguez, Otto, & Fernández-Palacios, 2022), including 93% of all native species with frequency >5% and 91% of species with >1% maximum cover and 81% of all introduced species. In functional community ecology, traits should be taken from all species that make up at least 80% of the relative plot cover (Pakeman & Quested, 2007).

The trait data compilation includes five morphological and biochemical leaf traits: leaf area (LA, mm^2) as the one-side surface area of the individual lamina, LDMC ($mg\,g^{-1}$) as the leaf dry mass per unit of water-saturated fresh mass, SLA ($mm^2\,mg^{-1}$) as the leaf area per unit of dry mass, leaf Nitrogen content (Nmass; $mg\,g^{-1}$) as the nitrogen content per unit of lamina dry mass, and leaf carbon content (Cmass; $mg\ g^{-1}$) as the carbon content per unit of lamina dry mass. Three reproductive traits were measured or extracted from the literature and trait databases such as TRY: seed mass (SM, g/1000 seeds), dispersal syndrome (animal, wind, unassisted) and pollination system (wind, animal). Animal dispersal includes endozoochory (9 species) and ectozoochory (20 species) by birds, lizards and possibly introduced rabbits. Plants with hydrochory are not present in this type of vegetation. Since some plants can have more than one dispersal mode (Vargas et al., 2015), the main dispersal mode was considered. Animal pollination in the target habitat is mainly related to insects and in rare cases additionally to birds and lizards. Finally, two traits related to plant growth and lifespan were obtained: stem-specific density (SSD; $mg\ mm^{-3}$) as dry mass per unit of fresh stem volume and growth form (fern, forb, graminoid, subshrub, shrub). In our study, 76% of forbs and 67% of graminoids are annuals.

Plant traits were not recorded on the plots of the chronosequence but measured in the field on La Palma (8 La Palma endemics) and Tenerife (70 shared native non-endemics and multi-island endemics; 49 Barajas Barbosa et al., 2023; 21 Ratier Backes et al., 2023). For the rest of the species (15 native non-endemic species, 11 introduced species), databases such as TRY (Kattge et al., 2020) were consulted (Table S2). For each species, ten to hundred leaves and one stem sample of each of three to five individuals located across the species' island distribution range were collected and analysed. Therefore, we consider that our data represent robust estimates of the intraspecific trait variation and can thus be used for quantitative community analyses. Furthermore, species turnover, not intraspecific variation, best explained total variation in rather plastic traits such as leaf area in endemic and non-endemic plant assemblages along environmental gradients in the coastal habitat on La Palma (Hanz, Beloiu, et al., 2022). However, we are aware that the sampled intraspecific trait variation does not reflect potential within-species trait changes along our successional gradient which could limit the interpretation of our results. In general, changes in average community trait values can be explained by both compositional change and within-species trait variability. Neglecting intraspecific trait variability may result in misinterpreting the response of communities to environmental changes (Lepš et al., 2011). The effect of intraspecific trait variability might under- or overestimate community-wide trends for specific traits depending on the type of environmental change and trait (Zheng et al., 2022).

Data for growth form, dispersal and pollination mode, that is traits which exhibit no intraspecific variation, were compiled from the literature (Table S2).

Our selected leaf and growth traits are associated with the functional continuum from acquisitive to conservative strategies (Díaz et al., 2016), whereas the reproductive traits such as dispersal type and seed mass can be related to the continuum from ruderal to stress or competitive strategies (Grime, 2002).

2.5 | Data analysis

We applied two approaches to study functional traits during primary succession. First, we analysed changes of single traits in relation to lava age and environmental factors using CWMs and linear models (LMs). Then, we followed a trait-based community-level approach using unconstrained and constrained ordination techniques (redundancy discriminatory analysis [RDA]) to reveal trends in the functional composition of successional communities. Finally, we tested changes in community taxonomic richness and functional diversity with time applying different indices. CWMs were calculated for each trait and each plot, using the functcomp function in the *FD* package in R (Laliberté et al., 2014). While a multi-trait approach informs us how trait combinations vary during succession, single-trait analyses focus on the variation of specific traits with lava flow age.

In the first step, we tested for significant differences in univariate relationships between individual CWM trait values and time treated as a factor with five lava age classes (<0.3, 0.3–1, 2–4, 6–8, >15 Ka) applying a non-parametric Kruskal–Wallis test followed by Dunn's test with Holm corrections for post hoc pairwise comparisons. Furthermore, we applied multiple linear regression with each CWM trait as a dependent variable and a set of environmental factors as independent variables. First, we checked for collinearity among environmental factors and selected the ecologically most meaningful ones from highly correlated variables (when correlation coefficients >0.7). We also tested for the effect of time since eruption (both included as factor or continuous variable). The seven historic lava flows are precisely dated, while the four older lava flows are given in age classes. However, in previous studies, lava age in the

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same chronosequence was treated as a continuous variable (Cabrera Rodríguez, Otto, & Fernández-Palacios, 2022; Irl et al., 2019). We ran linear (lm) models both for the whole age gradient and separately for only young lava flows to elucidate differences in early and late-successional stages. Explanatory variables were log- or square root transformed and scaled to mean zero to improve model fit and to meet assumptions for model residual (Shapiro test for normal distribution and studentized Breusch Pagan test for homoscedasticity). For the continuous but bounded (0,1) variables (dispersal and pollination mode), we applied generalized linear models (glm) with a quasibinomial distribution and logit function.

We checked for spatial autocorrelation of model residuals using the Moran's *I* statistics as implemented in the morantest function of the spdep packages in R (Bivand, 2022). Gabriel graph defined neighbours and three types of spatial weights (neighbour/non-neighbour, inverse distance weights, inverse squared distance weights) were applied. No spatial autocorrelation was found in residuals for all LMs. Differences in species richness and cover values for each species origin group along the lava flow chronosequence were evaluated by Dunn test with Holm correction; differences between species origin groups for the same lava flow age class were tested applying two-samples Wilcoxon test. Phylogenetic correction was not considered here since out of 79 genera only three (*Aeonium*, *Scilla* and *Sonchus*) with two or three species belong to in situ diversified lineages. The other species within the same genus represent different colonization events (Price et al., 2018) and are not phylogenetically closely related. However, there is a still an ongoing debate whether phylogenetic correction should be applied in trait analyses (Westoby et al., 1995, 2023).

In a second approach, we investigated the effects of environmental factors and age on the functional composition of successional communities by applying a RDA using the *rda* function in the *vegan* R library (Oksanen, 2017). Before running the RDA, a detrended correspondence analysis was performed to confirm that the linear ordination method was adequate for RDA (gradient lengths <3). The independent contributions of each environmental factor to explain the constrained variation were checked by applying partial RDA using the *rda* function including the condition expression. The significance of the RDA model was assessed with the *ANOVA* function based on 999 permutations.

We calculated, for each plot, three main components of functional diversity, using n-dimensional hypervolumes (Blonder, 2018): functional richness, functional dispersion and functional beta diversity applying the functions *kernel.alpha*, *kernel.dispersion* and *kernel.beta*, respectively, in the R package BAT (Mammola & Cardoso, 2020). We used a fixed kernel bandwidth for all groups using cross-validation as the kernel estimator method. Functional diversity metrics are based on hypervolumes estimated from the three first principal components using six continuous plant functional traits (SLA, LA, LDMC, SM, Nmass, Cmass). Functional richness is the total volume of a trait space while functional dispersion quantifies how spread or dense a given trait space is. Functional evenness quantifies how regular a given trait space is. Hypervolumes for each plot were calculated using the *kernel.build* function in the BAT package with *gower* distance and *Gaussian* kernel density estimation. Kernel.beta computes the pairwise comparisons of dissimilarity (β) between communities in different plots. We calculated the mean dissimilarity of all comparisons of a certain community/plot with the rest of the communities/plots. Introduced species were not included in the CWM and functional diversity analyses since they were almost absent and showed, if present, very low cover values (max. 5%). All statistical analyses were conducted in the R environment (R Core Team, 2023).

3 | RESULTS

The richness of endemic, non-endemic native and introduced species significantly increased with lava flow age. Introduced species were almost absent, especially on young substrate (Figure 2), and increased in richness only on older substrates. The richness of non-endemic natives increased until the oldest successional stage and was always significantly higher compared to endemics for each age class, except for the 6–8 Ka lava flows.

Vegetation cover was dominated by endemics along the entire chronosequence (significantly higher endemic than non-endemic native cover for each age class), non-endemic natives reached cover values up to 10% at old stages, introduced species did not play any role in structuring the vegetation and only reached 2%–4% cover at the 2–4 ka successional stages.

