Plant taxonomic and functional diversity along elevational gradients and their abiotic drivers

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“Observation of individual parts of trees or grass is by no means to be considered plant geography; rather plant geography traces the connections and relations by which all plants are bound together among themselves, designates in what lands they are found, in what atmospheric conditions they live [...].”

Alexander von Humboldt, *Florae Fribergensis Specimen* (1793);
translated by Hartshorne, 1958, p. 100

Contents

SUMMARY

Mountain ecosystems are unique hotspots of biodiversity which provide important ecosystem functions and services. They are also valuable study systems which comprise several environmental gradients, e.g., of climate, soil and area, and distinct vegetation types over short geographical distances. These environmental factors have been suggested as drivers of plant species diversity and the ecological strategies of the plant communities along elevational gradients. Anthropogenic disturbances, such as mountain roads, and non-native species, are additional factors which can cause changes in natural communities. Despite the long history of studies on vegetation changes along elevational gradients, the patterns and abiotic drivers of plant diversity are still debated.

In this thesis, I present three studies encompassing changes in species richness, functional composition and functional diversity, as well as abiotic drivers along the steep elevational gradient on Tenerife, Canary Islands. I have performed vegetation surveys in over 100 paired plots of 2 m x 50 m, along three mountain roads ranging from the coast to the crater of Teide at approximately 2300 m a.s.l. Each pair of plots consisted of one plot along the roadside and one plot starting 50 m away from the road. I installed soil temperature loggers and took soil samples in every plot. I collected leaf samples of the majority of species observed in the plots (189 out of ca. 270 species) and additional 664 leaf samples from eleven herbaceous species for the analysis of intraspecific trait variability. Leaf functional traits related to plant growth strategies were measured and used to assess changes at the individual, population and community levels in the three following studies:

(1) Here I investigated elevational changes of soil chemical properties, and the relative importance of temperature, disturbance and soil in shaping plant species richness, community trait means and functional diversity of leaf traits. Most of the analyzed chemical soil properties varied as expected along the elevational gradient, indicating better soil quality at lower elevations. Temperature and road disturbance had a positive effect on species richness, while temperature and soil chemical properties favored communities with a more acquisitive strategy. The overall results emphasize the importance of including data from local environmental conditions for climate, disturbance and fine-scale soil conditions in order to better understand biodiversity patterns.

(2) In the second study, I aimed to disentangle the main mechanisms underlying species richness patterns along elevational gradients using functional traits. Even though several mechanisms (related to climate, available land surface area and disturbance) might predict the observed elevational species richness pattern on Tenerife, the use of mechanism-specific expectations about the responses of leaf traits to elevation can allow to better evaluate the effect of each mechanism. Community means of most traits indicated shifts from acquisitive to conservative growth strategies, and functional diversity decreased along the elevational gradient, supporting the effect of filtering by temperature. The expected effect of disturbance on growth strategies was supported by the fact that roadside communities were overall more acquisitive than less disturbed communities away from the road.

(3) In the final study, I compared the intraspecific trait variability of native and non-native herbaceous species along the elevational gradient. Additionally, I analyzed the effect of elevation on within-population trait variability. Surprisingly, non-native species were overall less variable than native species. With increasing elevation, individuals from native species followed more conservative trait strategies, while non-native species showed almost no response to elevation. In contrast, within-population trait variability of non-native species decreased with increasing elevation for some traits, indicating that environmental filtering selects for intermediate trait values in non-native species that meet the requirements of various conditions.

The research work presented here contributes to the current understanding of the role of temperature, disturbance and soil properties in shaping the diversity and ecological strategy of communities and non-native species along elevational gradients. Such knowledge is important in order to better understand how the novel communities and ecosystems are responding to global change.

ZUSAMMENFASSUNG

Bergökosysteme sind einzigartige Hotspots der Biodiversität, die wichtige Ökosystemfunktionen und -leistungen erbringen. Bergökosysteme sind außerdem wertvolle Forschungsorte, die mehrere Umweltgradienten in Bezug auf Klima, Boden und verfügbarer Oberfläche repräsentieren, sowie unterschiedliche Vegetationstypen über kurze geografische Distanz beheimaten. Diese Umweltfaktoren werden als Treiber der Pflanzenartenvielfalt und der ökologischen Strategien der Pflanzengemeinschaften entlang von Höhengradienten angesehen. Anthropogene Störungen wie Bergstraßen und nichtheimische Arten sind weitere Faktoren, die zu Veränderungen der natürlichen Pflanzengemeinschaften führen können. Trotz der langen Forschungsgeschichte zu Vegetationsveränderungen entlang von Höhengradienten, werden die der Pflanzenvielfalt zugrunde liegenden Muster und deren abiotische Treiber weiterhin diskutiert.

In dieser Arbeit konzentriere ich mich auf drei Studien welche die Veränderungen des Pflanzenartenreichtums, der funktionellen Zusammensetzung und der funktionellen Diversität sowie der abiotischen Treiber entlang eines steilen Höhengradienten auf der Kanarischen Insel Teneriffa umfassen. Ich habe Vegetationsaufnahmen in über 100 Parzellen mit einer Größe von 2 m x 50 m entlang von drei Bergstraßen durchgeführt, die von der Küste bis zum Krater des Teide auf etwa 2300 m Meereshöhe reichten. An jedem Standort wurden Parzellen am Straßenrand und 50 m von der Straße entfernt vermessen. Ich installierte Bodentemperaturlogger, entnahm Bodenproben in jeder Parzelle, und sammelte Blattproben der Mehrheit der Arten, die in den Parzellen beobachtet wurden (189 von ca. 270 Arten). Weitere 664 Blattproben wurden von elf krautigen Arten für die Analyse der intraspezifischen Merkmalsvariabilität entnommen. Funktionelle Merkmale der Blätter in Relation zur Pflanzenwachstumsstrategie wurden bemessen und genutzt um Veränderungen auf Individuums-, Populations- und Communityebene in folgenden Studien zu beurteilen:

Im der ersten Studie untersuchte ich die chemischen Bodeneigenschaften auf Veränderungen entlang des Höhengradienten und die relative Bedeutung von Temperatur, Störungen und Boden bei der Gestaltung des Pflanzenartenreichtums, der Mittel der Communitytraits und der funktionellen Vielfalt von Blattmerkmalen. Die meisten der analysierten chemischen Bodeneigenschaften variierten wie erwartet entlang des Höhengradienten, was auf eine bessere Bodenqualität in niedrigeren Höhen hindeutet. Temperatur und Straßenstörungen wirkten sich positiv auf den Artenreichtum aus, während Temperatur und chemische Eigenschaften des Bodens Gemeinschaften mit einer akquisitorischen Wachstumsstrategie begünstigten. Summarisch betrachtet heben die Resultate die Wichtigkeit der Inkludierung von lokalen Daten hervor.

In der zweiten Studie stelle ich einen funktionalen Ansatz vor, um jene Hauptmechanismen zu entschlüsseln welche den Mustern des Artenreichtums entlang des Höhengradienten zugrunde liegen. Doch auch wenn diverse Mechanismen wie Klima, verfügbare Oberfläche und Störung, Aufschlüsse über die beobachteten Muster des Pflanzenartenreichtums entlang des Höhengradienten auf Teneriffa prognostizieren können, so erlaubt die Anwendung von Mechanismus-spezifischen Erwartungen und Reaktionen der Blattmerkmale in verschiedenen Höhenlagen eine bessere Evaluation eines jeden Effekts der Mechanismen. Die Mittel der Communitytraits der meisten Merkmale zeigten Verschiebungen von einer akquisitven hin zu einer eher konservativen Wachstumsstrategie auf. Die funktionelle Vielfalt hingegen nahm entlang des Höhengradienten ab. Die erwartete Auswirkung von Störungen auf die Wachstumsstrategien wurde ebenfalls durch die Tatsache gestützt, dass Communities am Straßenrand insgesamt akquisitiver waren als weniger gestörte Communities abseits der Straße.

In der dritten Studie vergleiche ich die intraspezifische Merkmalsvariabilität einheimischer und nicht einheimischer krautiger Arten entlang des Höhengradienten. Des Weiteren analysierte ich die Auswirkung der Höhenlage auf die Merkmalsvariabilität innerhalb einer Population. Überraschenderweise waren nicht einheimische Arten insgesamt weniger variabel als einheimische Arten. Mit zunehmender Höhe verfolgten Individuen einheimischer Arten konservativere Merkmalsstrategien, während nichtheimische Arten fast keine Reaktion auf die Höhe zeigten. Im Gegensatz dazu nahm die Merkmalsvariabilität innerhalb der Population von nicht einheimischen Arten mit zunehmender Höhe für einige Merkmale ab, was darauf hinweist, dass Environmental Filtering bei nicht einheimischen Arten jene selektiert, deren Eigenschaften die Anforderungen verschiedener Bedingungen erfüllen.

Die hier präsentierte Arbeit trägt zum gegenwärtigen Verständnis über die Rolle der Temperatur, Störung und Bodeneigenschaften und ihren Einfluss auf die Diversität und ökologische Strategien von Communities und nichtheimische Arten entlang des Höhengradienten, bei. Dieses Wissen ist wichtig um ein besseres Verständnis darüber zu erreichen, wie Novel-Communities und Ökosysteme auf den globalen Wandel reagieren.

CHAPTER 1

General introduction

Biodiversity and mountain ecosystems

Mountain ecosystems are unique hotspots of biodiversity and endemism, accommodating at least half of all terrestrial vascular plant species (Barthlott and al., 1996; Körner, 2007; Irl et al., 2015). High endemism and diversity in mountains are likely due to high levels of ecological and allopatric speciation facilitated by environmental heterogeneity and biogeographic isolation (Irl et al., 2015; Steinbauer et al., 2016; Noroozi et al., 2018). The steep changes in environmental conditions over short distances also allow for the existence of a variety of distinct vegetation types in close proximity, the so-called vegetation belts (Körner, 2003). Mountains are furthermore excellent study systems that serve as natural experiments as they comprise several environmental gradients, e.g., of climate, soil and area (Lomolino, 2001; Körner, 2007; Sanders and Rahbek, 2012). Their importance is further attributed to ecosystem functions and services such as freshwater storage and provision (Viviroli et al., 2003).

The environmental and biotic variation within mountain ecosystems piqued the interest of European naturalists in the 19th century, who started to document predictable changes in composition of the fauna and flora of mountains (von Humboldt, 1849; Bonnier and Flahault, 1878; Wallace, 1878; Lomolino, 2001). Humboldt’s observations in South America culminated with the publication of ‘Naturgemälde’, an annotated map showing the vegetation zonation along elevational gradients around the world (von Humboldt, 1849). During his excursion to Chimborazo and other mountains, including a stop on the volcanic island of Tenerife, he became aware of the close link between changes in vegetation and environmental conditions as he observed the flora and took physical measurements at different elevations (Pausas and Bond, 2019). Since then, diversity patterns along elevational gradients have been investigated world-wide through inventories and standardized sampling strategies (e.g., Haider et al., 2021; Lee et al., 2013; Merriam, 1890; Odland & Birks, 1999; Ohdo & Takahashi, 2020; Whittaker, 1960).

The underlying environmental factors that change along elevational gradients present different patterns themselves. For example, temperature decreases predictably with elevation by approximately 0.6 °C for each 100 m increase in elevation, with some variation due to latitude and weather patterns (Barry, 2008). Other factors, such as precipitation are more difficult to generalize. The most common precipitation pattern is one of increasing precipitation with elevation, but this can vary greatly in different climatic zones (McCain and Grytnes, 2010). Likewise, soil characteristics depend on the local geological history, origin of bedrock material and interacting climatic conditions (Köhler et al. 2006, Dinter et al. 2020). As these factors shaping soil characteristics (e.g., precipitation) do not necessarily change in a predictable way with elevation (Körner, 2007), also the changes of chemical soil properties might be complex (Grieve et al., 1990; Köhler et al., 2006). Available land area usually decreases with elevation, but it can also be lowest at mid-elevation on flat-topped mountains (McCain and Grytnes, 2010). Finally, there are additional environmental changes, such as fire regime and land-use history, which reflect local peculiarities and are impossible to generalize across mountain regions (Spehn et al., 2010).

Drivers of species richness patterns along elevational gradients and a functional-trait approach

Species richness patterns along elevational gradients were first assumed to simply mirror the latitudinal decrease in species richness (Rosenzweig, 2010). Nowadays, a variety of patterns of plant species richness have been studied, and the most commonly observed patterns are a hump-shaped pattern peaking at intermediate elevations and above this peak a linear decrease in diversity with increasing elevation (McCain and Grytnes, 2010; Sanders and Rahbek, 2012). Several theories have been proposed to explain these diversity patterns (Currie, 1991; Grytnes, 2003; Sanders and Rahbek, 2012; Vetaas et al., 2019), the most prominent of which consider changes in climate (Irl et al., 2015; Peters et al., 2016), area (Bachman et al., 2004; Romdal and Grytnes, 2007) and disturbance (Bunn et al., 2010). Even though support for those different factors has been found, disentangling their actual role is challenging, as the factors interact and are correlated with each other (e.g., disturbance is more prevalent at lower elevations, but also temperature decreases with increasing elevation). Collinearity among the different potential drivers results in similar predictions for the richness patterns from different theories, making it hard to test them (Nogués-Bravo et al., 2008; Vetaas, 2021). For example, in a mountain area where temperature and disturbance decrease with elevation both mechanisms related to temperature and disturbance would predict a decrease in species richness along the elevational gradient (McCain and Grytnes, 2010). Therefore, disentangling and quantifying their relative effect remains a central question in biogeography.

