







RESEARCH ARTICLE

Mechanisms behind elevational plant species richness patterns revealed by a trait-based approach

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Abstract

Aims: Elevational patterns of plant species richness may be caused by multiple underlying mechanisms, and the same pattern can be predicted by different mechanisms. Using the steep elevational gradient of Tenerife as a model system, we aimed to test if the application of a trait-based approach can help disentangle the role of potential mechanisms behind local elevational plant species richness patterns.

Location: Tenerife, Canary Islands, Spain.

Methods: Based on vegetation relevés from natural vegetation and disturbed roadside habitat, along an elevational gradient of 2300m, we observed a peak of plant species richness in the lowest third of the gradient. We considered three mechanisms potentially shaping this pattern: environmental filtering (temperature and precipitation), effects of area and disturbance. For these mechanisms, we hypothesized a distinct pattern of functional trait–elevation relationships. These were tested with *in-situ* data of nine functional leaf traits, from which we calculated community-weighted means (CWM) of traits and functional diversity (Rao's Q).

Results: While species richness was significantly positively correlated with temperature, area and disturbance, filtering through temperature was the only mechanism for which we could confirm most of our mechanism-specific hypotheses about elevational trait changes: with increasing elevation, CWMs of most traits indicated shifts from acquisitive to conservative growth strategies, and functional diversity decreased. The shift of growth strategies also supported the disturbance effect, as we found overall more acquisitive communities at roadsides compared to natural habitats.

Conclusions: Our results indicate that simple correlations between species richness and abiotic variables are not necessarily causal. Additional testing of mechanism-specific hypotheses for elevational patterns of both CWMs and functional diversity can help distinguishing between correlational and mechanistic relationships between species richness and environmental variables. The trait-based framework presented

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here can be fruitfully applied to better understand species richness patterns in other regions and across other types of environmental gradients.

KEYWORDS

altitude, biodiversity, community-weighted mean, environmental filtering, functional diversity, functional traits, mountain biogeography, species richness

1 | INTRODUCTION

Studies of variation in species richness along elevational gradients have a long history dating back to the early 19th century (e.g. von Humboldt, 1849). Since then, the most frequently described elevational patterns of plant species richness have been a peak at mid-elevation and decreasing richness with elevation (McCain & Grytnes, 2010). Mechanisms proposed to explain these patterns were related, for instance, to climate (Irl et al., 2015; Peters et al., 2019), land surface area (Bachman et al., 2004; Romdal & Grytnes, 2007), disturbance (Bunn et al., 2010), or a combination of more than one of these factors (Lee et al., 2013; Jiang et al., 2018). Nevertheless, teasing apart mechanisms leading to changes in species richness along elevational gradients is not trivial. On the one hand, different mechanisms might generate the same elevational species richness pattern. For instance, a pattern of decreasing species richness with increasing elevation can be explained by either filtering by temperature or the elevational reduction of available land surface area, because cold conditions and small areas at high elevations only allow for a small number of species (McCain & Grytnes, 2010). On the other hand, species richness patterns can emerge from the combined effect of more than one mechanism acting in different directions. For instance, a hump-shaped pattern can result from the interaction between climate filtering at high elevations and filtering by strong anthropogenic disturbance in the lowlands (Peters et al., 2019). A thorough understanding of the mechanisms shaping elevational species richness patterns is further complicated by the fact that several abiotic factors are intercorrelated along elevational gradients.

The positive relationships between species richness and both temperature and precipitation have been attributed to the fact that only specialist species are able to persist under extreme climatic conditions (de Bello et al., 2013), that is, very low temperatures or low amounts of precipitation. Larger areas can harbor larger species pools, and in mountains worldwide such a positive association between species richness and area of the elevational band has been observed (Bachman et al., 2004; Romdal & Grytnes, 2007). Elevational patterns of species richness can also be positively affected by disturbance, especially by mountain roads (Catford et al., 2012). Moderate levels of disturbance promote the co-existence of species through reduced competition (via biomass removal of dominant species) and the release of additional resources (Davis et al., 2000; Milbau et al., 2013). Available area, temperature and disturbance typically decrease with elevation, while precipitation predominantly

increases with elevation (but can differ depending on the prevailing weather patterns; McCain & Grytnes, 2010).

Since “elevation” summarizes all of these environmental gradients, how to tell apart their effects on species richness? Here, we suggest to use patterns of functional traits to reveal the contribution of different mechanisms. Functional traits are measurable characteristics of individuals which affect their growth, reproduction and survival (Violle et al., 2007). Trade-offs between traits associated with resource acquisition and investment in leaves constrain species and communities into a functional continuum from acquisitive (with fast nutrient uptake and fast growth of non-durable leaves) to conservative strategies (with slow nutrient uptake and slow growth of highly durable leaves; Wright et al., 2004; Díaz et al., 2016; Bruelheide et al., 2018). Typically, acquisitive strategies are found in resource-rich habitats (lowlands), while conservative strategies prevail under extreme conditions (highlands). Since both species richness and functional traits vary along environmental gradients (Read et al., 2014; Bruelheide et al., 2018), we assume that those mechanisms behind elevational species richness patterns that are related to environmental factors should also be reflected in elevational trait patterns (Lavorel & Garnier, 2002; Funk et al., 2017). For example filtering through temperature should not only restrict the number of species able to persist at high elevations, but also influence the functional characteristics of the community towards stress-tolerant trait values or strategies. Thus, for each potential mechanism behind an observed elevational species richness pattern, we can hypothesize an elevational pattern of functional traits. This includes the expectation that those mechanisms possibly driving species richness patterns, but related to factors not directly based on environmental conditions (e.g. an area effect; Bachman et al., 2004), should not affect community-weighted trait means (CWMs). Provided that the expected trait patterns differ for the different mechanisms, we can gain insight into each mechanism's importance.

Here, we use the steep elevational gradient on the island of Tenerife as a model system to test our approach. Species richness on Tenerife peaks in the lowest third of the elevational gradient (around 750 m a.s.l.), followed by a more linear decrease (Bacaro et al., 2015). This pattern might be driven – among others – by (i) climate filtering, (ii) the elevational reduction of available land surface area, and (iii) a disturbance effect (see below for hypothesized trait patterns linked to these three mechanisms). In Tenerife, temperature, area and disturbance decrease with elevation, while precipitation peaks at mid-elevation (Morales Matos & Pérez González, 2000).