With respect to cover-weighted growth forms, shrubs dominated the communities along the entire chronosequence (Figure 3). Forbs, comprised mainly of annuals, showed variation in relative abundances at the youngest stages, but generally low values for later stages. However, using only presence-absence data, forbs and graminoids increased with lava age, shrubs decreased, while ferns and subshrubs did not show a consistent trend with lava age.

Single-trait analyses showed that CWMs for SLA, LA, wind dispersal and wind pollination significantly decreased, while those of SM, SSD, LDMC, Nmass, Cmass, animal dispersal, unassisted dispersal and animal pollination significantly increased with lava flow age (Figure 4). For most traits, significant differences were observed between younger (<1 Ka, age classes 1 and 2) and older (>1 Ka, age classes 3, 4 and 5) lava flows. LMs including the entire time gradient confirmed that lava flow age had a significant effect on all traits (Table S1). However, some trait CWMs were also moderately related to precipitation, temperature and soil organic matter. For instance, precipitation positively affected SLA and LA, but a negative one on LDMC and SSD. Interestingly, when LMs were applied only to younger lava flows (<600 years), none of the explanatory variables including lava flow age resulted significant, indicating no clear temporal change nor environmental effects in traits in these earlier stages.

RDA confirmed the compositional change of plant traits along the chronosequence from species with high LA, dispersed and pollinated by wind on very young substrate to species with higher SM, Cmass, SSD, dispersed and pollinated by animals on older lava flows

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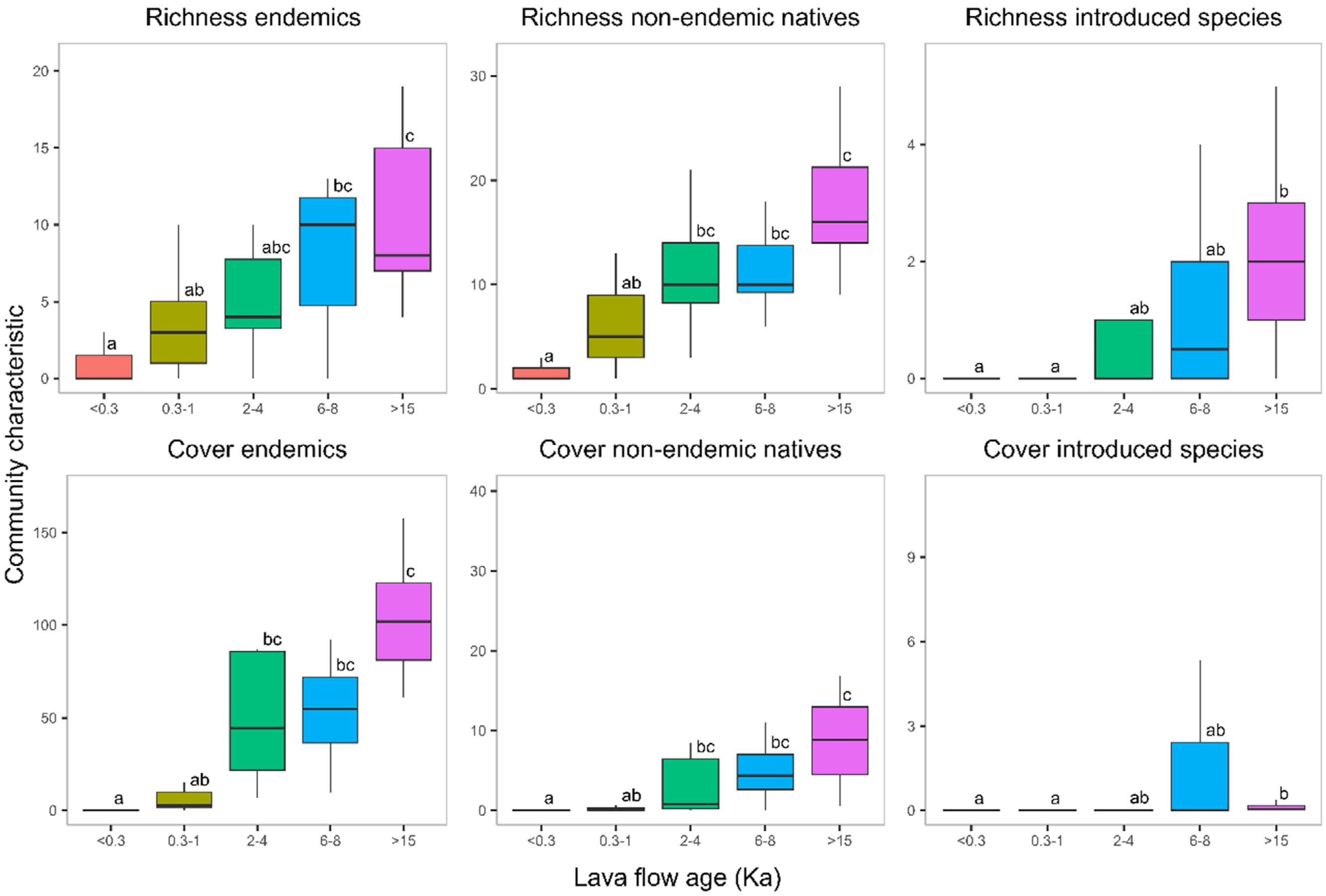

FIGURE 2 Temporal trends of species richness and cover of endemic, non-endemic native and introduced species in structuring plant communities during primary succession. Variation of taxonomic richness (number of species) and abundance (cover, expressed as %) along the chronosequence of lava flows (note the differences in the ordinates scale). Different letters indicate significant differences ($p < 0.05$) between age groups. The total cover can reach more than 100% due to the existence of different vegetation layers.

(Figure 5). However, SLA and herbaceous species (forbs, grasses) were related to precipitation and the second RDA axis. Partial RDA analyses revealed three significant explanatory variables, lava flow age (24.7% explained variance, $p < 0.001$) and soil organic matter (3.5% explained variance, $p < 0.05$) correlated with axis 1 and precipitation (2.7% explained variance, $p < 0.05$) correlated with the second axis.

Functional richness as well as functional dispersion significantly increased with lava flow age (Figure 6; Table S1). Again, differences were related to the changes from younger to older stages although a high variability for successional stage 0.3–1 Ka was observed. Functional beta diversity significantly decreased along the chronosequence due to changes in richness and not due to species replacement.

4 | DISCUSSION

Here, we present the first detailed study about plant functional traits and diversity, including leaf economic, and reproductive traits, during primary succession on the Canary Islands. We can highlight the following main results: (i) the richness of endemic and non-endemic native species strongly increased with lava flow age, while introduced species were almost absent and occurred only at very low abundances, if present; (ii) endemic shrubs dominated the vegetation structure along the entire chronosequence, but the presence of other growth forms increased with substrate age while contributing comparatively little to vegetation structure; (iii) both the single trait and trait compositional approach revealed that the composition of plants displaying core traits related to leaf economics and dispersal ability shifted with substrate age showing a change from acquisitive to conservative traits and from anemochory to zoochory, highlighting the importance of the leaf economic spectrum and the ruderal-competitive continuum in primary succession (Díaz et al., 2004, 2016; Grime, 2006; Wright et al., 2004). Substrate age also clearly influenced functional diversity indicating functional divergence during succession due to an increase in structural complexity and trait space. All these findings suggest an evolutionary adaptation of the Canarian lowland scrub to volcanism, a disturbance type that is quite common on most oceanic islands. Furthermore, we conclude that processes during primary succession on lava flows in the semi-arid subtropical climate of the Canary Islands are very slow compared