Plant functional traits are characteristics that affect plant performance (in terms of growth, survival and reproduction) at the individual level (Violle et al., 2007). They change along environmental gradients according to ecological strategies of resource acquisition and investment, which have been investigated from the individual up to the community level (Read et al., 2014; Reich, 2014; Bruelheide et al., 2018). For plants, these trait trade-offs or coordinations between traits are summarized in the leaf economics spectrum (LES) (Wright et al., 2004; Reich, 2014; Díaz et al., 2016). At one end of the spectrum, more conservative, slow growing species or individuals acquire nutrients slowly and invest in durable leaves, while at the other end of the spectrum more acquisitive, fast-growing plants acquire nutrients fast and produce leaves that are not as durable (Reich, 2014). High-elevation habitats are known to pose constraints on plant growth and survival via limited growing season and low temperatures, which cause lower photosynthetic rates and frost damage to tissues (Körner, 2003). Communities in these harsh environments tend to follow a more conservative strategy, reflected in traits that provide protection or a way to avoid damage (Bai et al., 2015; Schellenberger Costa et al., 2017; Llerena-Zambrano et al., 2021). At low elevations, less stressful conditions (milder climatic conditions, better soil conditions) tend to favor species with acquisitive strategies, which can quickly take up resources. Other environmental filters, such as disturbance and soil properties also alter the distribution of resources, affecting the characteristics of species which are able to survive in a particular place (Ordoñez et al., 2009; Midolo et al., 2021). Disturbance also is thought to favor acquisitive strategies by increasing environmental heterogeneity, empty space and other resources. Changes in soil conditions such as an increase in soil nutrients should favor acquisitive strategies (Ordoñez et al., 2009; Martinez-Almoyna et al., 2020).

Functional traits perspectives developed so far have focused on phylogenetic or functional diversity in order to investigate aspects of community assembly (Bello et al., 2017; López-Angulo et al., 2020). They also have shown that non-random processes can be disentangled from random ones by looking at patterns of functional diversity change with area or other environmental gradients (Dainese et al. 2015, Schrader et al. 2021). Functional traits are, therefore, a useful and promising tool to investigate the drivers behind spatial variation of diversity. This thesis expands the scope of these studies by looking not only at functional diversity changes across communities, but also including so-far neglected (but see Jiang et al. 2018) community mean traits of single traits in order to investigate the mechanisms behind species richness patterns.

Vulnerability of mountains to global change

Mountain ecosystems are particularly vulnerable to global change drivers such as climate change, biological invasions, anthropogenic disturbances and their interactions (Chakraborty, 2021). High-elevation areas are warming at an above-average rate (Auer et al., 2007; Gobiet et al., 2014), and the effects are already observed as an upslope migration of species towards cooler regions (Chen et al., 2011; Lenoir and Svenning, 2015; Chakraborty, 2021). Range shifts, however, are not limited to the high elevations, and are expected to increase species extinction risks along the whole elevation gradient, as species fail to track climatic shifts and encounter constraints in the available area due to topography and anthropogenic pressures (Lenoir and Svenning, 2015; Elsen et al., 2020).

Even though high mountains areas have remained relatively uninvaded (Pauchard et al., 2009; McDougall et al., 2011), non-native species have been frequently observed in mountain areas, as more species introduced in the lowlands make their way to higher elevations (Pauchard et al., 2009; Pyšek et al., 2011). Anthropogenic disturbances in remote mountain areas in the form of building of infrastructure, such as roads, and tourism have become more prevalent since the last century (Chakraborty, 2021). Road construction, traffic and maintenance activities, which include biomass removal, can affect the richness and composition of the roadside communities in multiple ways (Forman and Alexander, 1998; Catford et al., 2012; Milbau et al., 2013; Haider et al., 2018). For example, trampling and traffic on the road verges can cause soil compaction and have a negative effect on soil nutrient availability for plants (Johnston and Johnston, 2004; Makineci et al., 2007; Yang et al., 2016; Deljouei et al., 2018). Non-native species might also take advantage of the environmental heterogeneity created by road-related disturbance (increasing resources such as space and light) in order to establish and expand their elevational range (Johnston and Johnston, 2004; Jauni et al., 2015). Mountain roads have been shown to be common corridors that aid the spread of non-native species not only upwards (Alexander et al., 2011, 2016; Dainese et al., 2017), but also in a second direction of spread from the disturbed habitats on roadsides towards less disturbed habitats away from roads (McDougall et al., 2018). Even though disturbance usually decreases with increasing distance from the road, non-native species which are shade and moisture tolerant manage to invade natural communities (McDougall et al., 2018).

Non-native species spread into mountain regions and functional trait variability

The decrease of non-native species with elevation (Haider et al., 2018) can be explained by the effect of ecological filtering acting upon the lowland species pool (Alexander et al., 2011; Barni et al., 2012; Marini et al., 2013). Among introduced species, stress tolerance is not a typical characteristic. Hence, with increasing elevation and harshening of climatic conditions, only a limited subset consisting of climatic generalist species, with high dispersal ability or high plasticity manages to persist (Alexander et al., 2011; Seipel et al., 2012; Marini et al., 2013). Propagule limitation and biotic resistance from resident communities have also been suggested to prevent plant invasions into remote mountain areas (Zefferman et al., 2015). However, increasing human influence and associated pressures (propagule pressure and disturbance) are supposed to alleviate these limitations, and further support the spread of non-native species along elevational gradients (Marini et al., 2013).

A key factor allowing non-native species to successfully establish and spread into new regions is their ability to succeed under a range of novel environmental conditions, which might be enabled by high variability in functional traits exhibited within species (Davidson et al., 2011; Matesanz et al., 2012; Colautti and Barrett, 2013). The invasion capacity of non-native species along elevational gradients has been linked to certain traits (small seeds, acquisitive strategies; e.g. Leishman et al., 2007) and to high trait variability within the species (Davidson et al., 2011; Westerband et al., 2021). Intraspecific trait variability can be achieved via high phenotypic plasticity of the individuals (Ansari and Daehler, 2010), and genetic adaption to local environmental conditions (Monty and Mahy, 2009; Haider et al., 2012). Independently of the mechanism behind it, native species might present a certain level of intraspecific trait variability as a result from a long history of adaptation to the different environmental conditions across their elevational range. Differently, high levels of intraspecific variability on non-native species can result from the multiple introductions from various sources and can be useful for a species' spread to harsher high-elevation conditions. However, as of yet, only a few studies have explicitly compared the intraspecific trait variability of native and non-native species along environmental gradients (but see Alexander et al., 2009; Davidson et al., 2011).

Thesis scope and chapter summaries

In this dissertation, I have investigated elevational patterns of plant species richness, functional traits at the community, individual and population levels, as well as associated environmental gradients of soil characteristics, disturbance, temperature and precipitation along the slopes of the volcano Teide in Tenerife, Canary Islands (Fig. 1). To do so, I have performed vegetation surveys in 111 plots of a size of 2 m x 50 m along three mountain roads going from the coast to the crater of Teide at approximately 2300 m a.s.l. Plots along the roadside and 50 m away from the road were surveyed at each location. I installed soil temperature loggers, took soil samples, and collected leaf samples of the majority of species. Additional 664 leaf samples were taken from 11 herbaceous species for intraspecific trait variability analysis. Leaf traits were analyzed in the laboratory within the context of a larger sampling scheme, which included samples from 11 mountain regions from South and North America, Australia, Europe and Asia.

In chapter 2 "E*ffects of soil properties, temperature and disturbance on diversity and functional composition of plant communities along a steep elevational gradient on Tenerife"*, I asked how soil properties vary along elevation and how these properties, as well as temperature and disturbance, influence plant species richness, community trait means and functional diversity of leaf traits. Soil characteristics and their association to functional traits were analyzed in the context of the bachelor thesis of Larissa Frey, who I co-supervised. The chapter expanded on the thesis by integrating multiple other abiotic factors and using a Bayesian approach to assess the effects of the different abiotic conditions on vegetation properties. We hypothesized that lower elevation sites have better soil conditions for plant growth, and that these should have a positive effect on species richness, acquisitive trait strategies and functional diversity. Temperature and disturbance were expected to have a similar influence, though it is hard to predict which of the abiotic factors is more important.

In chapter 3 "*Mechanisms behind elevational plant species richness patterns revealed by a trait-based approach*", I proposed that functional traits can be used as a tool to distinguish between different potential mechanisms behind patterns of species richness along elevational gradients. In order to do so, I formulated sets of expectations for elevational patterns of leaf functional traits related to plant growth strategies according to three different mechanisms (related to climate, area and disturbance). The use of two different metrics of community functional composition, namely community-weighted mean and functional diversity, and the distinction between roadside and more natural vegetation plots allowed me to distinguish the sets of predictions according to each mechanism. The expectations were then compared to the observed patterns.

In chapter 4 "*Contrasting patterns of intraspecific trait variability in native and non-native plant species along an elevational gradient on Tenerife, Canary Islands*", I asked whether high intraspecific trait variability is a mechanism that allows non-native species to spread along elevation gradients. I hypothesized that non-native plant species with high intraspecific variation in functional traits might have spread to a broader elevational range than those with less intraspecific variation. The second chapter was built upon the master thesis of Paul Kühn, who I co-supervised. In this chapter, we compared intraspecific-trait variability of five non-native herbaceous species and six native species along their elevational ranges. We investigated whether intraspecific trait variability supports the spread of non-native species along the elevation gradient, and whether non-native species overall possess a higher capacity of functional trait adjustment.

In chapter 5, I synthesize the key findings resulting from my thesis. I discuss the links between the results from the individual chapters, their broader applicability to other mountain systems in the world, the limitations of my approach, and specific needs for future studies.

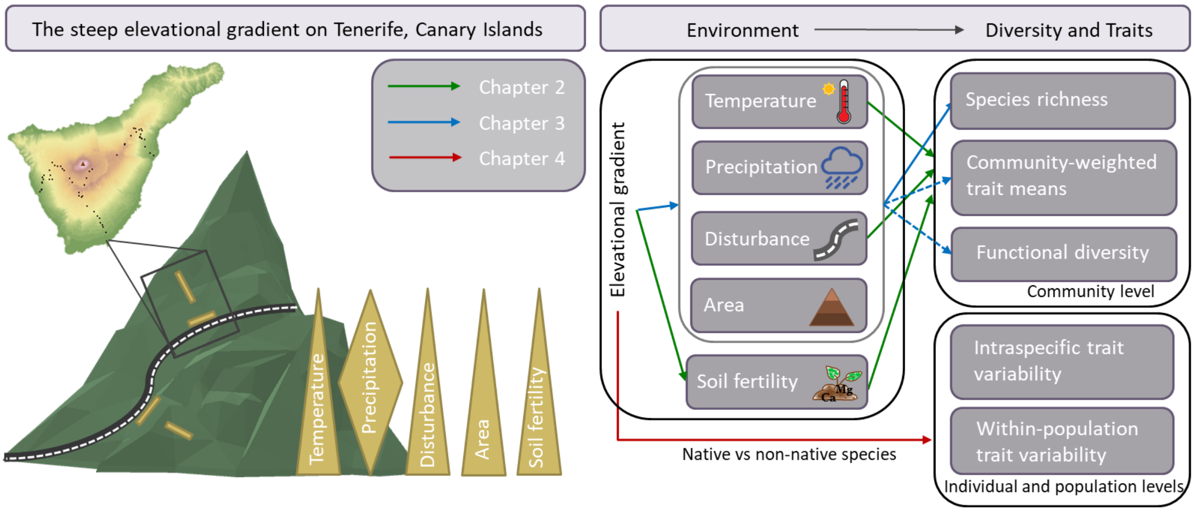

Figure 1. On the left side, sampling sites (56 black points) along three mountain roads, from the coast until the volcanic caldera of Las Cañadas on Tenerife; T-transects at each sampling site consisting of two perpendicular plots; and expected changes of environmental variables with elevation. On the right side, overview of predictors and responses of each chapter (linked by colored arrows). The dashed arrow means that these relationships were not directly tested (see details in chapter 3). Temperature,

precipitation, disturbance, area and soil fertility are the environmental variables summarized by the elevational gradient. Species richness, community-weighted trait means and functional diversity were analyzed at the community level; while intraspecific trait variability and within-population trait variability were analyzed at the individual and population levels, respectively.