1.1 | Generating region-specific hypotheses

In the following, we first explain for each mechanism how it typically affects trait patterns. Then, we link these general relationships to the Tenerife-specific elevational change of the factors underlying the respective mechanism. Based on this, we hypothesize how community trait characteristics related to growth strategies respond to elevation in our study area. Testing these expected trait–elevation relationships will help to assess which variables might have a mechanistic effect on species richness, compared to variables which might be statistically associated to species richness, but are not in a causal relationship with it.

1. *Climate filtering*: The effect of cold or drought stress is reflected in plant communities by functional shifts from more acquisitive to more conservative growth strategies (Ordoñez et al., 2009; de Bello et al., 2013). For example, specific leaf area typically decreases with decreasing water availability (e.g. Liu et al., 2017) and decreasing temperature (e.g. Körner, 1989; Rosbakh et al., 2015). Within a community, the few species persisting under extreme climatic conditions are similar in their functional traits (de Bello et al., 2013), which results in a lower functional diversity, as observed along gradients of temperature and precipitation, for example on Mt. Kilimanjaro (Schellenberger Costa et al., 2017) and on a Mediterranean mountain (Bricca et al., 2022).
2. *Area effect*: *Land surface area* per se does not have a direct ecological effect on plant individuals and thus, even though species richness should increase with area of the elevational bands (reflecting a larger source pool area), area should not cause a directional change in CWMs. There are only few studies that analyzed such a direct effect (e.g. Schrader et al., 2021). When taking into account only a passive sampling effect, larger areas with more species have a higher probability of containing species reflecting the extremes of the regional trait distribution and thus functional diversity might increase with area (Karadimou et al., 2016). Studies addressing the topic of functional diversity–area relationships are comparably recent, and only rarely focus on plants (Wang et al., 2013; Schrader et al., 2021).
3. *Disturbance effect*: In mountains, a typical form of anthropogenic disturbance are roads that lead from the lowlands up to high elevation. The gradient of disturbance caused by mountain roads is perpendicular to the elevational gradient and decreases from roadsides to adjacent natural vegetation. Road disturbance, specifically via road maintenance activities of biomass removal, trampling and driving on road verges, can favor species with a more acquisitive strategy through increasing the availability of resources (space, light, nutrients; Forman & Alexander, 1998). Thus, road disturbance might act as a filter that results in a shift of CWMs towards more acquisitive growth strategies (Forman & Alexander, 1998) and lower functional diversity (Mayfield et al., 2010). Alternatively, road disturbance might increase functional diversity by removing dominant species and allowing

weak competitors to survive, especially in highly productive areas, such as low elevations. However, we expect road disturbance to act mainly as a filter in Tenerife due to its high intensity and frequency.

Figure 1 shows for each of the three mechanisms potentially underlying the observed elevational species richness pattern in our study region the expected elevational patterns of community-weighted traits means (CWMs) of functional traits and functional diversity. Comparing the observed trait–elevation relationships to our mechanism-specific expectations will allow us to assess the influence of each mechanism on the observed elevational species richness pattern. Based on the general effects of temperature, precipitation, land surface area and disturbance on plant functional traits together with the elevational patterns of these abiotic factors in our model region, we formulate the following (competing) hypotheses:

1. Community-weighted means (CWMs) change from acquisitive to conservative strategies with increasing elevation as a consequence of climate filtering by temperature (Figure 1a). For the disturbance effect, CWMs of roadside (disturbed) communities shift towards values indicating a more acquisitive growth strategy compared to communities in natural vegetation (Figure 1a–c). Climate filtering by precipitation leads to highest acquisitiveness at mid-elevations (Figure 1b). CWMs do not change with elevation as a consequence of the area effect (Figure 1c).
2. Functional diversity decreases with elevation according to filtering by temperature (Figure 1d) and the area effect (Figure 1f), or peaks at mid-elevations according to filtering by precipitation (Figure 1e). Because of the filtering effect of disturbance, functional diversity is lower along roadsides compared to natural vegetation (Figure 1d–f).

2 | MATERIALS AND METHODS

2.1 | Study area

Tenerife is the largest island of the Canary Islands archipelago, located west of the African coast at 28.28°N, 16.15°W. In the center of the island, at ca. 2000m a.s.l., is the high plateau of the volcanic caldera Las Cañadas, from which the summit of Mount Teide rises up to 3718m a.s.l. Climate is strongly influenced by northeastern trade winds which form a cloud layer in the north of the island, distinguishing the more humid and temperate north from the hotter and arid south (Fernández-Palacios, 1992).

Temperature decreases along the elevational gradient with a lapse rate of approximately 0.5°C per 100m (Morales Matos & Pérez González, 2000). The prevailing trade winds cause precipitation to increase from the coast until mid-elevations. Towards the summit, precipitation has been reported to decrease again, but with high variability due to the island's complex topography (Morales Matos & Pérez González, 2000; AEMET, 2012). Due to the conical shape of

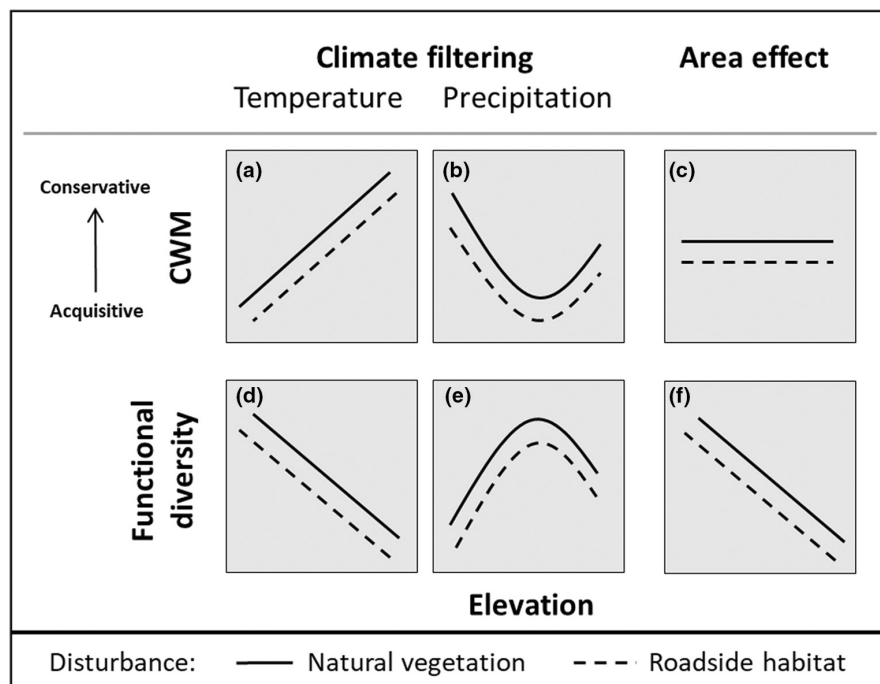


FIGURE 1 Expected elevational patterns of community-weighted traits means (CWMs) and functional diversity of leaf traits according to different mechanisms underlying the observed elevational species richness pattern in the study region of Tenerife. CWMs of leaf traits represent the average growth strategy of the community, i.e., conservative (high leaf dry matter content, for example) and acquisitive strategies (low leaf dry matter content).

the main volcano, land surface area of elevational bands decreases with elevation (Morales Matos & Pérez González, 2000).