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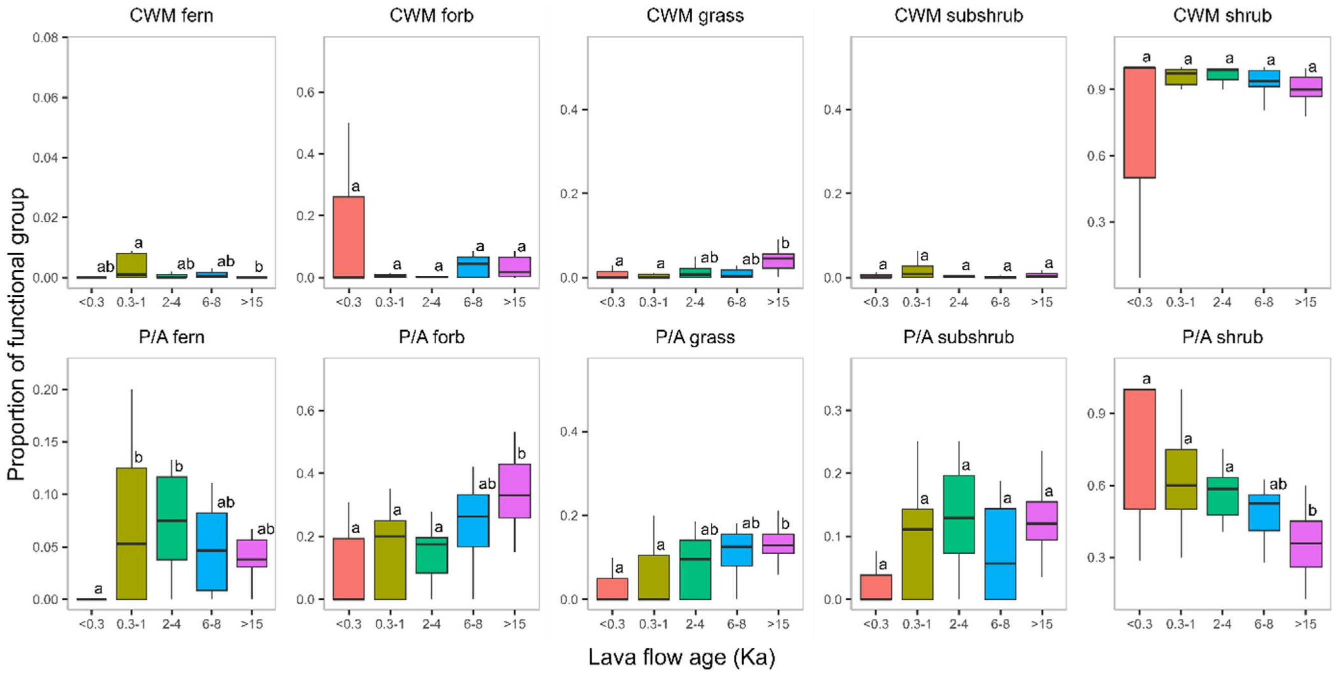

FIGURE 3 Temporal trends in the proportion of growth forms of endemic/non-endemic native species along the chronosequence showing community-weighted means (CWM) values calculated with abundance (cover) values (above) and represented by presence-absence data (below). Different letters indicate significant differences ($p < 0.05$) between age groups. Note the differences in the ordinates scale.

to tropical islands with a humid climate (Whittaker et al., 1989) and that major changes in taxonomic richness as well as functional trait composition and diversity occur only after 500 years since eruption.

4.1 | Richness, growth forms and species origin

Species richness strongly increased with time since eruption in the lowland scrub of La Palma. This finding is in accordance with observations of a series of other studies both on primary and secondary ecological succession (Cutler et al., 2008; Grishin et al., 1996; Magnússon et al., 2014; Otto et al., 2006). However, other studies report a hump-shaped temporal trajectory for species richness, especially during secondary succession due to a dominance of competitive shrub or tree species at later stages (del Moral & Poli Marchese, 2010; Dolezal et al., 2008; Prach & Walker, 2019). Earlier studies based only on species richness pattern questioned the evolutionary adaptation of endemics to early primary succession on the Canaries (Irl et al., 2019). However, our study, which includes species abundance and CWM analyses, reveals a consistent dominance of endemic shrubs along the entire chronosequence and a very low contribution of non-endemic natives belonging to all other growth forms in structuring the Canarian lowland scrub. This interesting result supports the idea of an evolutionary adaptation of this plant community to volcanism including early-, mid- and late-successional species. The great dominance of shrubs in early successional stages might be explained partly by substrate type. Previous studies on primary succession on islands highlighted the advantage of shrubs in colonizing lava flows compared to herbs due to their capacity to grow in cracks by extending their root system whereas herbs are more abundant on ash deposits (del Moral & Poli Marchese, 2010; Karadimou et al., 2018). Topography, substrate and volcanic disturbance type have been identified as factors influencing colonization processes during primary succession (del Moral & Grishin, 1999).

In general, endemic shrubs not only control the successional process during primary succession on La Palma but also dominate the entire native flora of the Canary Islands, especially the diversified flora (Barajas Barbosa et al., 2023; Fernández-Palacios et al., 2021). Many of these endemics belong to lineages that evolved insular secondary woodiness (Zizka et al., 2022), the evolutionary transition from herbaceous continental ancestors toward woody insular-derived species, which has been related to longevity and promotion of sexual outcrossing due to the scarcity of pollinators, seasonality or herbivory release or increased drought resistance (Whittaker et al., 2023).

4.2 | Functional traits

Our quantitative analyses of nine functional traits showed that plants with high SLA, LA, small seeds, wind dispersal and pollination as well as low leaf C mass, LDMC and SSD were dominant in early successional stages (<1 Ka), while the opposite trend occurred in species of late-successional stages. Hence, we detected two gradients or trade-offs of functional traits that co-occur during primary succession in agreement with general succession theory (Díaz et al., 2004; Grime, 2002; Westoby et al., 2002). The first gradient coincides with the leaf economic spectrum relating

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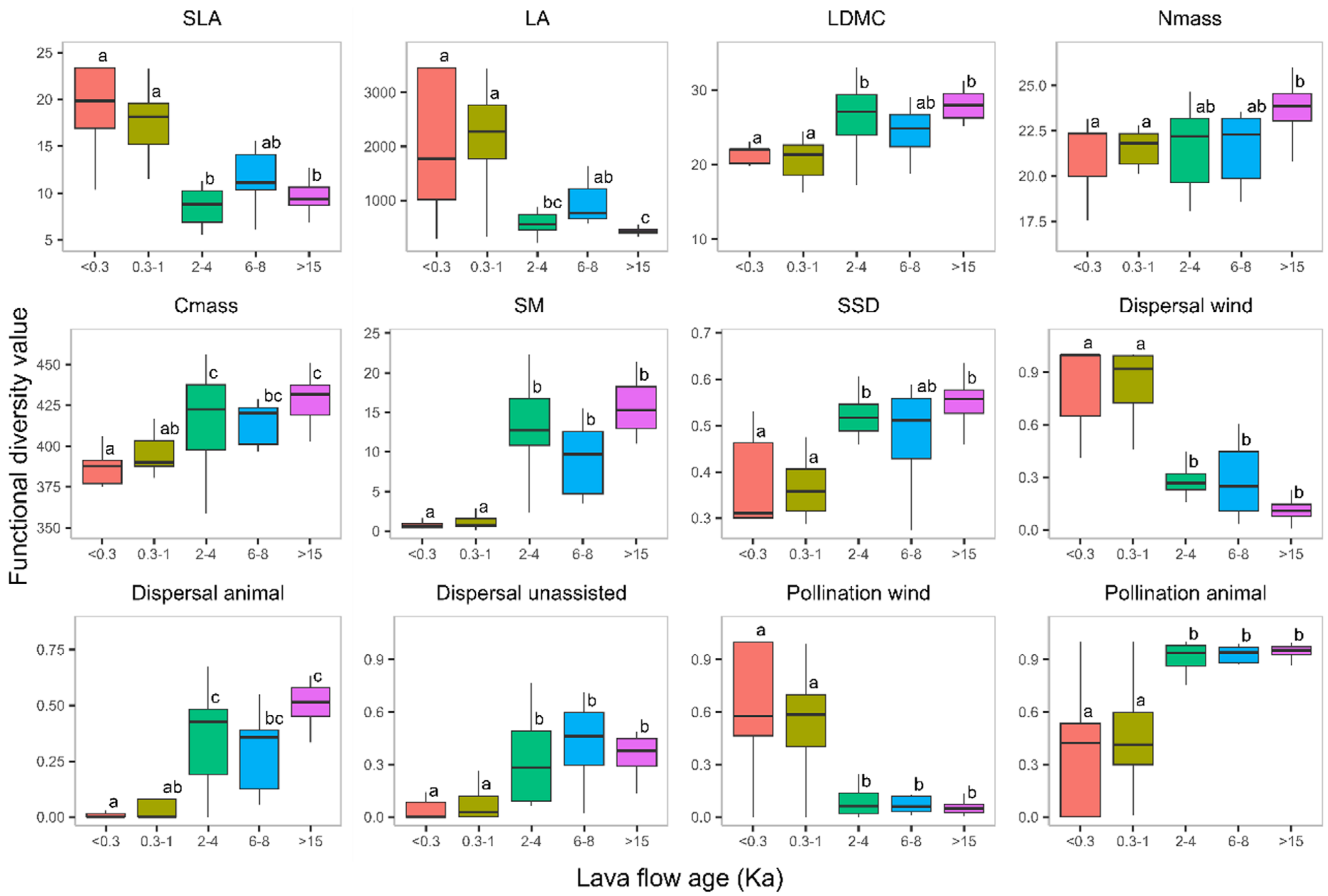

FIGURE 4 Community-weighted means (CWM) values of endemic/non-endemic native plant functional traits during primary succession along a chronosequence represented by five lava flow age classes. Different letters indicate significant differences ($p < 0.05$) between age groups. Cmass, leaf carbon content; LA, leaf area; LDMC, leaf dry matter content; Nmass, leaf nitrogen content; SLA, specific leaf area; SM, seed mass; SSD, stem specific density.

fast-growing species with an acquisitive strategy (high SLA, LA and low LDMC, SSD, C mass) with early successional communities and species with a more conservative strategy showing the opposite trait pattern (slow growth and higher leaf C) and an association with late-successional communities (Reich, 2014; Wright et al., 2004). Studies on leaf economic spectra in primary succession in continental settings confirmed this acquisitive–conservative gradient at least for some related traits such as SLA and SSD (SLA, leaf N, Caccianiga et al., 2006; SLA, SSD, Laine et al., 2018; SLA, Chang & HilleRisLambers, 2019; SLA, Greinwald et al., 2021). Support for the leaf economic spectrum also comes from several types of secondary succession in temperate grasslands, shrublands and forests (Craven et al., 2015; Purschke et al., 2013; Ratier Bakes et al., 2023).