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CHAPTER 2

Effects of soil properties, temperature and disturbance on diversity and functional composition of plant communities along a steep elevational gradient on Tenerife

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Effects of Soil Properties, Temperature and Disturbance on Diversity and Functional Composition of Plant Communities Along a Steep Elevational Gradient on Tenerife

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Elevational variation of vegetation has been of interest for centuries, and a prominent example for such pronounced vegetation changes can be found along the steep elevational gradient on Tenerife, Canary Islands, 200 km off the West-African cost. The 3,718-m ascent to the peak of the island volcano, Teide, offers a unique opportunity to investigate associated changes in vegetation. However, elevation is not a directly acting factor, but represents several natural environmental gradients. While the elevational variation of temperature is globally rather uniform and temperature effects on plant communities are well understood, much less is known about the region-specific elevational change of chemical soil properties and their impact on plant communities along elevational gradients. Because human interference takes place even at high-elevation areas, we considered human-induced disturbance as important third factor acting upon plant community assemblages. In our study, we compared the effects of soil properties, temperature and disturbance on species richness, functional identity and functional diversity of plant communities along the elevational gradient on Tenerife. We used pairs of study plots: directly adjacent to a road and in natural vegetation close by. In each plot, we did vegetation relevées, took soil samples, and installed temperature loggers. Additionally, we collected leaf samples to measure leaf functional traits of 80% of the recorded species. With increasing elevation, soil cation concentrations, cation exchange capacity (CEC) and pH decreased significantly, while the soil carbon to phosphorus ratio slightly peaked at mid-elevations. Temperature had the strongest effects, increasing species richness and favoring communities with fast resource acquisition. Species richness was higher at road verges, indicating the positive effect of reduced competition and artificially generated heterogeneity. However, we did not detect road effects on plant functional characteristics. Vice versa, we did not find soil effects on species richness, but increased concentrations of soil cations favored acquisitive communities. Surprisingly, we could not reveal any influence on community functional diversity. The importance of temperature aligns with findings from large-scale biogeographic studies. However, our results also emphasize that it is necessary to consider the effects of local abiotic drivers, like soil properties and disturbance, to understand variation in plant communities.

Keywords: species richness, mountains, climate gradient, altitudinal gradient, chemical soil properties, road disturbance, environmental filtering, plant functional traits

INTRODUCTION

Plant community changes and plant species distributions along elevational gradients are a century-old topic in biogeography (e.g., von Humboldt, 1849; Whittaker and Niering, 1965). A prominent example of a pronounced vegetation sequence described by Alexander von Humboldt (von Humboldt and Bonpland, 1831) occurs along the steep elevational gradient on the island of Tenerife, Canary Islands, 200 km west of the African coast. Along the slopes of Mount Teide, vegetation belts comprise coastal and thermo-sclerophyllous scrub at low elevations, forests of Canary Island pine (*Pinus canariensis* C. Sm.) at mid-elevations and alpine scrub within the high-elevation volcanic caldera (Fernández-Palacios, 1992; **Figure 1**). In addition to such elevational variation in taxonomic composition, elevational patterns of plant species richness were observed worldwide (e.g., McCain and Grytnes, 2010; Haider et al., 2018). More recently, studies also addressed how community functional identity and functional diversity vary along elevational gradients (Schellenberger Costa et al., 2017; Midolo et al., 2021).

Elevation *per se* is not directly acting upon vegetation, but represents a number of environmental conditions (Körner, 2007). Two major environmental components changing with elevation and relevant for shaping plant communities are temperature and chemical soil properties. Temperature decreases with increasing elevation in mountains worldwide and adiabatic lapse rates have been intensely studied (Barry, 2008). In contrast, elevational changes of chemical soil properties are less frequently studied, region-specific and depend on multiple factors, such as bedrock, soil age and climatic conditions (Köhler et al., 2006; Dinter et al., 2020). These factors may affect soil acidity as well as biochemical cycles which can in turn modify concentrations of plant available nutrients (Grieve et al., 1990; Köhler et al., 2006; Unger et al., 2012; Tan and Wang, 2016). Since the environmental conditions shaping chemical soil properties (e.g., precipitation) do not necessarily change linearly with elevation (Körner, 2007), also the change of chemical soil properties might not be linearly correlated with elevation.

Soil properties are often modified by human actions (Weil and Brady, 2016). In mountains, especially the building of road infrastructure, road maintenance activities and disturbance through vehicle traffic and trampling can cause severe physical and chemical changes of road verge soil (Forman and Alexander, 1998; Johnston and Johnston, 2004). This might include higher concentrations of nutrients and less acidic soil pH, for example as a consequence of road dust, and moister conditions from road drainage (Forman and Alexander, 1998; Müllerová et al., 2011). Vehicles accessing the road verge may also lead to higher bulk density of the soil, causing lower soil permeability and thus reduced water and nutrient flows (Johnston and Johnston, 2004; Makineci et al., 2007; Deljouei et al., 2018; Yang et al., 2018). Therefore, even though soil nutrient concentrations might not differ between road verges and more natural vegetation away from the road, nutrient availability for plants may be lower in close proximity to roads as the roots may experience difficulties in penetrating hard soil or oxygen stress due to less aeration (Stirzaker et al., 1996; Makineci et al., 2007).

Both warmer temperatures and better soil conditions (more nutrients and neutral pH) have been found to increase the number of species in plant communities (Laughlin et al., 2007; Liu et al., 2020). Road disturbance should reduce competition among plants, and thus also enable a larger number of species to co-exist (Catford et al., 2012; Milbau et al., 2013; Haider et al., 2018). Moreover, temperature and soil conditions have been recognized to modify the functional characteristics of plant communities (Schellenberger Costa et al., 2017). So-called plant functional traits link morphological and physiological features to a plants' performance (Violle et al., 2007). Functional traits measured at the individual level can be translated to the level of species assemblages via abundance-weighted community trait means and community functional diversity. Trade-offs between traits associated with resource acquisition vs. resource investment define opposing ecological strategies observed in plant species and communities. Hence, functional traits are suitable proxies to describe the competitive ability of species and the competition intensity within a community, respectively. Acquisitive strategies are characterized by fast nutrient uptake and fast growth of short-lived leaves, and therefore characteristic for species with high competitive ability, represented e.g., by high values for specific leaf area (SLA) and leaf nitrogen concentration. Vice versa, conservative strategies are related to slow nutrient uptake and slow growth of highly durable leaves, and therefore characteristic for species with high competitive ability, represented e.g., by high values for leaf dry matter content (LDMC) and high amounts of carbon in the leaves (Wright et al., 2004; Díaz et al., 2016).

Many studies have shown community leaf traits to shift from acquisitive to conservative strategies with increasing harshness of environmental conditions, such as temperature (Moles et al., 2014; Rosbakh et al., 2015; Bruelheide et al., 2018). However, fewer studies investigated functional trait responses at the community level to varying soil conditions, especially along elevational gradients (but see Gong et al., 2020; Midolo et al., 2021). Paralleling the effect of benign climatic conditions, better soil conditions with higher nutrient concentrations and intermediate pH should lead to more acquisitive plant communities, e.g., with higher SLA (Molina-Venegas et al., 2018)

FIGURE 1 | The elevational gradient sampled in Tenerife starts with **(A)** coastal vegetation and thermo-sclerophyllous scrub, followed by **(B)** forests of Canary Island pine (*Pinus canariensis* C. Sm.), and ending at the high elevation plateau of Las Cañadas with **(C)** high mountain scrub.

and higher concentrations of leaf nitrogen (Schellenberger Costa et al., 2017). In contrast, it was found that plant communities on nutrient-poor soil had lower leaf nutrient concentrations as well as lower SLA (Wright et al., 2017). Additionally, by increasing the availability of resources (space, light, nutrients), road disturbance also favors species and communities with a more acquisitive strategy (Forman and Alexander, 1998). An increase in SLA and a decrease of LDMC were observed at sites with experimental physical disturbance (Bernhardt-Römermann et al., 2011), and an increase in leaf nitrogen was found at high disturbance intensity (Carreño-Rocabado et al., 2012).

Environmental factors like temperature and chemical soil properties do not only affect community trait means, but also community functional diversity. Environmental filtering is assumed to constrain species traits to certain values (Keddy, 1992), resulting in a decrease of functional diversity under harsh environmental conditions, e.g., in areas where the climate is characterized by low temperatures (Jiang et al., 2018) or where the soil is very poor in nutrients or has extreme pH values. Studies of functional diversity along soil nutrient availability are scarce (but see Schellenberger Costa et al., 2017; López-Angulo et al., 2020; Midolo et al., 2021). Another important assembly mechanism driving the functional diversity of plant communities is the concept of limiting similarity (Macarthur and Levins, 1967; Mouillot et al., 2007). In this case, functional differences between co-existing species reduce competition, resulting in communities with high functional diversity (Mouillot et al., 2007). Another factor that comes into play is road disturbance. The removal of plant biomass and consequently of dominant competitors as part of road maintenance will allow the entry of more individuals into the community as competition for space, light and nutrients decreases. With the addition of more individuals, functional diversity should increase due to a pure sampling effect (Mayfield et al., 2010).

In our study, we investigated how environmental conditions modify plant community characteristics along a gradient on Tenerife spanning more than 2,300 m in elevation. Thereby, we asked: (1) How do soil properties change along the elevational gradient and how do soil properties differ between road verges and away-from road locations? (2) Which environmental factors (temperature, soil properties, and road disturbance) have the strongest effects on species richness, functional identity, and functional diversity of plant communities?

MATERIALS AND METHODS

Study Area

Our study was carried out on Tenerife, the largest of the Canary Islands, situated in the mid-Atlantic between 27° 38′ and 29° 25′ off the West-African coast. The highest point on the island is the summit of the volcano Mount Teide at 3,718 m a.s.l. The crossover of different weather system causes the humid air masses of the north-eastern trade winds to remain on the northern slopes. Consequently, the southern slopes of Tenerife, where this study's elevational gradients are located, are characterized by an arid and warm climate (Fernández-Palacios, 1992). Temperature decreases along the elevational gradient with a lapse rate of approximately 0.5°C per 100 m (Morales Matos and Pérez González, 2000). Precipitation increases from approximately 100 mm per year at the coast to a maximum of approximately 500 mm at mid-elevations and moderately decreases again toward the summit, but with high variability due to the island's complex topography (Morales Matos and Pérez González, 2000; AEMET, 2012). This characteristic distribution of precipitation and temperature, the history of volcanic activity, and the specific topography of the island, lead to the formation of many different types of soil (Morales Matos and Pérez González, 2000).

Study Design

Data collection took place in April and May 2018. All data and samples were retrieved from the permanent plots which were established in 2008 following the design of the standardized mountain road survey of the Mountain Invasion Research Network (MIREN) (Bacaro et al., 2015; Haider et al., 2021). Thereby, three roads on the island's southern slopes were selected, spanning from the coast to the crater of Mt. Teide. By dividing the elevational range of each road into 19 equal portions, 20 sampling locations were chosen evenly over an ascent of approximately 2,350 m. At each sampling location, two plots with 2 m × 50 m each were established, one directly adjacent and with the long side parallel to the road (hereinafter roadside plot), and a second one perpendicular to the roadside plot, at 50–100 m away from the road (hereinafter distant plot). Steep topography and private property prevented sampling in some locations, resulting in a total of 111 plots.

Vegetation Relevées and Leaf Trait Sampling

In each plot, all vascular plant species were identified, and their cover was visually estimated and recorded via classes from 1 to 7 (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%). For the leaf trait sampling, we primarily aimed to collect the most abundant and most frequent species, both native and non-native species, and all life forms (grasses, forbs, shrubs, and trees). For each species, we collected 10–50 leaves from one to three typical populations, so that the sampling covered the species' elevational distribution. Later, trait values of all populations of a species were averaged to get a single value for each trait of each species. With this approach, we obtained for each plot trait information of species making up at least 80% of the relative plot cover (except for five plots); an established threshold for a reliable characterization of the functional properties of a community (Pakeman and Quested, 2007). In total, 332 leaf samples for 189 species (out of 270 species recorded in the survey) were collected.

Leaf Trait Analysis

For a subset of the leaf samples, we conducted laboratory analyses of five traits associated with an acquisitive (SLA, leaf N, and leaf N:P ratio) and a conservative growth strategy (LDMC and leaf C:P ratio). In a second step, we used this subset of samples as "calibration samples" to predict the trait values for the remaining samples via the high-throughput method of near-infrared reflectance spectroscopy (NIRS) as described for example by Foley et al. (1998) and applied in previous projects (Kühn et al., 2021; see **Supplementary Material** for more details).