The natural vegetation along the southern slopes begins with coastal halophytic communities and thermo-sclerophyllous scrub up to 1000 m a.s.l., followed by forests of Canary Island pine (*Pinus canariensis*) up to 2000 m a.s.l. and summit scrub on the high plateau above the tree line (Appendix S1). A peak of species richness has been reported from the lower third of the elevational gradient, followed by decreasing species richness (Bacaro et al., 2015).

2.2 | Environmental data

Temperature and precipitation data for each sampling site were obtained from CHELSA (Karger et al., 2017), which is a global data set of interpolated climatic variables with a spatial resolution of 30'' over a time period of 34 years (1979–2013). Mean temperature and total precipitation of the main growing season (from March to May) were calculated for each sampling site. These variables were selected as indicators of available energy and water in the crucial time of the year for plant growth and survival. Mean temperatures ranged from 19.5°C at the coast to 9.6°C at the highest sampling sites. Growing-season precipitation was lowest with 39 mm at the coast and highest with 111 mm in the mid-elevational pine forest belt. To examine the relationship between plant species richness and land surface area, we divided the elevational gradient into 100-m vertical bands (which roughly corresponded to the elevational difference between our sampling sites). We used a digital elevation model of Tenerife from the Shuttle Radar Topography Mission (<https://www2.jpl.nasa.gov/srtm/>), which contains topographic data with an approximate resolution of 3'' (ca. 90 m × 90 m at the equator). The surface area for each band (polygon) was calculated with ArcGIS Desktop software

(version 10.5; ESRI). As a proxy for disturbance, plot type (road or interior) was used.

Our own data compilation confirmed the decrease of temperature and area with elevation, but we found a linear elevational increase of precipitation along the elevational gradient covered by our study (see Appendix S2). As expected, Spearman's rank correlation coefficients (ρ) among the three environmental factors indicate strong collinearity (Appendix S2). This strong collinearity poses a challenge when trying to determine the main mechanism behind the elevational changes of species richness.

2.3 | Sampling design

The project was conducted within the framework of the Mountain Invasion Research Network (MIREN; <http://www.mountaininvasion.org>), and we used the permanent plots established in 2008 according to the standardized protocol of the global MIREN survey (Arévalo et al., 2005; Haider et al., 2021). Fieldwork was carried out during the growing season from April to June 2018, along three roads on southwest, south, and southeast slopes, from close to the coast (24 m a.s.l.) up to 2377 m a.s.l. in the volcanic caldera (Figure 2a). Along the elevational extent of each road, 20 sampling sites were equally distributed (average elevational distance between sample sites was 123 m). Each sampling site consisted of two plots of 50 m × 2 m: one roadside plot with the long side parallel and directly adjacent to the road ("road plot"), and one non-roadside plot in natural vegetation located perpendicularly to the road and starting at a distance of 50 m from the road plot ("interior plot"; Figure 2b). Due to local conditions, such as steepness of the terrain and density of settlements, only 111 out of 120 plots could be implemented across a total elevational range of 2353 m.

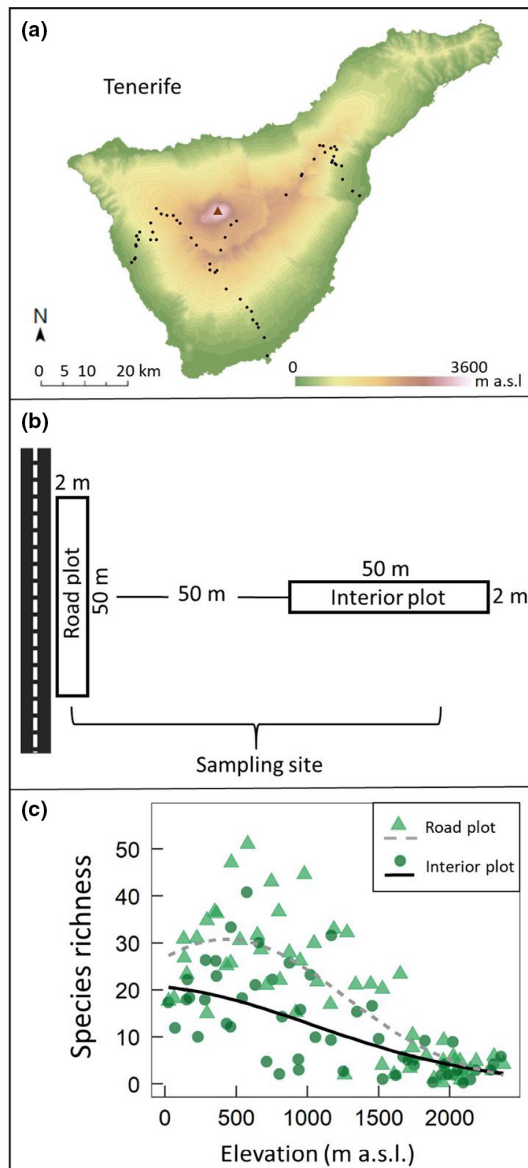


FIGURE 2 (a) Locations of sampling sites (56 black dots) along three mountain roads, starting at the coast and ending at the volcanic caldera of las Cañadas on Tenerife (Spain). The highest point on the island is the peak of Teide (3718 m a.s.l., brown triangle). (b) At each sampling site, two plots were established (road and interior plots), where all species were identified and their cover recorded. Populations for leaf sample collection were also chosen within these plots. (c) Observed relationship between species richness and elevation based on our data collection. Regression lines are based on model predictions.

2.4 | Vegetation relevés and trait sampling

In each plot, all vascular plant species were identified, and their cover recorded using seven classes (where class 1 corresponds to a cover of up to 1%; 2 = 1%–5%; 3 = 6%–25%; 4 = 26%–50%; 5 = 51%–75%; 6 = 76%–95% and 7 = 96%–100%).