High leaf N concentration has also been linked to the acquisitive strategy and positively correlates with SLA, LA, short life span and fast growth rates, especially at productive sites (Reich, 2014; Wright et al., 2004). For primary series, no clear trend in leaf N has been observed so far (Chang & HilleRisLambers, 2019; Dolezal et al., 2008). In our study, the few dominant pioneer shrubs on young lava flows possessed intermediate values of leaf N which only increased in the oldest successional stage, probably due to the dominance of the N fixing shrub *Retama rhodorhizoides* (Fabaceae). Hence, we observe a certain mismatch between leaf N and soil N, the limiting factor of the productivity on young volcanic soils (Vitousek et al., 1987). Nitrogen is almost non-existent in the basaltic bedrock and must accumulate either via biological fixation or dry deposition (Walker & Syers, 1976). And yet, the endemic ruderal shrubs on young lava flows are able to maintain an acquisitive strategy, possibly linked to a high N uptake and resorption efficiency as reported for pioneer shrubs growing on nutrient-poor sites in early primary succession (Zhong et al., 2021).

When analysing all explanatory variables, leaf N and forbs were associated with the second RDA axis and precipitation indicating the relationship of these traits with higher availability of nutrients and water representing better soil conditions (Cabrera Rodríguez, Otto, & Fernández-Palacios, 2022). However, the second RDA axis explained little of the overall trait variation compared to the first axis and, therefore, precipitation is not considered a key driver of trait change in our model system.

The second gradient represents plant regeneration/reproduction and is related to life-history traits such as pollination and

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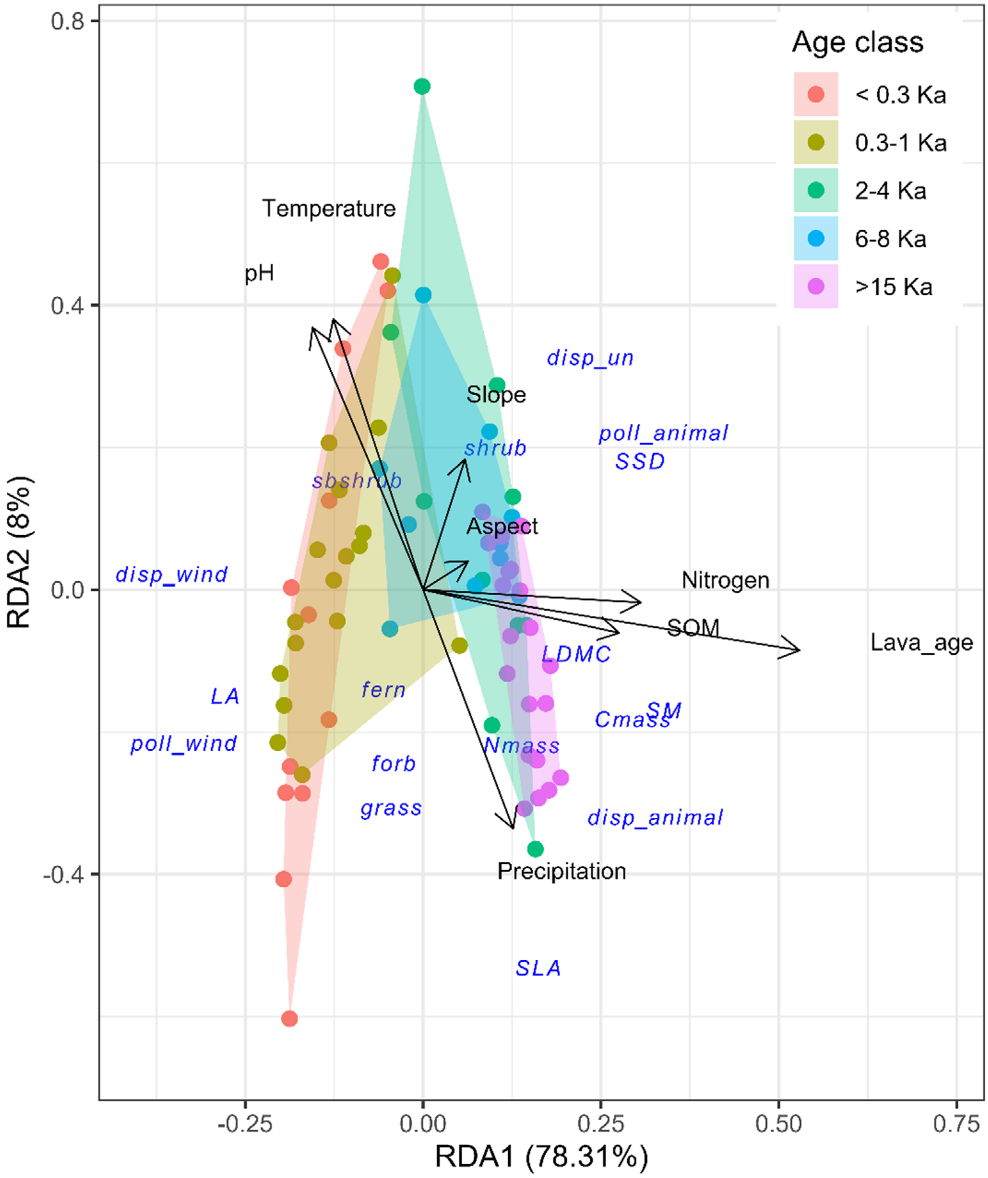

FIGURE 5 Redundancy discriminatory analysis biplot showing the distribution of endemic/non-endemic native plant traits in relation to lava flow age and environmental variables (Eigenvalue axis 1: 5.69, eigenvalue axis 2: 0.581. Total variance explained: 42.7%). Cmass, leaf carbon content; disp_animal, animal dispersal; disp_un, unassisted dispersal; disp_wind, wind dispersal; LA, leaf area; LDMC, leaf dry matter content; Nmass, leaf nitrogen content; poll_animal, animal pollination; poll_wind, wind pollination; SLA, specific leaf area; SM, seed mass; SOM, soil organic matter; SSD, stem specific density.

dispersal type, seed mass and growth rates. The particular importance of reproductive traits in governing colonization processes in primary succession has been highlighted for both continental and island settings (del Moral & Wood, 1993; Greinwald et al., 2021). The shifts in time from anemochory to zoochory and from small to large-seeded plants are common in primary succession both on islands and continents (Franzén et al., 2019; Fuller & del Moral, 2003; Korablev et al., 2020; Magnússon et al., 2014; Whittaker et al., 1989). Plant richness on young lava flows on La Palma is extremely low and the few typical endemic pioneer shrubs (*Kleinia neriifolia*, *Rumex lunaria* and *Schizogyne sericea*) are all wind dispersed, while *Rumex* is wind- and the others animal-pollinated. Endozoochorous shrubs (*Asparagus plocamoides*, *Rubia fruticosa*) and epizoochorous small shrubs (*Forsskaolea angustifolia*) or grasses are common in mid- to late-successional stages. The very sparse vegetation cover at early successional stages leads to a lower presence of lizards and birds compared to later successional shrub communities where they can hide and act as dispersers of fleshy-fruited plants with larger seeds, a mechanism described as positive feedback of endozoochory and vegetation structure (Whittaker et al., 1989). There are only a few wind-pollinated shrubs in our successional species pool indicating that pollination mode might not be a key trait in our study. However, where insects are rare, anemophily can represent a reproductive advantage to entomophily, as in early primary succession or, generally, on archipelagos where insect diversity is low (anemophily as island syndrome, Whittaker et al., 2023).