In the field, the calibration samples were kept in bags with a wet tissue to prevent water loss during the sampling day, then weighed and scanned with a flatbed scanner on the same day. Leaf area was calculated using WinFOLIA (Regent Instruments, Quebec, CA). The samples were subsequently dried for 72 h at 80°C in a drying oven and weighed again. LDMC was calculated as the ratio of leaf dry weight to leaf fresh weight, and SLA as the ratio of fresh leaf area to leaf dry weight (Kleyer et al., 2008; Pérez-Harguindeguy et al., 2013). The dry samples were milled into fine powder using a ball mill (MM 400, Retsch, Haan, DE). Following a nitric acid digestion and adding ammonium heptamolybdate and ascorbic acid, the concentration of leaf phosphorus was measured by visual assay with a Photometer SmartSpec^{TM} 3000 (BIO-RAD). The total carbon and nitrogen concentrations were measured via gas-chromatography with the Dumas method (Vario EL Cube, Elementar Analysensysteme, Langenselbold, DE). From these single element values, we calculated leaf N:P and leaf C:P ratio.

Species Richness, Community-Weighted Trait Means and Functional Diversity

Species richness was defined as the total number of species recorded per plot. Community-weighted trait means (CWMs) were calculated for each of the five leaf traits (SLA, LDMC, leaf N, leaf N:P ratio, leaf C:P ratio) and for each plot using the SYNCSA package (Debastiani and Pillar, 2012) in the R statistical environment (R Core Team, 2020):

$$\mathrm{CWM} = \sum_{i=1}^{N} p_i trait_i \tag{1}$$

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

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

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 cover 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. We included all five leaf traits in the calculation of Rao's Q (multi-trait functional diversity). The calculation of functional diversity was done with species trait values scaled to unit variance, in the FD package in R (Laliberté and Legendre, 2010). Elevational variation of CWMs, functional diversity (Rao's Q) and species richness and the effect of road proximity are shown in **Supplementary Figure 1** and **Supplementary Table 1**. See **Supplementary Table 2** for an overview of all the leaf trait, soil and temperature variables used in this study.

Soil Sampling and Soil Analysis

From three locations in each plot, we collected a bulked soil sample from the upper 10 cm of the mineral soil layer. The samples were sieved (<2 mm) and remaining, visible plant particles were removed. Soil pH was measured in 1 molar KCl. For gas-chromatographically measuring total soil carbon and nitrogen concentrations, fresh soil was dried for 72 h at 105°C and then milled to fine powder. To determine the concentrations of the base cations calcium, magnesium and potassium, fresh soil was percolated in a solution of 0.1 molar barium chloride. Afterward, the cation concentrations were measured by atomic absorption spectrometry (ContrAA 300 AAS, Analytik Jena, Jena, Germany). The concentration of hydrogen ions was measured by determining the pH of the percolates, and the cation exchange capacity (CEC) was calculated as the sum of ion equivalents of all measured exchangeable cations (Ca, K, Mg, and H). For the determination of bioavailable phosphorus, the soil samples were analyzed using the method proposed by Olsen (1954). Like for the leaf samples, the measurement of soil P was done photometrically after adding a molybdate reagent solution and an ascorbic acid solution. The ratios of N:P and of C:P were calculated.

Temperature Data

Near-surface soil temperature was measured using miniature loggers (HOBO 64K Pendant, with 0.53°C accuracy, Bourne, MA, United States). They were installed in the center of the roadside plot and 50 m away from it, at the start of the distant plot, at a depth of 3 cm below the soil surface. They were programmed to log at 1.5 h intervals from May 2018 until April 2019. Data quality control was done in R (R Core Team, 2020), and days with less than 13 measurements per day (out of 16) were excluded when calculating the daily averages, as well as months with less than 27 days with enough measurements. After data cleaning, daily and monthly averages and the bioclimatic variables Bio10 (mean temperature of the warmest quarter) and Bio11 (mean temperature of the coldest quarter) were calculated using the climvars package (Maclean and Gardner, 2021), which follows the definitions of WorldClim (Hijmans et al., 2005). By taking into account climate of different seasons and including the periods where temperature stress might be strongest for plant growth, survival and reproduction, these two bioclimatic variables are ecologically and physiologically relevant and are widely used in species distribution studies (Lembrechts et al., 2019). We did not choose to use annual means, for example, since they cover periods that have less influence on foliage. Temperature variation with elevation and proximity to roads is shown in **Supplementary Figure 2**.

Statistical Analysis

All statistical analyses were carried out in R version 4.1.0 (R Core Team, 2020). To get an overview about how the measured chemical soil properties are correlated, a principal component analysis (PCA) was performed (function "prcomp") and visualized with the R packages "FactoMineR" (Lê et al., 2008) and "factoextra" (Kassambara and Mundt, 2020).

To analyze elevational changes of chemical soil properties and the influence of road proximity, we used linear mixed-effects models (R package "lmerTest"; Kuznetsova et al., 2017). Models were fitted with each of the eight investigated soil variables as response, and elevation, proximity to roads (roadside or -distant plot) and their interaction as fixed effects. Sampling location nested in road identity was added as random factor. Elevation was scaled prior to analyses. Because the interaction term was never significant, a simplified model without the interaction was fitted. *P*-values were calculated from F-statistics of type III sum of squares with Satterthwaite approximation to estimate the denominator degrees of freedom. We visually checked, if model assumptions were met, and transformed the response variables if necessary. This was the case for soil N and soil Mg concentrations, soil C:P and N:P ratios (log-transformed) and for soil Ca and soil K concentration and CEC (square-root-transformed). Additionally, we fitted models with the same structure, but including the quadratic term of elevation, using its second-order polynomial. We compared the AIC (Akaike's Information Criterion) of linear and quadratic models and considered those with lower AIC as the better models. For soil pH, C:P ratio and K, the quadratic model had a lower AIC than the linear one.

To test and compare the effects of soil properties, temperature and road proximity, we used a multivariate generalized linear mixed model based on a Markov Chain Monte Carlo sampler ("MCMCglmm" function in the R package "MCMCglmm"; Hadfield, 2010). Response variables were the CWMs of SLA, LDMC, leaf N, leaf N:P, and leaf C:P, Rao's Q of these traits (multi-trait functional diversity) and species richness. All response variables were scaled and, if necessary, transformed prior to scaling. This was the case for SLA, leaf C:P ratio, Rao's Q, and species richness (log-transformed). As predictors we included temperature of the warmest and of the coldest quarter, proximity to roads (roadside or distant plot), and chemical soil properties, summarized by using the values of the first three axes of the PCA described above. We also permitted the interactions between road proximity and soil variables. All predictors were scaled, which allows to directly compare their effect sizes. The random effect of sampling location nested in road was added to control for the fact that all response variables were measured in the same plots. The model was fitted with a Gaussian distribution for all response variables. We ran the model with 100,000 iteration steps, discarded the first 10,000 samples as burn-in and thinned the remaining samples by storing every 25th iteration step.

RESULTS

Correlations Between Soil Properties

We found three major axes of variation in chemical soil properties. The first PCA axis summarized cation concentrations in the soil (hereafter referred to as "cation axis"), and explained 41.1% of the total variation (**Figures 2A,C**). The soil cations Ca, Mg and the CEC were strongly negatively correlated with the cation axis (i.e., high positive values along this axis mean a low concentration of soil Ca and soil Mg, and low CEC). The second

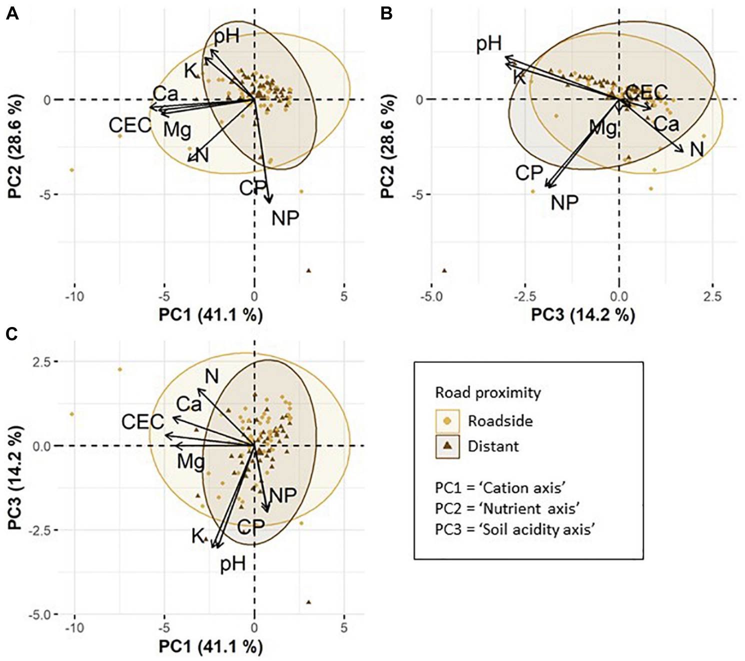

FIGURE 2 | Principle component analysis (PCA) based on eight chemical soil properties: pH, cation exchange capacity (CEC), soil nitrogen (N), carbon to phosphorus ratio (CP), nitrogen to phosphorus ratio (NP), calcium (Ca), magnesium (Mg), and potassium (K). Per cent values show the variance explained by PC1, PC2, and PC3. The ellipses are 95% confidence ellipses and visualize the variation in soil properties of roadside plots compared to distant plots. Larger symbols correspond to the ellipse centroids. **(A)** displays axes PC1 and PC2, **(B)** axes PC3 and PC 2 and **(C)** axes PC1 and PC3.

PCA axis summarized the concentration of soil N as well as soil C:P and N:P ratios (hereafter referred to as "nutrient axis"). This axis explained 28.6% of the total variation (**Figures 2A,B**). Soil N and both soil C:P and N:P ratios were negatively correlated with the nutrient axis. The third PCA axis summarized soil acidity and the concentration of soil K (hereafter referred to as "soil acidity axis"), explaining 14.2% of the total variation (**Figures 2B,C**). Soil pH and K were negatively correlated with the soil acidity axis.

Response of Soil Properties to Elevation and Road Proximity

Most of the investigated chemical soil properties (pH, Ca, K, Mg, and CEC) decreased significantly with increasing elevation (**Figures 3A,E–H** and **Table 1**). While soil Ca, Mg and CEC decreased continuously, pH and soil K decreased more steeply in the lower part of the elevational gradient. Soil C:P ratio peaked at mid elevations, while while soil N:P ratio did not respond to elevation (**Figures 3C,D** and **Table 1**). Soil pH values were significantly higher in roadside plots compared to distant plots (**Figure 3A** and **Table 1**). For concentrations of N and Mg, the opposite was observed (**Figures 3B,G** and **Table 1**).

Effects of Temperature, Soil Properties, and Road Proximity on Vegetation

Mean temperature of the warmest quarter had a positive effect on leaf N and a negative effect on leaf C:P ratio (**Figure 4** and **Supplementary Table 3**). Mean temperature of the coldest quarter had a positive effect on SLA and species richness (**Figure 4** and **Supplementary Table 3**). SLA increased with increasing CEC and soil cation concentrations (negative effect of the "cation axis," **Figure 4** and **Supplementary Table 3**). Species richness was higher in roadside plots compared to distant plots. Among the environmental variables tested, mean temperature of the coldest quarter had the strongest effects on vegetation characteristics (strongest on species richness, followed by the effect on SLA). The second strongest influence was exerted by mean temperature of the warmest quarter (on leaf N and second on leaf C:P ratio), followed by road proximity (on species richness) and soil cations (on SLA).

DISCUSSION

Elevational Responses of Chemical Soil Properties

Soil properties, such as soil acidity and the amount of nutrients, vary with environmental conditions and can reflect e.g., climatic differences, such as lower temperatures or aridity. This effect can be seen in particular along elevational gradients due to the strong environmental variation. In our study, the CEC, base cation concentrations (Ca, Mg, K) and pH decreased significantly along the elevational gradient on the south of Mt.