We collected leaf samples from the most abundant species and all life forms (grasses, forbs, shrubs and trees). By doing so, we obtained

trait values for species making up at least 80% of the relative plot cover (except for five plots; Appendix S3), which is an established threshold for a reliable characterization of the functional properties of a community (Pakeman & Queded, 2007). The trait samples consisted of 10–50 leaves from approximately seven individuals of a single species on the same plot. For each species, separate samples were taken from up to three different plots, corresponding to low-, intermediate and high-elevation points of the species' occurrence in the 2008 vegetation survey. The trait measurements were later aggregated into one value per species in order to focus on capturing elevational patterns at the inter-specific level, that is, based on species turnover and composition, rather than elevational within-species adjustments, which have been shown to be idiosyncratic (Kichenin et al., 2013). In total, we sampled leaves from 189 species (out of 270 recorded in the survey) and measured two eco-morphological (specific leaf area and leaf dry matter content) and seven biochemical leaf traits (leaf C, N, C:N ratio, P, Ca, K, Mg) which are associated with the functional continuum from acquisitive to conservative growth strategies (Appendix S3). Acquisitive strategies are related to high values of specific leaf area (SLA) and leaf nutrient concentrations, while conservative growth strategies are characterized by high leaf dry matter content (LDMC), high leaf carbon content, and high leaf carbon to nitrogen ratio (Reich et al., 1997). Beside reflecting fundamental physiological properties related to plant resource use and growth strategies, these leaf traits have been shown to respond to gradients of temperature (Wright et al., 2005), precipitation (Lang et al., 2019) and disturbance (McIntyre et al., 1999; Bernhardt-Römermann et al., 2011), being, therefore, appropriate traits to test our hypotheses. We additionally compiled data on two traits which are well established as traits affected by disturbance intensity and frequency: life span and woodiness. Due to the strong dominance of perennial woody species in the data set, we do not discuss these traits further (Appendix S3). For details about the trait measurements see Appendix S3.

2.5 | Species richness, community-weighted trait means and functional diversity

Species richness was calculated as the total number of species recorded per plot.

Community-weighted trait means (CWMs) were calculated for each trait and each plot, using the SYNCSEA package (Debastiani & Pillar, 2012) in R (R Core Team, 2020):

$$\text{CWM} = \sum_{i=1}^N p_i \text{trait}_i \quad (1)$$

where p_i is the relative cover of species i in the community, and trait_i is the trait value of species i .

To quantify functional diversity, we calculated Rao's quadratic entropy (Rao's Q ; Rao, 1982; Botta-Dukát, 2005) for each plot:

$$\text{Rao's } Q = \sum_{i=1}^{N-1} \sum_{j=i+1}^N p_i p_j d_{ij} \quad (2)$$

where the species' trait distances are weighted by their relative abundance in the community. N is the number of species in the plot, p_i and p_j are the relative abundances of species i and j , and d_{ij} is the trait distance between species i and j . Thus, Rao's Q gives the mean functional distance between any two species in a plot. The calculation of Rao's Q was done for each trait separately, and for all traits combined (multitrait Rao's Q ; scaling trait values to unit variance), using the *FD* package in R (Laliberté & Legendre, 2010), with the default Euclidean distance recommended for continuous traits. Before calculating multitrait Rao's Q , we checked for correlation among traits, and excluded correlated traits (leaf N, P and K). Therefore, we did not include these traits in any of the analyses. Additionally, we have performed logarithmic transformation to base ten previous to calculating Rao's Q for leaf Mg and leaf C:N ratio in order to ensure normality, as it has been proved to increase the robustness of functional indices relative to missing data (Májeková et al., 2016).

Because functional Rao's Q is calculated based on the species abundance matrix, it will inevitably exhibit a certain degree of association to community composition (correlation coefficient between Rao's Q and Simpson's diversity index for our data is 0.695). In order to account for the amount of variance explained by community composition alone, we followed the approach by Jucker et al. (Jucker et al., 2013), and used the residuals from the regression of Rao's Q and Simpson's diversity index as response variable in the elevational models described in subsection 2.6 *Statistical analyses*. We are thus able to assess the elevational patterns of functional diversity purely due to changes in traits and not influenced by community composition.

2.6 | Statistical analyses

In order to describe the pattern of species richness along the elevation gradient on Tenerife we fitted a linear mixed-effects model with $\log(x + 1)$ -transformed species richness as response to elevation (scaled to zero mean and unit variance), plot type (road or interior plot), and their two-way interaction. Sampling site nested in road identity (road 1, 2 or 3) was added as a random effect to account for the sampling design. To confirm our literature-based assumptions that species richness is positively correlated with temperature, precipitation, area and disturbance, we used the same model structure from the species richness–elevation model, but replaced elevation by each of the environmental variables.

We tested the responses of CWMs and functional diversity to elevation and plot type (i.e., natural vegetation vs. roadside habitat, Figure 1) by fitting a series of linear mixed-effects models. Each model was fitted with one response variable. As predictors, we used elevation (scaled to zero mean and unit variance), plot type as a factor and their interaction as fixed effects. Sampling site identity nested in road identity was added as a random effect.

All models were fitted with both a quadratic term (using the second-order polynomial of elevation) and the linear term of elevation, and both models were compared via Akaike's Information

Criterion (AIC). In total, 12 and 14 models were fitted with CWM and functional diversity as response variables respectively. The model with the lowest AIC was selected. All mixed-effects models were fitted in R version 3.5.3 (R Core Team, 2020) with the function “lmer” from the package *lmerTest* (Kuznetsova et al., 2017). p -Values were calculated from F -statistics of type III sum of squares with Satterthwaite approximation to estimate the denominator degrees of freedom.

Since models of CWMs against environmental variables have been shown to be affected by inflated Type I error rates (Peres-Neto et al., 2017; Zelený, 2018), we have adapted the double permutation test approach from Zelený (2018) for mixed models. The results show that our models are not affected by this issue, as the adjusted R^2 of our models are significantly higher than the average R^2 of the permuted models (both for trait and elevation permutations, Appendix S4).