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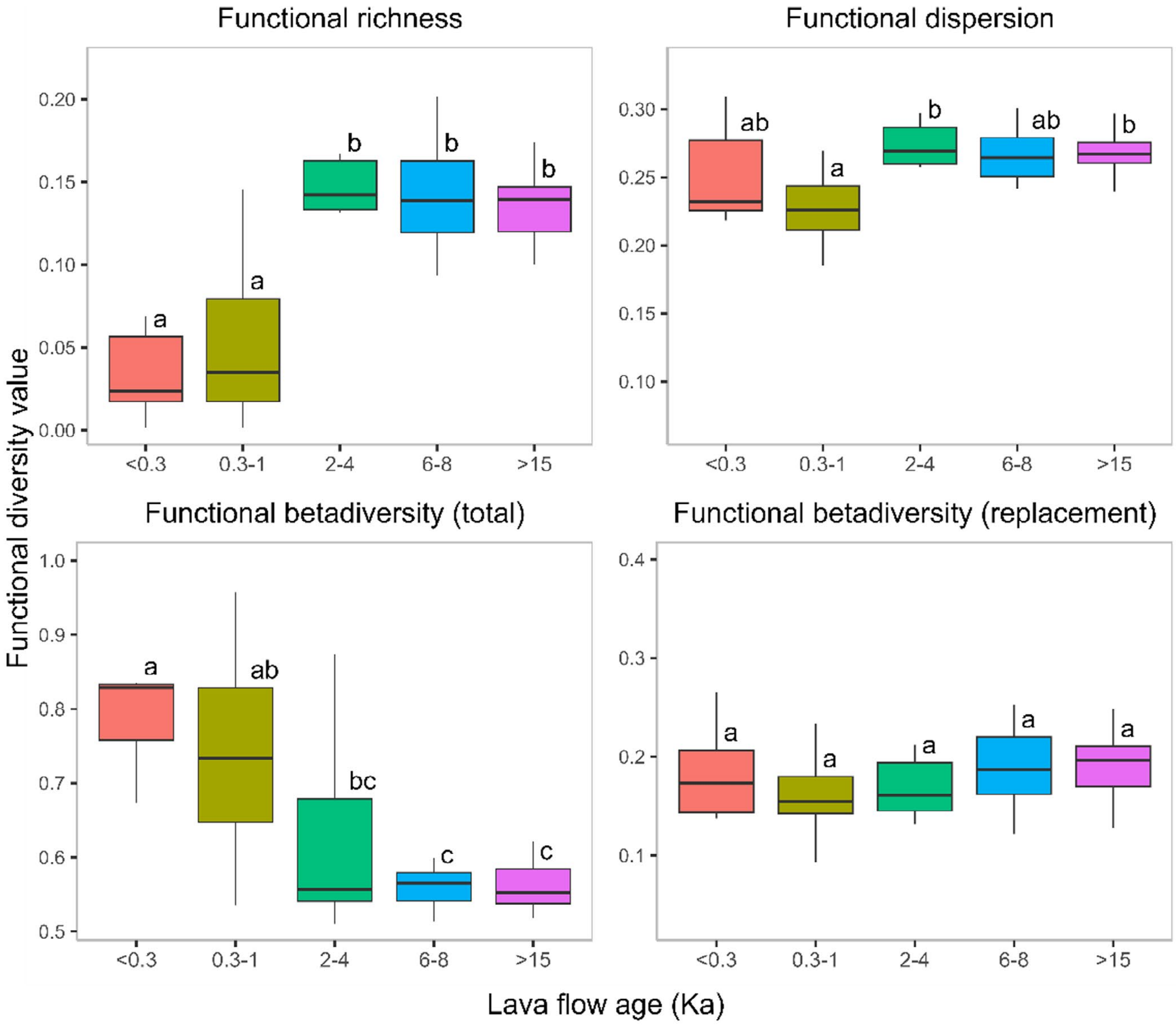

FIGURE 6 Changes of functional diversity of endemic/non-endemic native species during primary succession on La Palma Island. Functional richness, functional dispersion and functional beta diversity (total and only replacement) along the chronosequence. Different letters indicate significant differences ($p < 0.05$) between age groups.

The early successional ruderal endemic shrubs mentioned above have been termed "vaccine species" due to the important role they play in preventing the spread of invasive plants during primary and secondary succession and, in this way, strengthening the resistance of Canarian ecosystems against invasion (Fernández-Palacios et al., 2023). Those endemic shrubs often become invasive when introduced to other parts of the world, such as in the Mediterranean region (Villar-García et al., 2008). The fact that introduced species are almost absent and do not significantly alter successional trajectories on lava flows on the Canary Island might be related to strong environmental filtering (Bernardos et al., 2023; Cabrera Rodríguez, Otto, & Fernández-Palacios, 2022; Irl et al., 2019) and the evolutionary process of filling the island niche space with endemic pioneer species able to outcompete invasives (Fernández-Palacios et al., 2023). However, on other, more humid oceanic islands, such as Hawaii or La Réunion, invasives have been reported to colonize recent lava flows and strongly affect compositional change and diversity pattern during primary succession (Potgieter et al., 2014; Vitousek et al., 1987). Future trait-based studies might provide new insights into invasion and succession processes on islands.

Intraspecific variation in leaf traits has been detected along successional gradients, suggesting that local adaptation may also characterize plant communities (Alves et al., 2021), generally depending on the type of habitat and the selected trait (Lepš et al., 2011; Zheng et al., 2022). Nevertheless, other studies on forest secondary succession did not observe any important role of intraspecific trait variability on community assembly (Chai et al., 2019). Although species trait mean values used in our CWM approach capture intraspecific trait variation in relation to

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environmental variation on an island scale, uncertainty exist on how intraspecific trait shifts along the successional gradient, not accounted for in the present study, may influence our results and lead to a potential misinterpretation. However, we suggest that compositional change and not intraspecific variation count for most of the overall trait variation in our system. A recent study covering the same habitat and island revealed that within-species variability in leaf area and leaf thickness along an environmental gradient explained almost no overall trait variation supporting our idea (Hanz et al., 2022).

4.3 | Functional diversity

In the present study, functional richness, reflecting overall community niche space, increased with lava flow age. Similar results were reported for primary succession in continental regions (Greinwald et al., 2021). Furthermore, functional richness is usually strongly associated with species richness as in our case (Karadimou et al., 2018). We observed that communities in the second phase of primary succession showed consistently higher values of functional dispersion indicating a shift from trait convergence to divergence (Mouchet et al., 2010). Trait convergence usually results from abiotic filtering selecting for species with shared adaptations to a particular habitat, common in the early successional stage (Weiher & Keddy, 1995), while biotic interactions such as competition and facilitation lead to niche differentiation and functional divergence at late-successional stages (Mason et al., 2013). Moreover, our results of total functional beta diversity suggest that the trait composition of successional communities became more similar with time. However, this change is related to differences in richness since trait replacement was constant along the chronosequence and cannot be interpreted as trait convergence.

Overall, the harsh environmental conditions during early succession (Cabrera Rodríguez, Otto, & Fernández-Palacios, 2022) function as a strong abiotic filter for community assembly allowing only for a few shrubs with ruderal traits, joined by a few grasses and annuals, to colonize recent lava flows (<300 years). The next successional stage, which could be termed the transition stage, on older lava flows (0.3–1 Ka) is characterized by communities with a high variation both in taxonomic and functional richness as well as in vegetation structures. Depending on micro-environmental conditions, soil nutrient and vegetation development favour colonization of species with different traits. Hence, a general increase in both the number of species and trait combinations can be observed. The third successional stage refers to older lava flows (>1 Ka) where functional diversity seems to be already saturated although species richness and vegetation cover still increase. Interestingly, here, communities resemble functionally, but not structurally mature communities since their biomass has not yet reached its maximum. The incorporation of functionally similar species during late-successional stages indicates low competitive forces in community assembly.

5 | CONCLUSIONS

In general, our study system reflects a directional succession governed by strong abiotic selection of functional traits in the early stages followed by a gradual modification of the environment and an expansion of the niche space linked to the complementary effect based on functional differentiation mainly driven by facilitation (Mori et al., 2017). Interspecific competition between dominating shrubs like *Euphorbia* and *Retama* might exist at late-successional stages, but species accumulation and not competitive exclusion of species characterize the second phase of succession, supporting the tolerance model of succession (Connell & Slatyer, 1977). While the analysis of functional traits suggests a shift from convergence to divergence, the change in floristic composition supported convergence during primary succession where colonization is stochastic at the beginning and few endemic shrubs dominate late stages (Cabrera Rodríguez, Otto, & Fernández-Palacios, 2022). Hence, differences between the taxonomic and functional perspective of community assembly might exist (Fukami et al., 2005). Interestingly, endemic shrubs drive the trait shifts from acquisitive to conservative strategy and from anemochory to zoochory along the entire chronosequence while other life forms only contribute to functional diversity highlighting the importance of evolutionary processes in shaping plant functional traits on oceanic islands.