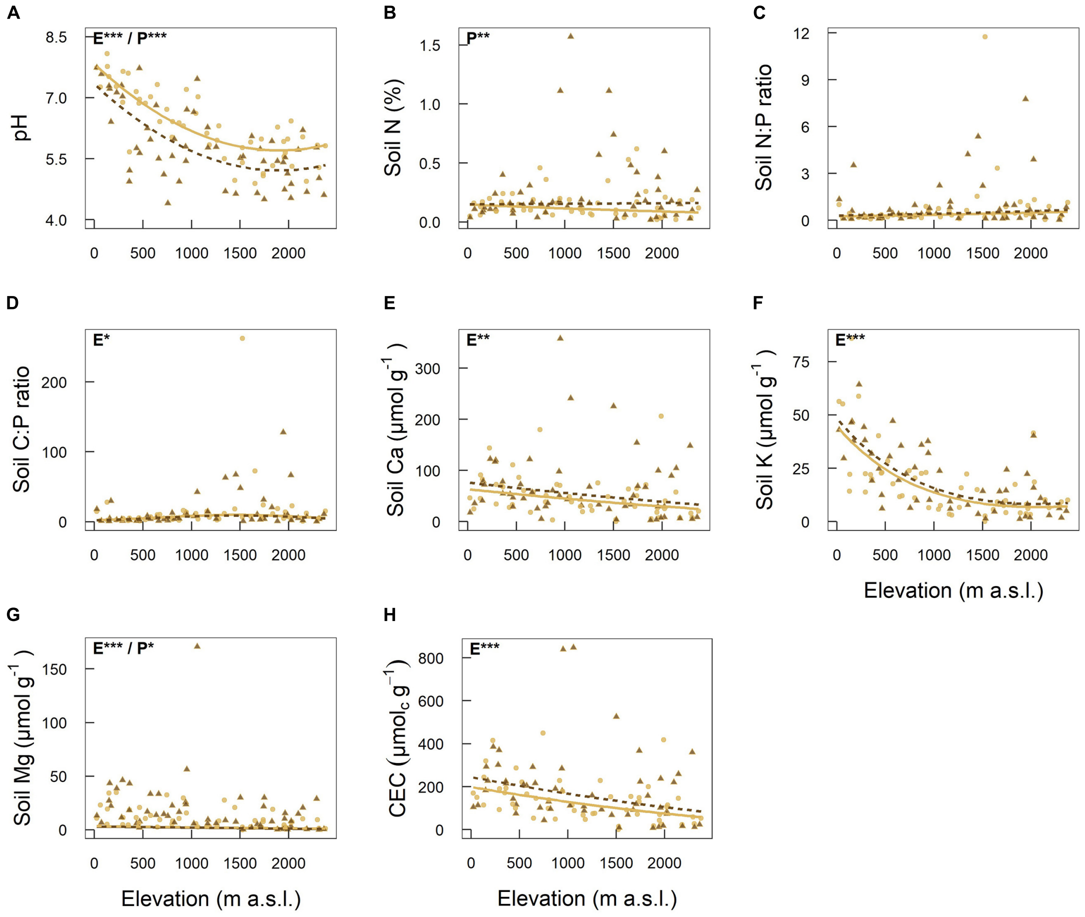

FIGURE 3 | Elevational variation of eight chemical soil properties: **(A)** pH, **(B)** Soil nitrogen, **(C)** Soil nitrogen to phosphorus ratio, **(D)** Soil carbon to phosphorus ratio, **(E)** Soil calcium, **(F)** Soil potassium, **(G)** Soil magnesium, **(H)** Cation exchange capacity. Linear mixed-effects models were fitted separately for each soil property as response to elevation (first or second-order polynomial), road proximity (roadside or distant plot), and their interaction. Sampling location nested in road identity, which corresponds to the sampling design, was included as random effect. Light brown continuous lines and circles represent plots next to the road (roadside plots). Dark brown dashed lines and triangles represent plots away from the road in natural vegetation (distant plots). For soil pH, C:P ratio and K the model including the quadratic term of elevation had a higher explanatory power (lower AIC) compared to the model including only the linear term of elevation. Significant terms are indicated at the top left of each plot: "E" corresponds to elevation and "P" to road proximity. Significance levels are indicated as follows: < 0.001 = ***, < 0.01 = **, < 0.05 = *.

Teide, on Tenerife. This elevational response of exchangeable cations is overall consistent with the results of another study conducted from mid to high elevations (1,400–3,100 m a.s.l.) on the northeastern slopes of Mt. Teide (Köhler et al., 2006), and was also found, for example, on the Galápagos Islands (Dinter et al., 2020). In contrast, a study conducted in the equatorial Andes did not observe clear elevational changes of soil base cations (Unger et al., 2012), and in Costa Rica, CEC, Ca and Mg concentrations were found to be highest at the highest elevation sampled (2,600 m a.s.l.; Grieve et al., 1990). Soil nutrient concentrations depend on multiple factors which do not necessarily change linearly with elevation (Körner, 2007). Differences in bedrock, soil age, climatic conditions or vegetation between regions result in region-specific soil property changes along elevational gradients (Köhler et al., 2006; Dinter et al., 2020). The distinct vegetational cover along the elevational gradient and thus input of litter between the study site in the equatorial Andes (Unger et al., 2012) and our study makes it difficult to sufficiently compare the results. Although soil age and bedrock are similar on the study site in Costa Rica, the investigated soil shows much greater depth and different structure. In contrast to our results, soil pH was found to increase from mid-elevations toward the tree line (around 2,100 m a.s.l.) on the northeastern slopes Mt. Teide (Köhler et al., 2006). These opposing responses of soil pH in the same mountain system are likely to be caused by different elevational patterns of precipitation: annual precipitation mainly increased within our studied elevational gradient from the coast (~100 mm/y)

TABLE 1 | Results from linear mixed-effects models to analyze the effects of elevation and road proximity (roadside or distant plot) on chemical soil properties.

		Estimate	DenDF	*F*	*p*
Soil pH	Elevation	0.253	48.882	50.797	**<0.001**
	Road proximity (distant)	−0.492	51.171	25.799	**<0.001**
Soil N	Elevation	−0.077	51.422	0.523	0.472
	Road proximity (distant)	0.333	51.017	7.392	**0.009**
Soil N:P ratio	Elevation	0.2303	50.206	3.266	0.077
	Road proximity (distant)	0.1777	50.658	1.393	0.243
Soil C:P ratio	Elevation	−0.323	50.240	4.895	**0.011**
	Road proximity (distant)	−0.1073	50.502	0.422	0.519
Soil Ca	Elevation	−0.896	51.058	7.912	**0.007**
	Road proximity (distant)	0.781	52.725	1.691	0.199
Soil K	Elevation	0.411	50.560	39.361	**<0.001**
	Road proximity (distant)	0.266	52.119	1.673	0.202
Soil Mg	Elevation	−0.721	50.436	27.108	**<0.001**
	Road proximity (distant)	0.350	51.889	4.224	**0.045**
CEC	Elevation	−1.937	51.334	15.963	**<0.001**
	Road proximity (distant)	1.560	52.923	3.021	0.088

Given are model estimates, denominator degrees of freedom (DenDF), F-values and p-values. To meet the model assumptions, soil N, N:P ratio, C:P ratio, and Mg were transformed using decadic logarithm, soil Ca, K, and CEC were transformed using the square root. For soil pH, C:P ratio and K the quadratic model (including the second-order polynomial of elevation), which had a lower AIC than the linear one, was used. Significant effects ($p < 0.05$*) are highlighted in bold.*

to the Canary pine forest belt (∼500 mm/y), plateauing in the highest study plots. Vice versa, the lowest part of the elevational gradient studied by Köhler et al. (2006) was located in the most humid belt at mid-elevations (∼1,050 mm/y), and precipitation decreased from there toward higher elevations (480 mm/y measured at 2,160 m a.s.l., in short distance to our highest study plots; Köhler et al., 2006). Hence, pH seems to be negatively correlated to precipitation and thus soil moisture—a pattern also reported from elevational gradients, for example, on Hawaii (Vitousek and Chadwick, 2013), on the Galápagos Islands (Dinter et al., 2020), and in Italy (Dixon et al., 2016).

In our study, soil C:P ratio peaked at mid-elevations, within the belt of Canary pine forest. A high ratio of soil C:P might indicate an efficient use of phosphorus by plants and microorganisms (Zhang et al., 2016), which in our case is likely to be supported by moister conditions in this elevational belt. On the other hand, the decomposition of pine needles is a slow process, potentially slowing down the relocation of phosphorus from dead plant material into the soil. At higher elevations, colder temperatures might further reduce decomposition rates and thus also increase the soil C:P ratio. The latter was found for example in a study in Northern China, where the soil C:P ratio significantly increased with elevation (Xu et al., 2019).

Soil N and N:P ratio showed no significant variation along our studied gradient. In our study, soil analyses were only conducted on mineral soil which has lower N concentrations than the organic layer. It was found that N concentrations were highest in the organic layers due to decomposing litter (Köhler et al., 2006). Thus, the increased litter in the pine forest resulted in higher N concentrations in mid-elevation soil samples which were, however, not significantly different to other samples. The lack of significant elevational changes of N and P coincides with the results of the studies conducted on the northeastern slope of Mt. Teide on Tenerife (Köhler et al., 2006), in the equatorial Andes (Unger et al., 2012), and on Mt. Gongga in China (Tan and Wang, 2016). Overall, young soils of volcanic origin—as found on Tenerife—are usually poorly developed and have lower nutrient concentrations and lower CEC compared to older soils (Köhler et al., 2006; Tan and Wang, 2016).

Road Effects on Soil Properties

We found significantly higher concentrations of soil N and Mg in plots away from the road compared to plots adjacent to the road. This contradicts our expectation that road verge soil

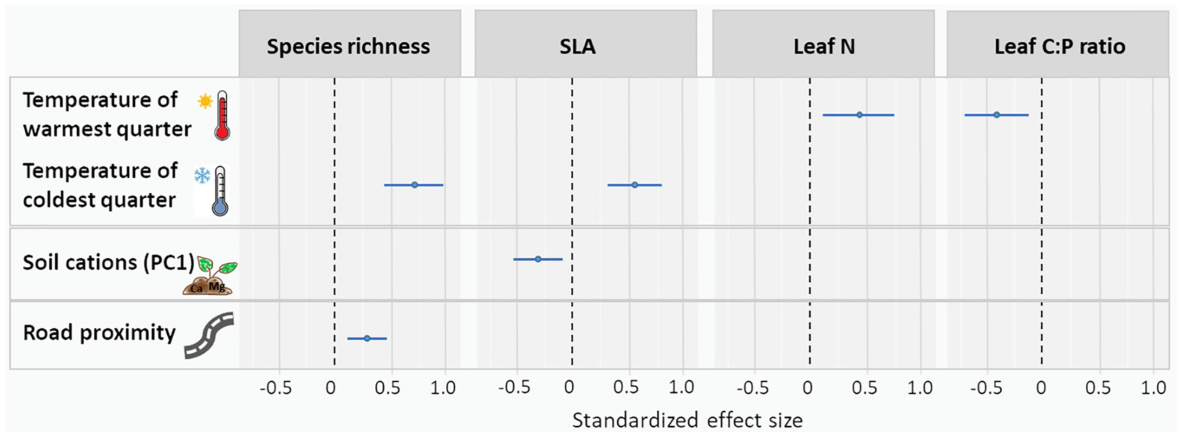

FIGURE 4 | Standardized effect size of mean temperature of warmest quarter, mean temperature of coldest quarter, soil cations (summarized through the first axis of the PCA) and road proximity on CWMs of plant functional traits (SLA [$mm^2\ mg^{-1}$], leaf N [%], and leaf C:P [$g\ g^{-1}$]) and species richness. Only significant effects are shown. For complete results, see **Supplementary Table 3**.

might contain higher nutrient concentrations as a consequence, for example, of road dust, and moister conditions from road drainage (Forman and Alexander, 1998; Müllerová et al., 2011). Our results might be explained by higher bulk density caused by vehicles accessing the road verge which might lead to lower soil permeability and reduced water infiltration (i.e., greater surface runoff) and nutrient flows (Johnston and Johnston, 2004; Makineci et al., 2007; Deljouei et al., 2018; Yang et al., 2018). Other studies which investigated the effect of road proximity on soil nutrients also found higher soil N and soil Mg concentrations away from the road. They explained this increase of nutrients by higher vegetation density and higher N mineralization rates (Johnston and Johnston, 2004; Deljouei et al., 2018). Moreover, along roads, due to mechanical disturbance mainly through vehicles, finer soil material is removed and the more coarse-grained mineral soils have lower concentrations of the major nutrients P and N as well as of exchangeable cations (Johnston and Johnston, 2004).

Besides the resulting disturbance along roadsides, the construction of roads might have severe impacts on soil properties. These are especially strong, if alkaline construction material is used in naturally acidic environments (Müllerová et al., 2011). As a consequence, soil pH might increase next to roads—as found in our study as well as in other regions (Müllerová et al., 2011; Deljouei et al., 2018).

Effects of Temperature, Soil Properties, and Road Disturbance on Vegetation

The main objective of our study was to evaluate how two important components of the environment—chemical soil properties and temperature—shape vegetation characteristics along the elevational gradient on Tenerife. Moreover, we analyzed the influence of roads on vegetation, and how the effects of soil are modified through road proximity. The strongest effects detected on different vegetation aspects analyzed in this study was that of temperature of the coldest and the warmest quarter, both variables decreasing with elevation. Species richness and SLA (acquisitive trait) significantly increased with mean winter temperature, and leaf N (acquisitive trait) increased with mean summer temperature, while leaf C:P ratio (conservative trait) decreased with mean summer temperature (**Figure 4**). The effect of temperature on vegetation has been widely studied (Kreft and Jetz, 2007; Šímová et al., 2011) and shifts of functional traits toward more conservative trait values with decreasing temperature and increasing elevation have been observed (Read et al., 2014; Schellenberger Costa et al., 2017). Cold temperatures and frost affect plants by causing physiological stress via cellular membrane damage on leaves and lower metabolic activities, which ultimately affect growth and reproduction (Yadav, 2010). At the high elevations of Mt. Teide, where we measured winter temperatures in the soil as cold as 1.7°C (**Supplementary Figure 1**), the specialist sclerophyllous shrubs dominate the communities. They seem to cope with the extreme conditions by having smaller, thicker leaves (low SLA) with high carbon content and low nutrient concentrations (high leaf C:P ratio). Because only specialist species are able to survive in such harsh conditions at high elevations, temperature also has a filtering effect on species richness toward colder sites, as observed as well on the neighboring island La Palma (Irl et al., 2015), but also at the global scale (Wright et al., 2017; Bruelheide et al., 2018) and e.g., for Kilimanjaro (Peters et al., 2019).