3 | RESULTS

3.1 | Species richness patterns

We observed an overall decrease of species richness with elevation with a small peak around 600m a.s.l. ($F_{1,51.8} = 71.48$, $p < 0.01$; Figure 2c). Road plots exhibited overall higher species richness compared to interior plots ($F_{1,52.7} = 26.88$, $p < 0.01$; Figure 2c). Species richness differences between road plots and interior plots decreased with elevation (elevation-by-plot type interaction) ($F_{1,52.7} = 3.19$, $p = 0.05$; Figure 2c). Species richness showed a hump-shaped relationship with mean temperature of the growing season ($F_{1,51.48} = 67.49$, $p < 0.001$; Appendix S5) and land surface area ($F_{1,51.02} = 41.92$, $p < 0.001$), and an exponentially decreasing relationship with precipitation of the growing season ($F_{1,51.88} = 29.32$, $p < 0.001$). Roadside plots had significantly higher species richness: $F_{1,52.43} = 24.08$, $p < 0.001$; area: $F_{1,52.27} = 26.32$, $p < 0.001$; disturbance: $F_{1,49.29} = 25.5$, $p < 0.001$. The increase in species richness on roadside plots compared to interior vegetation was stronger at intermediate temperatures (temperature-by-plot type interaction; $F_{1,52.46} = 3.23$, $p = 0.048$).

3.2 | Trait–elevation relationships

Elevation had a significant effect on the community-weighted means (CWMs) of all traits studied. However, traits related to conservative growth strategies (LDMC, leaf C and leaf C:N ratio) did not change with elevation in a consistent way. LDMC was highest at low elevations, lowest at mid-elevations, and had mostly intermediate values at high elevations (Figure 3a, Table 1). Leaf C showed a flattening increase with elevation, and leaf C:N ratio a mid-elevational peak (Figure 3b,c). We observed a significant linear decrease with elevation of the traits related to acquisitive strategies SLA, leaf Ca and Mg (Figure 3d–f).

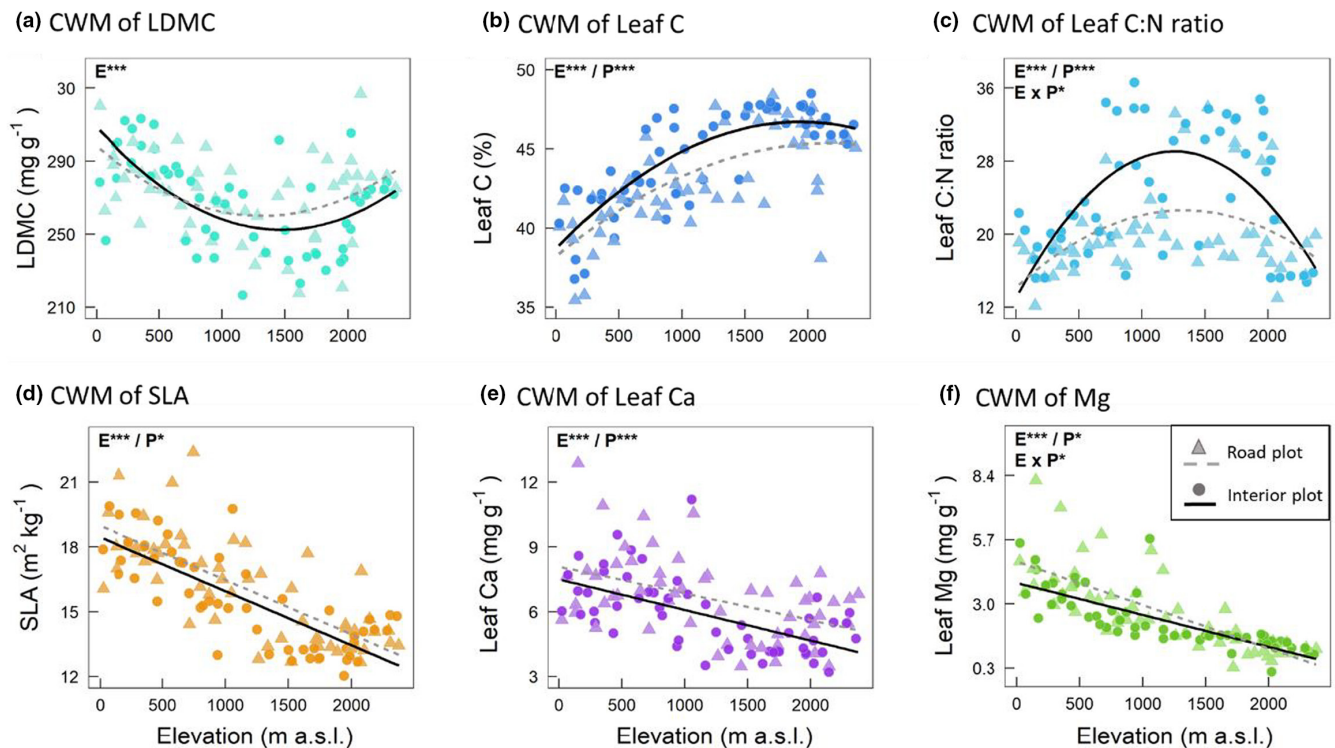


FIGURE 3 Relationship between elevation and community-weighted means (CWM) of six functional leaf traits. Regression lines are based on model predictions. For leaf dry matter content (LDMC), leaf C, leaf C:N ratio, the model including the quadratic term of elevation had a higher explanatory power compared to the model including only the linear term of elevation. Significant terms are listed at the top of each panel (E = elevation, P = plot type, E × P = elevation-by-plot type interaction). Significance levels: ***, <0.001; **, <0.01; * <0.05. SLA, specific leaf area.

Across the whole elevational gradient, communities from road plots showed a significant shift to a more acquisitive growth strategy when compared to communities from interior plots for all traits except for LDMC (lower leaf C and C:N ratio; higher SLA, leaf Ca and Mg). The shift was greatest at mid-elevations for leaf C:N ratio. Leaf Mg had more acquisitive values for roadside than interior plots at low elevations, but the difference disappeared at higher elevations (Table 1).

Functional diversity (residuals of Rao's Q against species diversity) of most of the single traits decreased with elevation, as did the multitrait Rao's Q (Figure 4, Table 1). For LDMC, leaf C:N ratio and leaf Mg, Rao's Q showed a hump-shaped relationship with elevation. Communities along roadsides exhibited higher functional diversity than communities in the interior plots for leaf Mg, while the difference disappeared at high elevation. Rao's Q of leaf C showed no significant relationship with elevation nor plot type.

4 | DISCUSSION

From the set of hypotheses proposed to explain the species richness patterns along the elevational gradient on Tenerife (Figure 1), our results suggest that filtering through temperature is the most important mechanism, together with an additional effect of disturbance. This conclusion is based on the significant pairwise

relationships between species richness, elevation and the abiotic factors, and consistent elevational patterns of functional traits. In contrast, we did not expect significant changes of functional traits along elevation, if available area were the dominating abiotic factor, and therefore we consider it unlikely that an area effect is the main mechanism behind the elevational species richness pattern. We also found no evidence that precipitation is an important driver of the elevational richness pattern, since the trait-elevation relationships did not match our expected patterns for this factor.