AUTHOR CONTRIBUTIONS

Rüdiger Otto, Francisco Cabrera Rodríguez and José María Fernández-Palacios conceived the original idea; Rüdiger Otto, Julian Schrader and José María Fernández-Palacios prepared the first manuscript. Francisco Cabrera Rodríguez, Natalia Sierra Cornejo, Martha Paola Barajas Barbosa, Holger Kreft, Dagmar Hanz, Severin D. H. Irl and Amanda Ratier Backes provided data; Rüdiger Otto performed the statistical analyses. All authors discussed the results and commented on the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The Trait data are deposited in the repository of the University of La Laguna (ULL), Spain, http://riull.ull.es/xmlui/handle/915/41739

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Floristic data are deposited in the Mendeley Data repository, V1, https://doi.org/10.17632/wbbf7b6xby.1 (Cabrera Rodríguez, Otto & Fernández-Palacios, 2022).

ORCID

Rüdiger Otto https://orcid.org/0000-0002-2764-8443
Julian Schrader https://orcid.org/0000-0002-8392-211X
Natalia Sierra Cornejo https://orcid.org/0000-0003-0851-3292
Martha Paola Barajas Barbosa https://orcid.org/0000-0002-9040-0766
Holger Kreft https://orcid.org/0000-0003-4471-8236
Dagmar Hanz https://orcid.org/0000-0002-8821-9044
Severin D. H. Irl https://orcid.org/0000-0002-1734-8607
Amanda Ratier Backes https://orcid.org/0000-0002-7229-578X
José María Fernández-Palacios https://orcid.org/0000-0001-9741-6878

REFERENCES

ArcGIS 9.3. (2008). ESRI® ArcMapTM 9.3. Available at http://www.esri.com

Alves, A. M., Espírito-Santo, M. M., Silva, J. O., Faccion, G., Sanchez-Azofeifa, A., & Ferreira, K. F. (2021). Successional and intraspecific variations in leaf traits, spectral reflectance indices and herbivory in a Brazilian tropical dry Forest. *Frontiers in Forests and Global Change*, *4*, 780299. https://doi.org/10.3389/ffgc.2021.780299

Arévalo, J. R., Delgado, J. D., Otto, R., Naranjo, A., Salas, M., & Fernández-Palacios, J. M. (2005). Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and gran Canaria (Canary Islands). *Perspectives in Plant Ecology, Evolution and Systematics*, *7*, 185–202. https://doi.org/10.1016/j.ppees.2005.09.003

Barajas Barbosa, M. P., Craven, D., Weigelt, P., Denelle, P., Otto, R., Díaz, S., Price, J., Fernández-Palacios, J. M., & Kreft, H. (2023). Assembly of functional diversity in an oceanic island flora. *Nature*, *619*, 545–550. https://doi.org/10.1038/s41586-023-06305-z

Barton, K. E., & Fortunel, C. (2023). Island plant functional syndromes and competition with invasive species. *Journal of Biogeography*, *50*, 641–653. https://doi.org/10.1111/jbi.14568

Beierkuhnlein, C., Walentowitz, A., & Welss, W. (2021). FloCan—A revised checklist for the flora of the Canary Islands. *Diversity*, *13*(10), 480. https://doi.org/10.3390/d13100480

Bernardos, M., Cornejo, N. S., Torres Hassan, A. D., Cabrera, R., & Arévalo, J. R. (2023). Road impact on plant colonization in the arid Timanfaya National Park. *Plants*, *12*, 3568. https://doi.org/10.3390/plants12203568

Bivand, R. (2022). R packages for analyzing spatial data: A comparative case study with areal data. *Geographical Analysis*, *54*(3), 488–518. https://doi.org/10.1111/gean.12319

Blonder, B. (2018). Hypervolume concepts in niche- and trait-based ecology. *Ecography*, *41*, 441–1455. https://doi.org/10.1111/ecog.03187

Cabrera Rodríguez, F., Otto Dittmann, R., & Fernández-Palacios, J. M. (2022). *Changes in soil chemical properties and plant species composition during primary succession on an oceanic island* (Supplementary Material). University of La Laguna, V1, https://doi.org/10.17632/wbbf7b6xby.1

Cabrera Rodríguez, F., Otto, R., & Fernández-Palacios, J. M. (2022). Changes in soil chemical properties and plant species composition during primary succession on an oceanic island. *Journal of Vegetation Science*, *33*, 1–13. https://doi.org/10.1111/jvs.13137

Caccianiga, M., Luzzaro, A., Pierce, S., Ceriani, R. M., Cerabolini, B., & Eriksson, O. (2006). The functional basis of a primary succession resolved by CSR classification. *Oikos*, *112*(1), 10–20.

Callaway, R. M., & Walker, L. R. (1997). Competition and facilitation: A synthetic approach to interactions in plant communities. *Ecology*, *78*(7), 1958–1965. https://doi.org/10.1890/0012-9658(1997)078[1958:CAFASA]2.0.CO;2

Canfield, R. H. (1941). Application of the line interception method in sampling range vegetation. *Journal of Forestry*, *39*, 388–394.

Carracedo, J. C., Badiola, E. R., Guillou, H., de la Nuez, J., & Pérez Torrados, F. J. (2001). Geology and volcanology of La Palma and El Hierro, Western canaries. *Estudios Geológicos*, *57*, 175–273. https://doi.org/10.3989/egeol.01575-6134

Chai, Y., Dang, H., Yue, M., Xu, J., Zhang, L., Quan, J., Guo, Y., Li, T., Wang, L., Wang, M., & Liu, X. (2019). The role of intraspecific trait variability and soil properties in community assembly during forest secondary succession. *Ecosphere*, *10*(11), e02940. https://doi.org/10.1002/ecs2.2940

Chang, C. C., & HilleRisLambers, J. (2019). Trait and phylogenetic patterns reveal deterministic community assembly mechanisms on Mount St. Helens. *Plant Ecology*, *220*, 1–24. https://doi.org/10.1007/s11258-019-00944-x

Chang, C. C., & Turner, B. L. (2019). Ecological succession in a changing world. *Journal of Ecology*, *107*, 503–509. https://doi.org/10.1111/1365-2745.13132

Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, *111*, 1119–1144.

Cornelissen, J., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D., Reich, P., ter Steege, H., Morgan, H. D. G., Van der Heijden, M., Pausas, J. G. H., & Poorter, H. (2003). Handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*, 335–380. https://doi.org/10.1071/BT02124

Craven, D., Hall, J. S., Berlyn, G. P., Ashton, M. S., & van Breugel, M. (2015). Changing gears during succession: Shifting functional strategies in young tropical secondary forests. *Oecologia*, *179*(1), 293–305. https://doi.org/10.1007/s00442-015-3339-x

Cutler, N. A., Belyea, L. R., & Dugmore, A. J. (2008). The spatiotemporal dynamics of a primary succession. *Journal of Ecology*, *96*, 231–246. https://doi.org/10.1111/j.1365-2745.2007.01344.x

Cutts, V., Hanz, D. M., Barajas-Barbosa, M. P., Schrodt, F., Steinbauer, M. J., Beierkuhnlein, C., Denelle, P., Fernández-Palacios, J. M., Gaüzère, P., Grenié, M., Irl, S. D. H., Kraft, N., Kreft, H., Maitner, B., Munoz, F., Thuiller, W., Violle, C., Weigelt, P., Field, R., & Algar, A. C. (2023). Links to rare climates do not translate into distinct traits for island endemics. *Ecology Letters*, *26*(4), 504–515. https://doi.org/10.1111/ele.14169

del Arco Aguilar, M. J., González González, R., Garzón Machado, V., & Pizarro-Hernández, B. (2010). Actual and potential natural vegetation on the Canary Islands and its conservation status. *Biodiversity and Conservation*, *19*, 3089–3140. https://doi.org/10.1007/s10531-010-9881-2

del Moral, R., & Grishin, S. Y. (1999). Chapter 5. Volcanic disturbances and ecosystem recovery. In L. R. Walker (Ed.), *Ecosystems of disturbed ground* (pp. 137–145). Elsevier.

del Moral, R., & Poli Marchese, E. P. (2010). Flroristic change during early primary succession on lava, Mount Etna, Sicily. *Braun-Blanquetia*, *46*, 225–234.

del Moral, R., & Wood, D. M. (1993). Early primary succession on the volcano Mount St. Helens. *Journal of Vegetation Science*, *4*, 223–234. https://doi.org/10.2307/3236108

Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Martí, G., Grime, J. P., Zarrinkamar, F., Asri, Y.,