In our study, soil cation concentrations were the only chemical soil properties exerting a significant effect on the vegetation. SLA increased with increasing soil Ca and Mg concentrations and higher CEC. More favorable soil conditions at low elevations (with higher Ca, Mg and CEC) seem to be an important factor—in addition to temperature—which favors species with acquisitive strategies in these communities. As soil conditions get less favorable (i.e., with increasing elevation), the communities are characterized by a more conservative strategy with smaller SLA. Our results deviate from those found at Mt. Kilimanjaro, where soil nutrients (N, P, Ca, Na, K) had a negative effect on LDMC, and a positive effect on leaf N and leaf P, but not on SLA (Schellenberger Costa et al., 2017). Despite the different single results in terms of which traits were affected by soil nutrients, the overall result from Schellenberger Costa et al. (2017) also showed soil nutrients to favor acquisitive strategies. The lack of an effect from our soil nutrient axis (determined by soil N concentration, soil C:P, and N:P ratio) might be due to the very low concentrations of N and P in the poorly developed soils at Mt. Teide, as also found in another study on Tenerife (Köhler et al., 2006) and in general for Mediterranean soils (Torrent, 2005). Even though the N concentrations we found in the soil along the southern slopes of Tenerife spanned over a wide range (0.02–1.57%), comparable to values found in alpine grasslands (0.2–1.2%, Körner, 2003), only a few sites contained more soil N than found by Köhler et al. (2006) on the northern slopes (0.02–0.26%). The overall poorly developed soils in our study area might also explain why we could not detect a positive effect of soil quality on species richness, although soil quality, and species richness almost paralleled each other along the elevational gradient.

We expected species richness to be higher next to roads compared to non-road habitats, because of the disturbance in the roadside habitats, which should weaken competition among plants through an increase in bare soil, light and nutrients and thus allow more species to co-exist (Catford et al., 2012). Indeed, communities at the road verge harbored more species than the communities away from the road in our study region. However, this was likely primarily because of the heterogeneity generated by the human activities associated to roads and more available space and light than increased nutrient availability (lower soil N and Mg concentrations next to the road). The removal of biomass during road maintenance in Tenerife, for example, prevents continuous cover of highly competitive species by creating empty spots and opportunities for other species to grow. We also expected disturbance to favor species with acquisitive traits, such as high SLA (McIntyre et al., 1999; Bernhardt-Römermann et al., 2011), which allow for a quick uptake and use of the available resources. However, in our study, CWMs of the functional traits investigated did not differ between communities next to and away from the road. This finding, together with the absence of an increase in functional diversity next to roads, is surprising and difficult to explain. A possible explanation might be that during the warmest quarter, temperature in roadside plots was significantly higher than in distant plots (**Supplementary Material**). Therefore, the effect of road disturbance might have been captured by the overall stronger effect of temperature. Alternatively, the new species favored by disturbance at roadsides might be functionally similar and thus do not significantly contribute to functional diversity or changes in CWMs.

We found no support for the expected interaction between soil properties and road disturbance. We expected that the same amount of soil nutrients or cations, for example, would have a different impact on roadside vegetation compared to the distant vegetation, as these nutrients might not be available for plant uptake due to higher soil compaction from vehicle traffic. However, these interacting effects were not detected in any of the vegetation characteristics analyzed here. This might be explained by a less pronounced difference in soil bulk density or grain size distribution in roadside and distant plots than we presumed, and therefore a similar nutrient availability for plants.

Surprisingly, functional diversity was not affected by any of the environmental factors considered. While other studies found functional diversity to decrease through environmental filtering (but see Schellenberger Costa et al., 2017; López-Angulo et al., 2020; Midolo et al., 2021) and to increase through competition (Mayfield et al., 2010), we could not detect any differences. While our selection of traits was done carefully in order to encompass the aspects of vegetation relevant to our questions, we also acknowledge that the leaf traits considered in this study do not capture all dimensions of trait variation. For example, seed and dispersal traits may also be important for community assembly (although not independent of life form, which make them less suitable for this study). Since the studied environmental variables are all related to competition intensity, we consider the choice of leaf traits related to the species' competitive and growth ability as appropriate. Thus, regarding the lack of a response of functional diversity in the study presented here, we emphasize that although elevation is often criticized of being merely an umbrella term, it also combines the effects of several environmental factors, thus revealing ecological patterns which cannot be detected with individual analyses of single variables (Körner, 2007).

In our study, temperature had the strongest effects on vegetation characteristics along the elevational gradient of Tenerife—stronger than chemical soil properties and disturbance. As decreasing temperature gradients are general patterns in mountains, our findings align with observations from elevational gradients in other regions. In addition, our results are in accordance with studies explaining broad-scale patterns of species richness and functional trait variation, particularly those looking at continental and global geographic patterns (Hawkins et al., 2003; Kreft and Jetz, 2007; Šímová et al., 2011; Bruelheide et al., 2018). While elevational temperature patterns are quite linear, soil patterns are more idiosyncratic, and thus not simply transferrable across regions. At the species level, a global compilation study found soil measured at the same site as the traits to be a more important driver of trait variation than temperature data extracted from smaller resolution sources (Ordoñez et al., 2009; but see Liu et al., 2017). Together with the results from our regional study, this emphasizes the importance of including data from local environmental conditions for climate, disturbance and fine-scale soil conditions for understanding biodiversity patterns.

DATA AVAILABILITY STATEMENT

The dataset presented in this article is available at the Dryad Digital Repository, https://doi.org/10.5061/dryad.66t1g1k37.

AUTHOR CONTRIBUTIONS

AR, LF, and SH conceived the ideas and analyzed the data. AR conducted the fieldwork and collected the vegetation data with help from SH and JA. AR and LF conducted the chemical soil and leaf analysis, respectively. AR and LF led the writing with important contributions from SH. All authors revised drafts of the manuscript, and approved the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.758160/full#supplementary-material

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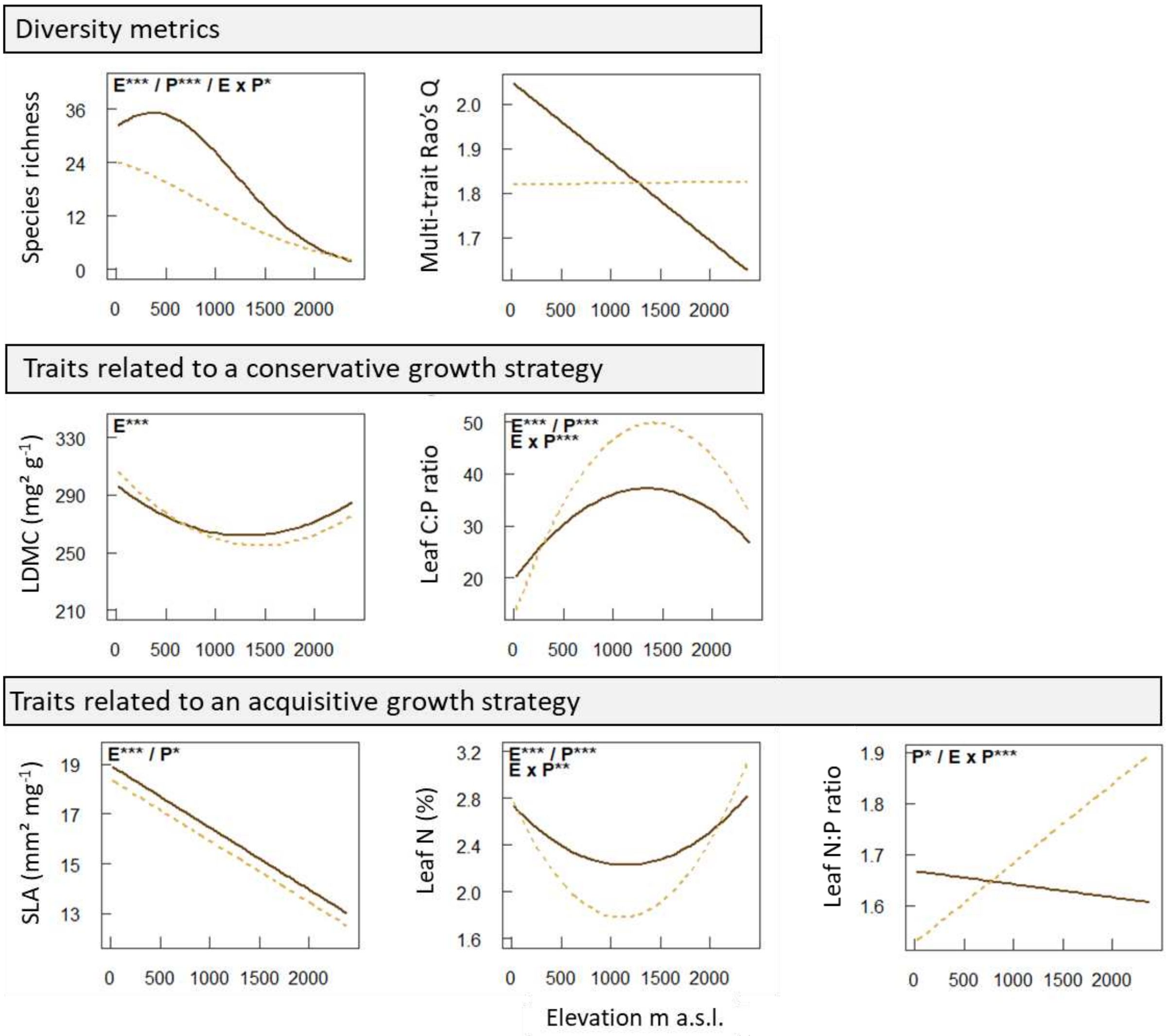
Supplementary Material

Trait predictions with near-infrared spectroscopy

The leaf samples used in this study were analyzed within a larger pool of samples from mountain ranges around the world, which amounted to almost 3000 samples. In order to obtain trait values for such a large dataset, a subset of samples was selected from the total pool of samples for laboratory analyses ('calibration samples'), and the trait values for the remaining samples were predicted via near-infrared reflectance spectroscopy (NIRS), as described by Foley et al. (1998) and applied for example by Davrinche and Haider (2021), Kühn et al. (2021), Proß et al. (2021) and Petit Bon et al. (2020). Calibration samples were selected to include species from different families and life-forms in order to cover a large trait variation (approximately 30 samples from each of the 10 mountain regions). Leaf powder of all samples (calibration and non-calibration samples) was scanned with a stationary NIR spectrometer (MPA, Bruker Optik, Ettlingen, Germany). Samples were scanned three times and the average spectrum over the three measurements was calculated for each sample. Secondly, separate prediction models were created for each trait based on the laboratory results and reflectance data of the calibration samples using Partial Least Square Regression, after an automated selection of the best spectral pre-treatment (software OPUS version 7.1, Bruker Optik, Ettlingen, Germany). Finally, using these models and the spectroscopy data, trait values for all samples were predicted. Trait values for the same species were averaged, so that we had one value per trait per species.



Supplementary Figure 1. Elevational changes of species richness, functional diversity (multi-trait Rao's Q) and community-weighted means (CWM) of five functional leaf traits. Linear mixed-effects models were fitted for CWM of the response variables, with elevation, proximity to road (roadside or distant plot), and their interaction as fixed effects (Supplementary Table 1). Sampling location nested in road, which corresponds to the sampling design, was included as random effect. Regression lines are based on model predictions. Dark brown continuous lines represent plots next to the road (roadside plots). Light brown dashed lines represent plots away from the road in natural vegetation (distant plots). For each response variable, we fitted one model containing only the linear term of elevation and another model using the second-order polynomial of elevation. We compared the AIC (Akaike's Information Criterion) of both models, and considered those with lower AIC as the better models. For LDMC, leaf C:P ratio and leaf N, 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 = proximity to road, E x P = elevation-by-proximity to road interaction). Significance levels < 0.001 = ***, < 0.01 = **, < 0.05 = *.

Supplementary Table 1: Results from linear mixed-effects models to analyze the effects of elevation and road proximity (roadside or distant plot) on species richness, functional diversity (multi-trait Rao's Q) and community-weighted means of five functional leaf traits. Given are model estimates, denominator degrees of freedom (DenDF), *F*-values and *p*-values. To meet the model assumptions, species richness and leaf C:P ratio were transformed using decadic logarithm, multi-trait Rao's Q was transformed using the square root. For species richness, LDMC, leaf C:P ratio, leaf N and leaf N:P ratio the quadratic model (including the second-order polynomial of elevation), which had a lower AIC than the linear one, was used. Significant effects (p<0.05) are highlighted in bold.