4.1 | Filtering through temperature as a main driver of the elevational species richness pattern

Species richness significantly decreased with elevation and increased with temperature. Both relationships are in line with observations from almost all climatic zones and continents (Grytnes, 2003; Field et al., 2009; Xu et al., 2017; Peters et al., 2019). The novelty of our study is that we can more confidently assign causality to these relationships, because our observed trait-elevation relationships match the assumptions for climate filtering. Specifically, the decrease of most traits' functional diversity with increasing elevation is consistent with the assumption of species being increasingly filtered out by cold stress at higher elevations, where only species with similar

TABLE 1 Results from linear mixed-effects models for community-weighted trait means (CWMs) of functional traits and functional trait diversity (FD) of single traits as well as all traits combined (multitrait) as response to elevation, plot type (road or interior plot) and their interaction.

	Elevation		Plot type		Elevation × plot type	
	df	F	df	F	df	F
LDMC						
CWM	49.66	13.19***	48.71	1.51	48.32	2.49
FD	53.22	3.75*	52.90	0.45	52.45	0.36
Leaf C						
CWM	47.37	45.70***	46.26	+24.07***	45.92	0.63
FD	54.25	0.87	53.31	0.71	53.26	0.75
Leaf C:N						
CWM	51.80	13.83***	50.08	+28.65***	49.71	5.01*
FD	52.89	6.41**	52.38	1.23	51.93	0.12
SLA						
CWM	52.24	54.73***	51.50	-6.26*	51.12	2.06
FD	102.67	4.50*	101.95	2.09	101.96	2.83
Leaf Ca						
CWM	53.17	25.99***	51.99	-13.48***	51.70	0.34
FD	54.07	7.99**	53.35	0.00	53.29	0.04
Leaf Mg						
CWM	53.41	115.64***	52.66	-5.44*	52.32	5.59*
FD	53.04	7.02**	52.75	3.26	52.29	3.33*
Multitrait						
FD	54.44	6.93*	53.21	0.90	53.16	0.94

Note: *F*-values and *p*-values, taken from type III sum of squares, are indicated in bold text when significant. For CWMs of leaf dry matter content (LDMC), leaf carbon (leaf C) and leaf carbon to nitrogen ratio (C:N ratio), and for FD of LDMC, C:N ratio and leaf Mg, the model including the quadratic term of elevation had a higher explanatory power compared to the model including only the linear term of elevation. Significant effects are highlighted in bold. Significance levels: ***, <0.001; **, <0.01; *, <0.05. Positive or negative signs next to *F*-values for plot type represent the sign of the estimate, meaning a higher or lower value respectively, for interior plots compared to road plots.

appropriate trait values (e.g. low SLA and high leaf C) are able to persist (de Bello et al., 2013). Additionally, as hypothesized for filtering through temperature, community-weighted means of traits linked to a conservative strategy (except for LDMC) increased and community-weighted means of traits related to an acquisitive strategy decreased with elevation, at least across the lower half of the elevational gradient. Generally, it is assumed that cold stress at higher elevations affects especially structural leaf traits; specifically, small leaves with high tissue density (low SLA, high LDMC) and high levels of carbon can help prevent damage from frost and wind (Körner, 2003). Even on a subtropical island like Tenerife, the formation of extracellular ice, which happens on Tenerife from ca. 1500 m a.s.l. upwards (Fernández-Palacios, 1992), is considered as one of the main ways through which cold stress affects plants. A positive correlation between SLA and mean annual temperature was observed, for example, in grasslands in the European Alps (Rosbakh et al., 2015), while a negative correlation between leaf carbon and temperature was reported on Mount Kilimanjaro (Schellenberger Costa et al., 2017). In contrast, high temperature stress and low water availability might explain the high LDMC

values in the low-elevation communities (Fernández-Palacios & Nicolás, 1995).

Following our expectations for community trait responses to temperature, leaf nutrient concentrations decreased with elevation but for leaf C:N ratio (and leaf N, P and K, results not shown) only until mid-elevations. The reversed response of these traits in the upper part of the elevational gradient suggests that the role of climatic filtering through temperature might be more complex than expected, and not limited to a direct positive effect on plant activity and growth. Rather, tissue formation constraints imposed at high elevation may inhibit the dilution of N and other nutrients in leaf tissue, leading to an accumulation of these nutrients at high elevations (Körner, 1989; Read et al., 2014). Another possible explanation is the high dominance at high elevations of N-fixing legume shrubs, such as *Adenocarpus viscosus* and *Cytisus supranubius*, which might contribute to low levels of the leaf C:N ratio (Irl et al., 2020). Furthermore, the low nutrient values of Canary Island pine (*Pinus canariensis*) observed in the mid-elevational vegetation belt likely reflect the very low nutrient values of this dominant species (leaf N = 1.43%, leaf P = 0.67 mg g⁻¹ and leaf K = 5.54 mg g⁻¹; see also Köhler et al., 2006