13652745, 2025, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.70033 by Martin Luther University Halle-Wittenberg, Wiley Online Library on [18/08/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Band, S. R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M. C., Shirvany, F. A., … Zak, M. R. (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, *15*(3), 295–304. https://doi.org/10.1111/j.1654-1103.2004.tb02266.x

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I. C., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*(7585), 167–171. https://doi.org/10.1038/nature16489

Dolezal, J., Homma, K., Takahashi, K., Vyatkina, M. P., Yakubov, V., Vetrova, V. P., & Hara, T. (2008). Primary succession following deglaciation at Koryto glacier valley, Kamchatka. *Arctic, Antarctic, and Alpine Research*, *40*, 309–322. https://doi.org/10.1657/1523-0430(06-123)

Elias, R., & Dias, E. (2009). Effects of landslides on the mountain vegetation of Flores Island, Azores. *Journal of Vegetation Science*, *20*, 706–717. https://doi.org/10.1111/j.1654-1103.2009.01070.x

Fernández-Palacios, J. M., Otto, R., Borregaard, M. K., Kreft, H., Price, J. P., Steinbauer, M. J., Weigelt, P., & Whittaker, R. J. (2021). Evolutionary winners are ecological losers among oceanic island plants. *Journal of Biogeography*, *48*(9), 2186–2198. https://doi.org/10.1111/jbi.14143

Fernández-Palacios, J. M., Schrader, J., de Nascimento, L., Irl, S. D. H., Sánchez-Pinto, L., & Otto, R. (2023). Are plant communities on the Canary Islands resistant to plant invasion? *Diversity and Distributions*, *29*(1), 51–60. https://doi.org/10.1111/ddi.13650

Franzén, M., Dieker, P., Schrader, J., & Helm, A. (2019). Rapid plant colonization of the forelands of a vanishing glacier is strongly associated with species traits. *Arctic, Antarctic, and Alpine Research*, *51*(1), 366–378. https://doi.org/10.1080/15230430.2019.1646574

Fukami, T., Martijn Bezemer, T., Mortimer, S. R., & van der Putten, W. H. (2005). Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters*, *8*(12), 1283–1290. https://doi.org/10.1111/j.1461-0248.2005.00829.x

Fuller, R. N., & del Moral, R. (2003). The role of refugia and dispersal in primary succession on Mount St. Helens, Washington. *Journal of Vegetation Science*, *14*, 637–644. https://doi.org/10.1111/j.1654-1103.2003.tb02195.x

Gallardo, A., Fernández-Palacios, J. M., Bermúdez, A., de Nascimento, L., Durán, J., García Velázquez, L., Méndez, J., & Rodríguez, A. (2020). The pedogenic Walker and Syers model under high atmospheric P deposition rates. *Biogeochemistry*, *148*, 237–253.

Garzón-Machado, V., Otto, R., & del Arco Aguilar, M. J. (2013). Bioclimatic and vegetation mapping of a topographically complex oceanic island applying different interpolation techniques. *International Journal of Biometeorology*, *58*, 887–899. https://doi.org/10.1007/s00484-013-0670-y

Greinwald, K., Gebauer, T., Musso, A., & Scherer-Lorenzen, M. (2021). Similar successional development of functional community structure in glacier forelands despite contrasting bedrocks. *Journal of Vegetation Science*, *32*, e12993. https://doi.org/10.1111/jvs.12993

Grime, J. P. (2002). *Plant strategies, vegetation processes, and ecosystem properties* (2nd ed.). Wiley.

Grime, J. P. (2006). Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science*, *17*, 255–260.

Grishin, S. Y., del Moral, R. D., Krestov, P. V., & Verkholat, V. P. (1996). Succession following the catastrophic eruption of Ksudach volcano (Kamchatka, 1907). *Vegetatio*, *127*, 129–153. https://doi.org/10.1007/BF00044637

Hanz, D. M., Beloiu, M., Wipfler, R., Beierkuhnlein, C., Field, R., Jentsch, A., Vetaas, O. R., & Irl, S. D. H. (2022). High species turnover and low intraspecific trait variation in endemic and non-endemic plant species assemblages on an oceanic island. *Journal of Vegetation Science*, *33*, e13120. https://doi.org/10.1111/jvs.13120

Hanz, D. M., Cutts, V., Barajas-Barbosa, M. P., Algar, A. C., Beierkuhnlein, C., Fernández-Palacios, J. M., Field, R., Kreft, H., Steinbauer, M. J., Weigelt, P., & Irl, S. D. H. (2022). Climatic and biogeographical drivers of functional diversity in the flora of the Canary Islands. *Global Ecology and Biogeography*, *31*, 1313–1331. https://doi.org/10.1111/geb.13507

Irl, S. D., Schweiger, A. H., Hoffmann, S., Beierkuhnlein, C., Hartmann, H., Pickel, T., & Jentsch, A. (2019). Spatiotemporal dynamics of plant diversity and endemism during primary succession on an oceanic-volcanic island. *Journal of Vegetation Science*, *30*, 587–598. https://doi.org/10.1111/jvs.12765

Irl, S. D. H., Schweiger, A. H., Steinbauer, M. J., Ah-Peng, C., Arévalo, J. R., Beierkuhnlein, C., Chiarucci, A., Daehler, C. C., Fernández-Palacios, J. M., Flores, O., Kueffer, C., Maděra, P., Otto, R., Schweiger, J. M. I., Strasberg, D., & Jentsch, A. (2021). Human impact, climate and dispersal strategies determine plant invasion on islands. *Journal of Biogeography*, *48*(8), 1889–1903. https://doi.org/10.1111/jbi.14119

Karadimou, E., Kallimanis, A. S., Tsiripidis, I., Raus, T., Bergmeier, E., & Dimopoulos, P. (2018). Functional diversity changes over 100 yr of primary succession on a volcanic island: Insights into assembly processes. *Ecosphere*, *9*, e02374. https://doi.org/10.1002/ecs2.2374

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar, C. C., Aleixo, I., Ali, H., … Wirth, C. (2020). TRY plant trait database-enhanced coverage and open access. *Global Change Biology*, *26*, 119–188.

Kitayama, K., Mueller-Dombois, D., & Vitousek, P. M. (1995). Primary succession of Hawaiian montane rain forest on a chronosequence of eight lava flows. *Journal of Vegetation Science*, *6*, 211–222. https://doi.org/10.2307/3236216

Korablev, A., Smirnov, V., Neshataeva, V., Kuzmin, I., & Nekrasov, T. (2020). Plant dispersal strategies in primary succession on the Tolbachinsky Dol volcanic plateau (Russia). *Journal of Vegetation Science*, *31*, 954–966. https://doi.org/10.1111/jvs.12901

Laine, A. M., Selänpää, T., Oksanen, J., Sevakivi, M., & Tuittila, E.-S. (2018). Plant diversity and functional trait composition during mire development. *Mires and Peat*, *21*(21), 1–19. https://doi.org/10.19189/MaP.2017.OMB.280

Laliberté, E., Legendre, P., & Shipley, B. (2014). *FD: measuring functional diversity from multiple traits, and other tools for functional ecology*. R package version 1.0-12.3.

Laughlin, D. C. (2024). Unifying functional and population ecology to test the adaptive value of traits. *Biological Reviews*, *99*, 1976–1991. https://doi.org/10.1111/brv.13107

Lepš, J., Bello, F. d., Šmilauer, P., & Doležal, J. (2011). Community trait response to environment: Disentangling species turnover vs intraspecific trait variability effects. *Ecography*, *34*(5), 856–863. https://doi.org/10.1111/j.1600-0587.2010.06904.x

Magnússon, B., Magnússon, S. H., Ólafsson, E., & Sigurdsson, B. D. (2014). Plant colonization, succession and ecosystem development on Surtsey with reference to neighbouring islands. *Biogeosciences*, *11*, 5521–5537. https://doi.org/10.5194/bg-11-5521-2014

Mammola, S., & Cardoso, P. (2020). Functional diversity metrics using kernel density n-dimensional hypervolumes. *Methods in Ecology and Evolution*, *11*, 986–995. https://doi.org/10.1111/2041-210x.13424

Mason, N. W., Bello, F., Mouillot, D., Pavoine, S., & Dray, S. (2013). A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, *24*(5), 794–806. https://doi.org/10.1111/jvs.12013

Matson, P. (1990). Plant-soil interactions in primary succession at Hawaii Volcanoes National Park. *Oecologia*, *85*(2), 241–246. http://www.jstor.org/stable/4219504

13652745, 2025, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.70033 by Martin Luther University Halle-Wittenberg, Wiley Online Library on [18/08/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Moles, A. T., & Westoby, M. (2004). Seed size and plant strategy across the whole life cycle. *Oikos*, *81*(1), 1–23.