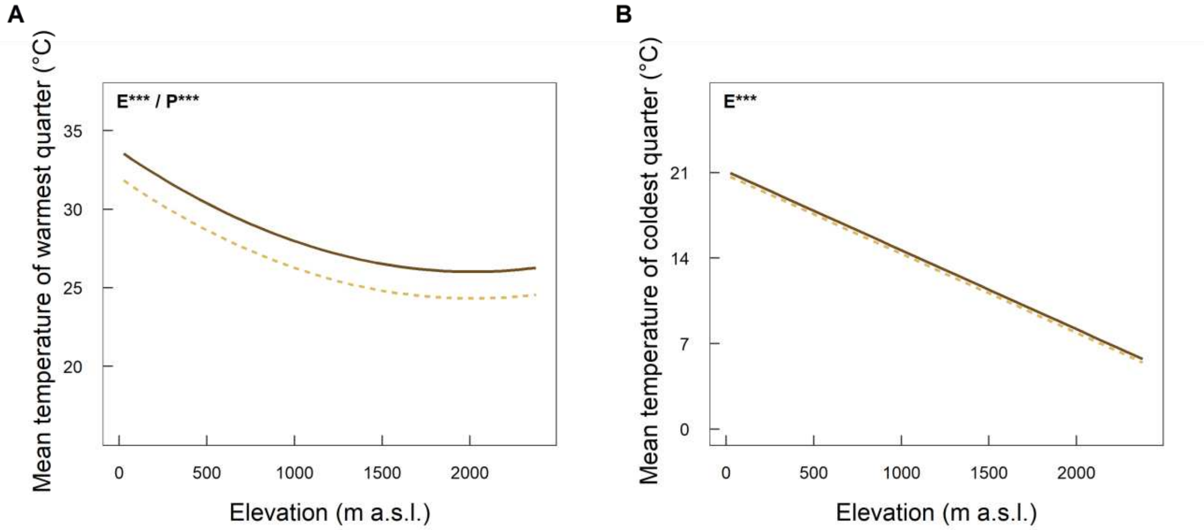
		Estimate	DenDF	*F*	*p*
Species richness	Elevation	-0.297	51.835	71.483	**<0.001**
	Road proximity (distant)	-0.413	52.740	26.883	**<0.001**
	Elev x Road proximity	0.158	52.677	3.186	**0.049**
multi-trait Rao's Q	Elevation	-0.128	51.080	1.162	0.286
	Road proximity (distant)	-0.015	50.559	0.020	0.886
	Elev x Road proximity	0.130	50.432	1.619	0.209
LDMC	Elevation	93.576	49.654	13.190	**<0.001**
	Road proximity (distant)	-3.693	48.710	1.510	0.225
	Elev x Road proximity	17.384	48.316	2.491	0.093
Leaf C:P ratio	Elevation	-0.122	51.714	11.080	**<0.001**
	Road proximity (distant)	0.181	50.211	18.726	**<0.001**
	Elev x Road proximity	-0.083	40.803	4.086	**0.023**
SLA	Elevation	-1.799	53.170	108.116	**<0.001**
	Road proximity (distant)	-0.517	52.806	5.967	0.199
	Elev x Road proximity	0.010	52.763	0.002	0.963
Leaf N	Elevation	1.784	52.414	11.821	**<0.001**
	Road proximity (distant)	-0.238	50.365	16.052	**<0.001**
	Elev x Road proximity	1.964	50.037	5.897	**0.005**
Leaf N:P ratio	Elevation	-0.019	52.136	1.849	0.180
	Road proximity (distant)	0.077	51.889	4.555	**0.038**

	Elev x Road proximity	0.130	51.527	12.829	**<0.001**

Supplementary Table 2. Mean values, abbreviations and units of the variables used to determine the effect of environmental factors on plant communities. The first group contains the analyzed soil chemical properties, the second group the determined leaf chemical properties as well as morphological plant traits, and the third group represents the applied climate data.

	Variable	Abbreviation	Unit	Mean
Soil	pH	Soil pH	-	6.05
	Cation exchange capacity	Soil CEC	$\mu mol_c\ g^{-1}$	164.16
	Calcium	Soil Ca	$\mu mol\ g^{-1}$	58.19
	Magnesium	Soil Mg	$\mu mol\ g^{-1}$	14.39
	Potassium	Soil K	$\mu mol\ g^{-1}$	18.76
	Phosphorous	Soil P	$\mu mol\ g^{-1}$	0.5
	Nitrogen	Soil N	%	0.2
	Carbon to phosphorus ratio	Soil C:P ratio	g/g	14.29
	Nitrogen to phosphorus ratio	Soil N:P ratio	g/g	0.83
Vegetation	Species richness	SR	-	17.16
	Specific leaf area	SLA	$mm^2\ mg^{-1}$	15.76
	Calcium	Leaf Ca	$mg\ g^{-1}$	6.42
	Magnesium	Leaf Mg	$mg\ g^{-1}$	2.56
	Potassium	Leaf K	$mg\ g^{-1}$	16.62
	Phosphorus	Leaf P	$mg\ g^{-1}$	1.47
	Nitrogen	Leaf N	%	2.31
	Carbon to phosphorus ratio	Leaf C:P ratio	g/g	35.00
	Nitrogen to phosphorus ratio	Leaf N:P ratio	g/g	1.67
Climate	Mean temperature of the warmest quarter	Bio10	°C	27.34
	Mean temperature of the coldest quarter	Bio11	°C	13.18

Elevational temperature patterns



Supplementary Figure 2. Elevational changes of mean temperature of warmest quarter (Bio10) and mean temperature of coldest quarter (Bio11) as defined by WorldClim (Hijmans et al., 2005). We fitted linear mixed-effects models in R (R Core Team, 2020; R-package 'lmerTest', Kuznetsova et al., 2017) with Bio10 and Bio11 as response variables, and elevation, road proximity (roadside or distant), and their interaction as predictors. Sampling location nested in road identity was added as a random effect to account for the sampling design. Regression lines are based on model predictions. Continuous dark brown lines represent plots next to the road (roadside plots). Dashed lines represent plots away from the road in natural vegetation (distant plots). For each response variable, we fitted one model containing only the linear term of elevation and another model using the second-order polynomial of elevation. We compared the AIC (Akaike's Information Criterion) of both models, and considered those with lower AIC as the better models. For mean temperature of the warmest quarter, the model including the quadratic term of elevation had a higher explanatory power compared to the model including only the linear term of elevation. Mean temperature of the warmest quarter showed an exponential decrease with elevation ($F_{2,52.9} = 22.582$, $p < 0.001$), and mean temperature of the coldest quarter a linear decrease ($F_{1,53.7} = 311.862$, $p < 0.001$). Roadside plots showed significantly higher mean temperature of the warmest quarter compared to distant plots ($F_{1,51.73} = 13.546$, $p < 0.001$), but there was no difference for mean temperature of the coldest quarter ($F_{1,53.0} = 0.545$, $p = 0.464$). The response to elevation did not differ between roadside and distant (no significant elevation-by-road proximity interaction; Bio10: $F_{2,51.86} = 1.574$, $p = 0.226$; Bio11: $F_{1,53.6} = 0.0001$, $p = 0.991$).

Supplementary Table 3. Results of multivariate generalized linear mixed model. Response variables were the CWM of SLA, LDMC, leaf N, and leaf C:P and N:P ratios, Rao's Q of these traits (multi-trait functional diversity) and species richness. As predictors we included mean temperature of the warmest and of the coldest quarter (Bio10 and Bio11, respectively), proximity to roads (roadside or distant), and soil properties, summarized by using the values of the first three axes of the PCA (Figure 2). We also permitted the interactions between road proximity and soil variables. We show the standardized effect sizes (post.mean), lower and upper values of the 95% credible interval (lower 95% CI and upper 95% CI, respectively) and p-values. Significant effects (p<0.05) are highlighted in bold. The prior was specified as prior = list(R = list(V = diag(7)/3, n = 6), G = list(G1 = list(V = diag(7)/3, n = 6), G2 = list(V = diag(7)/3, n = 6))).

		SLA	LDMC	Leaf N	Leaf C:P ratio	Leaf N:P ratio	SR	FD
Bio10	post.mean	0.184	0.230	0.448	-0.424	-0.158	0.023	0.076
	lower 95% CI	-0.036	-0.057	0.156	-0.696	-0.445	-0.223	-0.243
	upper 95% CI	0.421	0.508	0.753	-0.149	0.133	0.272	0.419
	p-value	0.110	0.114	**0.004**	**0.003**	0.283	0.857	0.653
Bio11	post.mean	0.550	0.252	-0.308	-0.131	-0.314	0.709	0.112
	lower 95% CI	0.290	-0.087	-0.634	-0.425	-0.657	0.438	-0.254
	upper 95% CI	0.794	0.547	0.018	0.196	0.008	0.978	0.482
	p-value	**0.001**	0.124	0.067	0.410	0.069	**<0.001**	0.544
PC1	post.mean	-0.291	0.007	-0.079	0.094	0.034	-0.140	-0.040
	lower 95% CI	-0.516	-0.278	-0.371	-0.160	-0.241	-0.362	-0.351
	upper 95% CI	-0.082	0.266	0.191	0.361	0.311	0.105	0.285
	p-value	**0.012**	0.949	0.580	0.483	0.791	0.251	0.807
PC2	post.mean	-0.024	0.039	0.115	-0.027	0.086	-0.185	-0.173
	lower 95% CI	-0.219	-0.213	-0.143	-0.261	-0.152	-0.410	-0.437
	upper 95% CI	0.164	0.294	0.372	0.216	0.354	0.027	0.119
	p-value	0.831	0.762	0.411	0.818	0.519	0.097	0.237
PC3	post.mean	0.008	-0.075	-0.030	-0.074	-0.211	0.087	0.061
	lower 95% CI	-0.191	-0.324	-0.309	-0.348	-0.477	-0.147	-0.237
	upper 95% CI	0.213	0.194	0.227	0.161	0.040	0.302	0.372
	p-value	0.934	0.568	0.832	0.561	0.111	0.423	0.696

Road proximity	post.mean	0.092	-0.024	0.155	-0.170	-0.129	0.281	0.019
	lower 95% CI	-0.059	-0.218	-0.054	-0.357	-0.325	0.105	-0.199
	upper 95% CI	0.252	0.190	0.371	0.036	0.086	0.459	0.285
	p-value	0.261	0.805	0.154	0.097	0.226	**0.002**	0.860
PC1 x Disturbance	post.mean	-0.038	0.148	-0.043	-0.103	-0.206	-0.099	-0.201
	lower 95% CI	-0.238	-0.091	-0.317	-0.345	-0.472	-0.324	-0.495
	upper 95% CI	0.156	0.418	0.215	0.140	0.051	0.118	0.084
	p-value	0.713	0.266	0.751	0.411	0.123	0.382	0.184
PC2 x Disturbance	post.mean	-0.156	-0.046	-0.126	0.186	0.160	-0.090	-0.062
	lower 95% CI	-0.324	-0.261	-0.358	-0.013	-0.052	-0.281	-0.315
	upper 95% CI	0.014	0.187	0.087	0.388	0.375	0.090	0.177
	p-value	0.069	0.669	0.258	0.066	0.139	0.336	0.616
PC3 x Disturbance	post.mean	-0.125	-0.144	-0.102	0.106	0.045	-0.134	-0.069
	lower 95% CI	-0.285	-0.350	-0.308	-0.076	-0.149	-0.314	-0.311
	upper 95% CI	0.042	0.059	0.107	0.312	0.260	0.043	0.163
	p-value	0.131	0.166	0.338	0.283	0.671	0.140	0.571

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CHAPTER 3

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

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This chapter is under revision in *Oecologia* as

Ratier Backes, A., Römermann, C., Alexander, J.M., Arévalo, J.R., Keil, P., Padrón-Mederos, M.A., Trogisch, S., & Haider, S. Mechanisms behind elevational plant species richness patterns revealed by a trait-based approach.

Abstract

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. Based on vegetation relevés in natural vegetation and disturbed roadsides we observed a peak of plant species richness in the lowest third of the elevational gradient. We considered three mechanisms potentially shaping this pattern: environmental filtering (temperature and precipitation), effects of area and disturbance. For each mechanism, we hypothesized a distinct pattern of trait-elevation relationships. These were tested with in-situ data of nine functional leaf traits, from which we calculated community-weighted trait means (CWM) and functional diversity. 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 elevational shift of growth strategies also supported the disturbance effect, and as expected we also found overall more acquisitive communities at roadsides compared to natural habitats. Our results suggest that 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.

Keywords: functional diversity, functional traits, community-weighted mean, environmental filtering, community assembly.