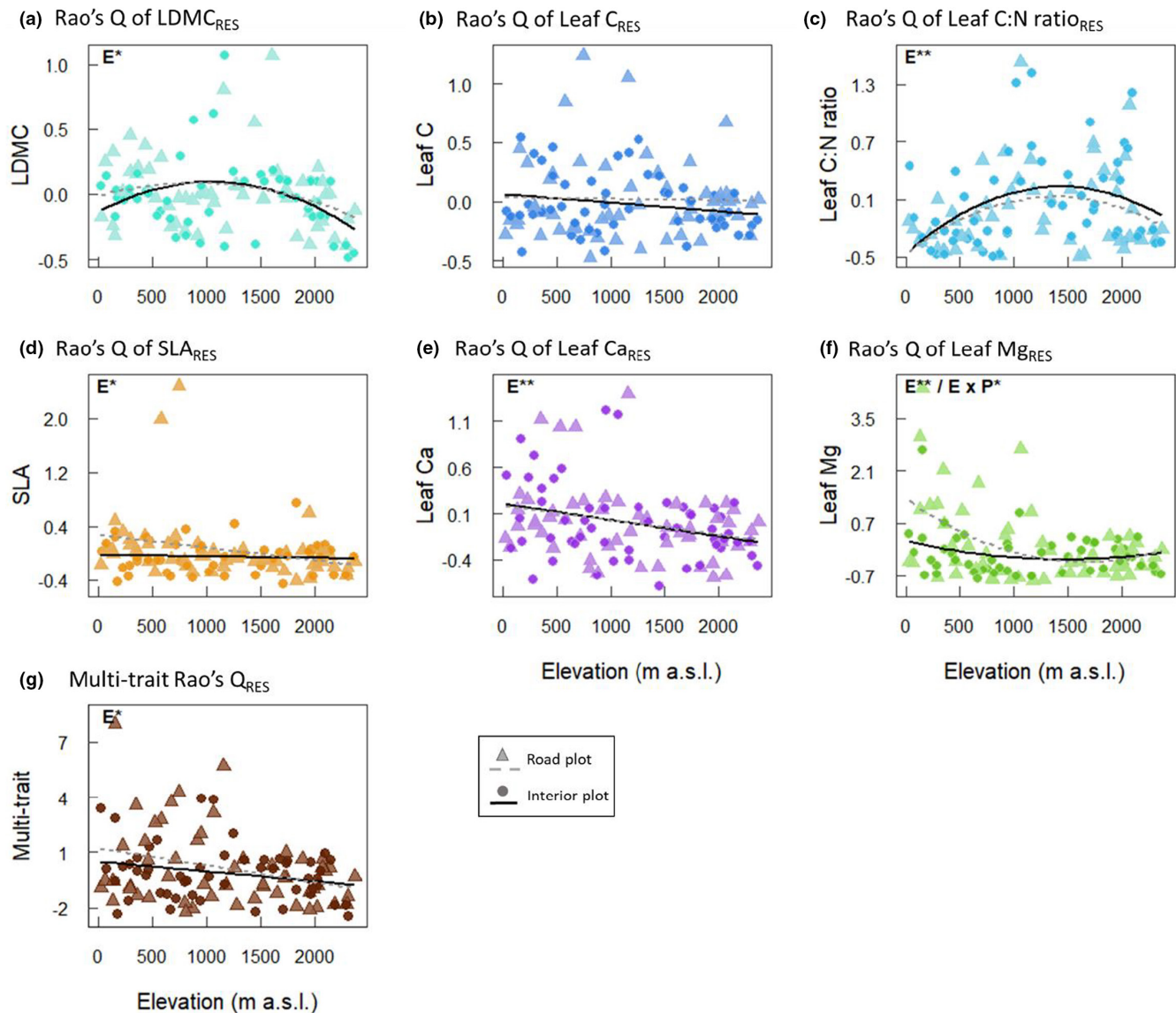


FIGURE 4 Relationship between elevation and functional diversity (Rao's Q) of six functional leaf traits and multitrait functional diversity. The residuals of Rao's Q of each trait and multitrait against Simpson's diversity index was used as predictor. Regression lines are based on model predictions. Significant terms are listed on top of each plot (E = elevation, P = plot type, E × P = elevation-by-plot type interaction). Significance levels: ***, <0.001; **, <0.01; *, <0.05. LDMC leaf dry matter content; SLA, specific leaf area.

and Appendix S6). Evergreen conifers tend to have lower nutrient requirements, since they do not renew their photosynthetic organs as often as other life forms (Ericsson, 1994).

While the observed pattern for functional diversity is also consistent with our hypotheses for an area effect, the expected effects of decreasing temperature with increasing elevation were observed in both community-aggregated trait values and functional diversity.

The high importance of temperature is in line with other studies explaining broad-scale patterns of plant diversity, particularly those looking at continental and global geographic patterns (Hawkins et al., 2003; Kreft & Jetz, 2007; Šimová et al., 2011). However, most of these studies report temperature in combination with water availability as the main driver of species richness (arguably through increased productivity; Storch et al., 2018), with the exception of

Šimová et al. (2011) who also found temperature, and specifically the effect of extreme thermal constraints, as the main predictor of species richness. In accordance to the "climatic tolerance hypothesis" (Terborgh, 1973; Šimová et al., 2011), which proposes that temperature acts as a filter on species distribution and diversity, our results suggest that the temperature filter leads to the exclusion of fast-growing species which cannot cope with increasing cold stress.

4.2 | Effect of disturbance on species richness–elevation patterns

Road disturbance significantly increased species richness. In our study area, disturbance along roadsides was caused by driving and

trampling on the road verges, but also through maintenance activities like mowing, which all resulted in a removal of biomass and thus a reduction of competition between plants. Higher species richness along roadsides in particular was also observed, for example, in Norway, but also other types of disturbance (e.g. logging) were reported to favor species co-existence (Biswas & Mallik, 2010).

As disturbance is known to favor species able to quickly capture available nutrients and grow (McIntyre et al., 1999; Fortunel et al., 2009; Schellenberger Costa et al., 2017), we expected to find more acquisitive trait syndromes along roadsides, where disturbance is higher. Indeed, our results showed that communities in disturbed roadside habitats had higher SLA and leaf nutrients, but lower leaf C and C:N ratio compared to communities in the less human-disturbed natural vegetation. We observed, however, the opposite for LDMC, starting at mid-elevations. Specifically at higher elevations, the extreme temperature conditions next to roads (very hot in summer and very cold in winter) might cause LDMC to increase along roadsides as a means to cope with such temperature fluctuations (Delgado et al., 2007).

Road disturbance exerted a positive effect on functional diversity for leaf Mg, with higher functional diversity on roadside plots compared to natural vegetation. This questions our initial hypothesis that disturbance acts as a filter favoring only acquisitive species. Rather, reduced competition through disturbance might increase heterogeneity in community, by reducing dominant species and thus allowing for communities composed of species with both conservative and acquisitive traits. Furthermore, non-native species might be contributing to these patterns, as they often possess different trait syndromes than native species and are typically more abundant at low elevations and in disturbed habitats like roadsides (Seipel et al., 2012; Alexander et al., 2016). Non-native species were indeed more frequent in roadside plots compared to interior plots, and almost absent at high elevations (Appendix S7).