Mori, A. S., Osono, T., Cornelissen, J. H. C., Craine, J., & Uchida, M. (2017). Biodiversity–ecosystem function relationships change through primary succession. *Oikos*, *126*, 1637–1649.

Mouchet, M. A., Villéger, S., Mason, N. W. H., & Mouillot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, *24*, 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Oksanen, F. J. (2017). *Vegan: Community ecology package*. R package version 2.4-3. https://CRAN.R-project.org/package=vegan

Ottaviani, G., Keppel, G., Götzenberger, L., Harrison, S., Opedal, Ø. H., Conti, L., Liancourt, P., Klimešová, J., Silveira, F. A. O., Jiménez-Alfaro, B., Negoita, L., Doležal, J., Hájek, M., Ibanez, T., Méndez-Castro, F. E., & Chytrý, M. (2020). Linking plant functional ecology to island biogeography. *Trends in Plant Science*, *25*(4), 329–339. https://doi.org/10.1016/j.tplants.2019.12.022

Otto, R., Arteaga, M. A., Delgado, J. D., Arévalo, J. R., Blandino, C., & Fernández-Palacios, J. M. (2014). Road edge effect and elevation patterns of native and alien plants on an oceanic island (Tenerife, Canary Islands). *Folia Geobotanica*, *49*, 65–82. https://doi.org/10.1007/s12224-013-9159-z

Otto, R., Krüsi, B. O., Burga, C. A., & Fernández-Palacios, J. M. (2006). Old-field succession along a precipitation gradient in the semi-arid coastal region of Tenerife. *Journal of Arid Environments*, *65*, 156–178. https://doi.org/10.1016/j.jaridenv.2005.07.005

Pakeman, R. J., & Quested, H. M. (2007). Sampling plant functional traits: What proportion of the species need to be measured? *Applied Vegetation Science*, *10*, 91–96. https://doi.org/10.1111/j.1654-109X.2007.tb00507.x

Pavanetto, N., Carmona, C. P., Laanisto, L., Niinemets, Ü., & Puglielli, G. (2024). Trait dimensions of abiotic stress tolerance in woody plants of the northern hemisphere. *Global Ecology and Biogeography*, *33*, 272–285. https://doi.org/10.1111/geb.13788

Pickett, S. T. A. (1989). Space-for-time substitution as an alternative to long-term studies. In G. E. Likens (Ed.), *Long-term studies in ecology* (pp. 110–135). Springer.

Potgieter, L. J., Wilson, J. R. U., Strasberg, D., & Richardson, D. M. (2014). Casuarina invasion alters primary succession on lava flows on La Réunion island. *Biotropica*, *46*, 268–275. https://doi.org/10.1111/btp.12103

Prach, K., & Walker, L. R. (2019). Differences between primary and secondary plant succession among biomes of the world. *Journal of Ecology*, *107*, 510–516. https://doi.org/10.1111/1365-2745.13078

Price, J. P., Otto, R., Menezes de Sequeira, M., Kueffer, C., Schaefer, H., Caujapé-Castelss, J., & Fernández-Palacios, J. M. (2018). Colonization and diversification shape species-area relationships in three Macaronesian archipelagos. *Journal of Biogeography*, *45*, 2027–2039. https://doi.org/10.1111/jbi.13396

Purschke, O., Schmid, B. C., Sykes, M. T., Poschlod, P., Michalski, S. G., Durka, W., Kühn, I., Winter, M., & Prentice, H. C. (2013). Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: Insights into assembly processes. *Journal of Ecology*, *101*, 857–866. https://doi.org/10.1111/1365-2745.12098

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Ratier Backes, A., Römermann, C., Alexander, J. M., Arévalo, J. R., Keil, P., Padrón-Mederos, M. A., Trogisch, S., & Haider, S. (2023). Mechanisms behind elevational plant species richness patterns revealed by a trait-based approach. *Journal of Vegetation Science*, *34*(1), e13171. https://doi.org/10.1111/jvs.13171

Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*, 275–301. https://doi.org/10.1111/1365-2745.12211

Schrader, J. (2020). Plants on small islands: Using taxonomic and functional diversity to unravel community assembly processes and the small-island effect. *Frontiers of Biogeography*, *12*, e47361. https://doi.org/10.21425/F5FBG47361

Schrader, J., Westoby, M., Wright, I. J., & Kreft, H. (2021). Disentangling direct and indirect effects of island area on plant functional trait distributions. *Journal of Biogeography*, *48*(8), 2098–2110.

Schrader, J., Wright, I. J., Kreft, H., & Westoby, M. (2021). A roadmap to plant functional island biogeography. *Biological Reviews*, *96*(6), 2851–2870. https://doi.org/10.1111/brv.12782

Vargas, P., Arjona, Y., Manuel Nogales, M., & Heleno, R. H. (2015). Long-distance dispersal to oceanic islands: Success of plants with multiple diaspore specializations. *AoB Plants*, *7*, plv073.

Villar García, J. L., Alonso Vargas, M. Á., & de la Torre García, A. (2008). The invasion of Senecio kleinia, an endemic plant of the Canary Islands, on the south–eastern Spanish coastline. *Bouteloua*, *4*, 41–46.

Vitousek, P. M., Walker, L. R., Whiteaker, L. D., & Matson, P. A. (1993). Nutrient limitations to plant growth during primary succession in Hawaii volcanoes National Park. *Biogeochemistry*, *23*, 197–215. https://doi.org/10.1007/BF00023752

Vitousek, P. M., Walker, L. R., Whiteaker, L. D., Mueller-Dombois, D., & Matson, P. A. (1987). Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science*, *238*, 802–804. https://doi.org/10.1126/science.238.4828.802

Walker, L. R., & del Moral, R. (2003). *Primary succession and ecosystem rehabilitation*. Cambridge University Press.

Walker, L. R., Wardle, D. A., Bardgett, R. D., & Clarkson, B. D. (2010). The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology*, *98*, 725–736. https://doi.org/10.1111/j.1365-2745.2010.01664.x

Walker, T. W., & Syers, J. K. (1976). The fate of phosphorus during pedogenesis. *Geoderma*, *15*, 1–19. https://doi.org/10.1016/0016-7061(76)90066-5

Weiher, E., & Keddy, P. A. (1995). Assembly rules, null models, and trait dispersion: New questions from old patterns. *Oikos*, *74*(1), 159–164. https://doi.org/10.2307/3545686

Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., & Wright, I. J. (2002). Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, *33*, 125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452

Westoby, M., Leishman, M. R., & Lord, J. M. (1995). On misinterpreting the 'phylogenetic correction'. *Journal of Ecology*, *83*, 531–534. https://doi.org/10.2307/2261605

Westoby, M., & Wright, I. J. (2006). Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution*, *21*(5), 261–268. https://doi.org/10.1016/j.tree.2006.02.004

Westoby, M., Yates, L., Holland, B., & Halliwell, B. (2023). Phylogenetically conservative trait correlation: Quantification and interpretation. *Journal of Ecology*, *111*, 2105–2117. https://doi.org/10.1111/1365-2745.14150

Whittaker, R., Bush, M., & Richards, K. (1989). Plant recolonization and vegetation succession on the Krakatau Islands, Indonesia. *Ecological Monographs*, *59*, 59–123.

Whittaker, R., Matthew, M., & Fernández-Palacios, J. M. (2023). *Geo-environmental dynamics, ecology, evolution, human impact, and conservation* (3rd ed.). Oxford University Press.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827. https://doi.org/10.1038/nature02403

Zheng, S., Didham, R. K., Yu, M., & Webber, B. L. (2022). Species-level CWM values mask contrasting intra- versus interspecific trait shifts

13652745, 2025, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.70033 by Martin Luther University Halle-Wittenberg, Wiley Online Library on [18/08/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

at subtropical forest edges. *Ecography*, *2022*(5), e05837. https://doi.org/10.1111/ecog.05837

Zhong, H., Zhou, J., Wong, W. S., Cross, A., & Lambers, H. (2021). Exceptional nitrogen-resorption efficiency enables *Maireana* species (Chenopodiaceae) to function as pioneers at a mine-restoration site. *Science of the Total Environment*, *779*, 146420. https://doi.org/10.1016/j.scitotenv.2021.146420

Zizka, A., Onstein, R. E., Rozzi, R., Weigelt, P., Kreft, H., Steinbauer, M. J., Bruelheide, H., & Lens, F. (2022). The evolution of insular woodiness. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(37), e2208629119. https://doi.org/10.1073/pnas.2208629119

SUPPORTING INFORMATION

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

Table S1. Results of linear models (function lm, package stats) with individual CWM traits as dependent variables and abiotic factors as explanatory variables.

Table S2. List of recorded plant species and traits.

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