4.3 | No support for filtering through precipitation

In contrast to our assumptions based on the literature that precipitation peaks at intermediate elevations (1200–1500m) in Tenerife (AEMET, 2012) and that precipitation favors species richness (McCain & Grytnes, 2010), we observed a linear increase of precipitation with elevation and the number of species decreased with increasing precipitation (Appendices S2 and S5). Hence, our hypotheses regarding elevational trait changes driven by precipitation not only need to be revised, but in the specific case of Tenerife, the generally assumed positive association between precipitation and species richness does not apply. Surprisingly, dry conditions do not seem to be a crucial environmental limitation to species richness at low elevations on Tenerife, as has been shown for other systems (e.g. temperate grasslands in southeastern Ontario, Serafini et al., 2019) or as predicted under climate change (e.g. Li et al., 2020). The lack of a trait response to precipitation is in line with a global meta-analysis of Moles et al. (2012) who compiled over 400,000 species-site combinations and found that plant functional traits at the species level were more strongly

correlated with mean annual temperature than with mean annual precipitation. Our results suggest that precipitation might be more important for determining the main vegetation type along our elevational gradient (open vegetation at low and high elevations vs forest at mid-elevations; Fernández-Palacios, 1992) than for driving species richness across the vegetation zones. Thus, precipitation might be a useful predictor for species richness within the same vegetation type (e.g. Qiu et al., 2016), but not across vegetation zones along elevational gradients.

Additionally, the spatial resolution and the source of the precipitation data used in this study might not be adequate to capture the trait variation in mountainous regions. Especially for precipitation on the highly heterogeneous mountain slopes, the grid cells size obtained from CHELSA might be too coarse, and pointing to the need for microclimatic data (Lembrechts et al., 2019). Also, precipitation might not be a good proxy for the actual amount of water available for plants, as soil water retention capacity and percolation might be decoupled from precipitation levels (Moles et al., 2014), and the volcanic soils in Tenerife have low water retention capacity as revealed by our own measurements of soil moisture (Gallardo, 2016). For example, in the Canary Island pine vegetation belt, air humidity is a key factor to consider, as the vegetation in this belt strongly benefits from the so-called horizontal rain formed on the long pine needles.

4.4 | No support for an area effect

Although area decreased with elevation and was positively correlated with species richness, we could not confirm an effect of area on species richness. The elevational changes of CWMs are in contrast to our expectation for an area effect, which we hypothesized to result in a random trait distribution along the elevational gradient. We thus question the importance of area per se as a mechanism shaping mountain diversity, mainly because of its typically strong correlation with temperature in mountains. Also, Lee et al. (2013) found for the Baekdudaegan Mountains in South Korea that area was a subordinate factor explaining elevational patterns of plant species richness when compared to climatic predictors. The effect of area might still be relevant in an evolutionary context of speciation and extinction, or for analysis of phylogenetic diversity (Wang et al., 2013; de Bello et al., 2017; Chun & Lee, 2018), but of minor importance when analyzing more recent or local community assembly processes (Rosenzweig, 1992). Also, a different set of studies which interpret the area effect as resulting from habitat heterogeneity might capture a different relevant aspect of the area effect which is not addressed in this study (Nilsson et al., 1988).

4.5 | Trait-based approach to interpret elevational species richness patterns

Abiotic factors and related mechanisms have a predictable effect on functional traits (Diaz et al., 2004; Bruelheide et al., 2018). Thus

we can evaluate their relevance in determining elevational species richness patterns by elaborating ecologically meaningful hypotheses of how traits should change along the elevational gradient (Dainese et al., 2015). Importantly, the analysis of both CWMs and functional diversity allowed a better distinction between the processes, which is even more relevant with an increasing number of mechanisms tested. In our case, the decrease of functional diversity with elevation would have supported filtering through temperature (Irl et al., 2015; Peters et al., 2019) as well as an effect of area (Bachman et al., 2004; Romdal & Grytnes, 2007), whereas patterns of community trait means were consistent with our predictions for filtering by temperature (Rosbakh et al., 2015; Schellenberger Costa et al., 2017), but not with an effect of area. The analysis of both trait means and functional diversity is also advantageous because different factors might act at different spatial scales. For example, climate factors have a filtering effect on the species pool at larger scales, while disturbance typically acts at more local scales. Such local scale factors might have a strong impact on biotic interactions, which are especially relevant for determining functional diversity (see also de Bello et al., 2013).

The traits selected in our study capture only one of the axes of plant strategies, namely the leaf economics spectrum (Wright et al., 2004). We did not evaluate other dimensions of trait variation which encompass aspects of reproduction, dispersal and competition (Westoby, 1998; Díaz et al., 2016; Carmona et al., 2021). For example, filtering through temperature might primarily act upon growth-related traits, while disturbance might additionally select for species with small, but highly numerous seeds (Grime, 1977; Douma et al., 2012). Thus, the predictions for elevational trait patterns resulting from different mechanisms driving species richness might be further expanded with regard to different groups of traits.

Even though several mechanisms might predict the observed elevational species richness pattern on Tenerife, the responses of leaf traits to elevation only supported the importance of filtering through temperature and disturbance. Thus, the functional trait approach enabled us to distinguish between proximate (correlational) and more ultimate (mechanistic) relationships between species richness and environmental variables. Our hypotheses-driven framework builds on recent studies which have used the responses of functional traits to environmental gradients to investigate community assembly (Götzenberger et al., 2012; Jiang et al., 2018; Scherrer et al., 2019). While most studies so far have focused on using phylogenetic and multitrait functional diversity (Dainese et al., 2015) and/or distinguishing between random and non-random assembly processes (Scherrer et al., 2019), our approach also includes single trait metrics and multiple abiotic drivers. It can be transferred to other systems and gradients, and it can also help to further understand how species richness will be affected through global change, specifically through climate change and increasing impact by human-induced disturbance.

AUTHOR CONTRIBUTIONS

Amanda Ratier Backes, Sylvia Haider and Christine Römermann conceived the ideas; Amanda Ratier Backes conducted the fieldwork

and collected the data with help from Sylvia Haider, Stefan Trogisch, José Ramón Arévalo and Miguel Antonio Padrón-Mederos; Amanda Ratier Backes analyzed the data with assistance from Sylvia Haider and Petr Keil. Amanda Ratier Backes led the writing with important contributions from Sylvia Haider, Christine Römermann, Jake M. Alexander and Petr Keil. All authors revised several drafts of the manuscript, and approved the final version.

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DATA AVAILABILITY STATEMENT

The plot level data used in the analyses of this manuscript are available at Zenodo: <https://doi.org/10.5281/zenodo.7473130>.

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SUPPORTING INFORMATION

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

Appendix S1. Vegetation changes along the elevational gradient.

Appendix S2. Data compilation of abiotic factors.

Appendix S3. Leaf trait sampling and analyses.



Appendix S4. Double permutation test for community-weighted means (CWM) along elevation.

Appendix S5. Species richness in response to abiotic factors.

Appendix S6. Elevational changes of community-weighted means and functional diversity excluding *Pinus canariensis*.

Appendix S7. Elevational changes of community-weighted means and functional diversity for all species (native and non-native) and only native species.

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