Introduction

Studies of variation in species richness along elevational gradients have a long history dating back to the early 19th century (e.g. 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 and 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 and Grytnes, 2007), disturbance (Bunn et al., 2010), or to 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 caused by both filtering by temperature and 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 and Grytnes, 2010). On the other hand, species richness patterns can emerge from the combined effect of more than one mechanism. For instance, a hump-shaped pattern can result from the interaction between climatic 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 elevational gradients contain several environmental factors which are often intercorrelated.

Species richness has been observed to increase with temperature and precipitation (e.g. Irl et al., 2015), with available area (e.g. Romdal & Grytnes, 2007) and up to a certain threshold with disturbance (intermediate disturbance hypothesis; e.g. Catford et al., 2012). 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 harsh climatic conditions (de Bello et al., 2013), i.e. 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 and Grytnes, 2007). Species richness can also be positively affected by disturbance, as long as its frequency and intensity do not exceed a certain threshold (Kowarik, 2008; Catford et al., 2012). These moderate levels of disturbance promote the co-existence of species through reduced competition 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 patterns vary among mountains.

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; Bruelheide et al., 2018; Díaz et al., 2016; Wright et al., 2004). Typically, acquisitive strategies are found in resource-rich, benign habitats (lowlands), while conservative strategies prevail under harsh 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 and Garnier, 2002; Funk et al., 2017). For example filtering through temperature should not only restrict the number of species able to persist in high elevations, but also influence the functional characteristics of the community towards stress-tolerant traits. 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, 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 hypothesised trait patterns linked to these three mechanisms). In Tenerife, temperature, area and disturbance decrease with elevation, while precipitation peaks at mid-elevation (Morales Matos and Pérez González, 2000).

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.

(i) *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, SLA typically decreases with decreasing water availability (e.g. Liu et al. 2017) and decreasing temperature (e.g. Rosbakh et al., 2015; Körner et al., 1989). 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).

(ii) 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 community-weighted trait means. There are only few studies that analysed such a direct effect (but see Schrader, Westoby, et al., 2021). Other factors often associated with area, such as habitat heterogeneity, are not considered here as an area effect. When taking into account only a passive sampling effect, larger areas with more species have a higher probability to contain 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).

(iii) Disturbance effect: In mountains, a typical form of anthropogenic disturbance are roads, which lead from the lowlands up to high elevation. Thus, two orthogonal gradients of disturbance occur: a decrease of disturbance from roadsides to adjacent natural vegetation, and the parallel elevational decrease of disturbance in both roadsides and natural vegetation. Road disturbance, specifically via road maintenance activities of biomass removal, trampling and driving on road verges, can favour 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 community-weighted trait means towards more acquisitive growth strategies (Forman and Alexander, 1998) and lower functional diversity (Mayfield et al., 2010).

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 conservative and acquisitive 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) of conservative traits increase, and CWMs of acquisitive traits decrease, with increasing elevation as a consequence of climate filtering by temperature (Fig. 1 a1, a2) and the effect of disturbance (Fig. 1 d1, d2). For the disturbance effect, CWMs of roadside (disturbed) communities shift towards values indicating a more acquisitive growth strategy compared to communities in natural vegetation (Fig. 1 d1, d2). Climate filtering by precipitation leads to highest acquisitiveness at mid-elevations (Fig. 1 b1, b2). CWMs do not change with elevation as a consequence of the area effect (Fig. 1 c1, c2).

(2) Functional diversity decreases with elevation according to filtering by temperature (Fig. 1 a3) and the area effect (Fig. 1 c3), increases with elevation through the effect of disturbance (Fig. 1 d3), or peaks at mid-elevations according to filtering by precipitation (Fig. 1 b3). Because of the filtering effect of disturbance (Fig. 1 d3), functional diversity is lower along roadsides compared to natural vegetation.

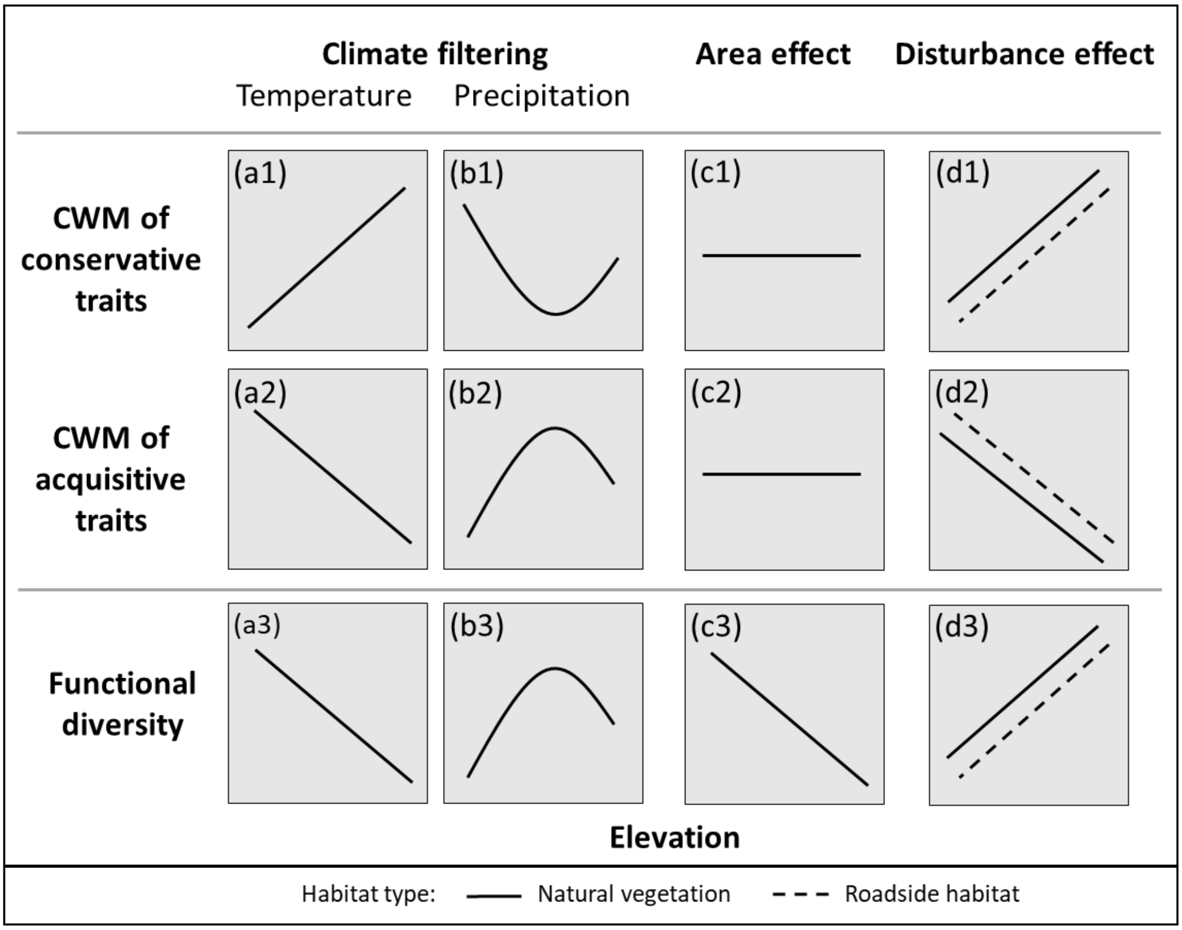

Figure 1. Expected elevational patterns of community-weighted traits means (CWMs) of conservative and acquisitive traits and functional diversity according to different mechanisms underlying the observed elevational species richness pattern in our study region, Tenerife. Continuous black and dashed grey lines represent the patterns in natural vegetation and roadside habitat, respectively.

Materials and methods

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. 2000 m a.s.l., is the high plateau of the volcanic caldera Las Cañadas, from which the summit of Mount Teide rises up to 3718 m 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 100 m (Morales Matos and 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 and Pérez González, 2000; AEMET, 2012). Our own data compilation confirmed the decrease of temperature with elevation, but we found a linear elevational increase of precipitation along the elevational gradient covered by our study (see Online Resource 1). Due to the conical shape of the main volcano, land surface area of elevational bands decreases with elevation (Morales Matos and Pérez González, 2000). Similarly to most mountain regions, human influence and hence human-induced disturbance decreases with elevation on Tenerife (Otto et al., 2014). Both patterns were confirmed by our own calculations (area) and field estimations (disturbance; Online Resource 1).

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* C. Sm.) up to 2000 m a.s.l. and summit scrub on the high plateau above the tree line (Online Resource 2). 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).

Sampling design

The project was conducted within the framework of the Mountain Invasion Research Network (MIREN; http://www.mountaininvasions.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 (Fig. 2 a). Along the elevational extent of each road, 20 sampling sites were equally distributed (average elevational distance between sample sites was 123 m). At each sample site, a so-called T-transect was established, which consists of two plots of 50 m x 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') (Fig. 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.

Vegetation relevés and trait sampling

In each plot, all vascular plant species were identified, and their cover recorded via classes from 1 to 7 (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%).

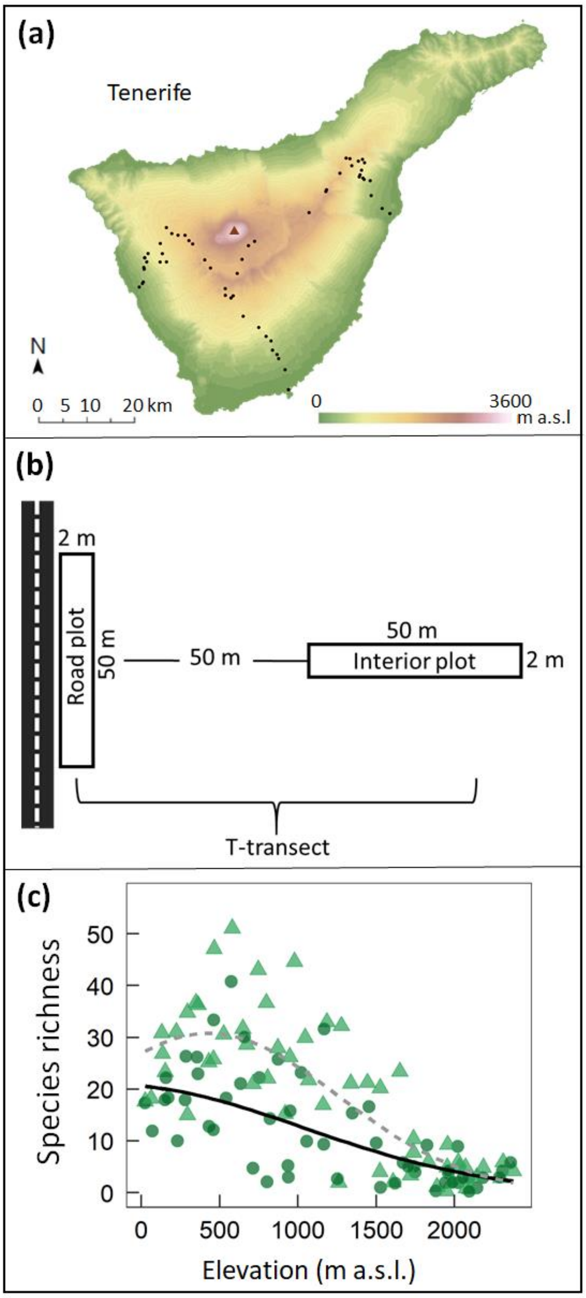

Figure 2. (a) Locations of sampling sites (56 black points) along three mountain roads, starting at the coast and ending at the volcanic caldera of Las Cañadas on Tenerife. The highest point on the island is the peak of Teide (brown triangle). (b) At each sampling site a T-transect consisting of two plots was established, 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. The gray dashed line and light-colored triangles represent plots next to the roadside (road plots). The black continuous line and dark-colored circles represent plots away from the road in natural vegetation (interior plots). Regression lines are based on model predictions.

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; Online Resource 3), which is an established threshold for a reliable characterization of the functional properties of a community (Pakeman and Quested, 2007). The trait samples consisted of 10-50 leaves from ca. 7 individuals of a single species on the same plot. For each species, separate samples were taken from up to three different plots, depending on the elevational distribution of the species. The trait measurements were later aggregated into one value per species in order to focus on capturing elevational patterns at the interspecific level, i.e. based on species turnover, rather than elevational within-species adjustments. 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 (Online Resource 3). 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). For details about the trait measurements Online Resource 3.

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 SYNCSA package (Pillar & Duarte, 2010) in R (R Core Team, 2020):

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

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; Botta-Dukát, 2005; Rao, 1982) 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 (multi-trait Rao's Q; scaling trait values to unit variance), using the FD package in R (Laliberté and Legendre, 2010). We chose Rao's Q because it is weakly related to species richness and sensitive to assembly rules (Mouchet et al., 2010).

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 (second-order polynomial), plot type (road or interior plot), and their 2-way interaction. Transect identity nested in road identity 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 mechanistic variables.

We tested the responses of CWMs and functional diversity to elevation and plot type (i.e., natural vegetation vs. roadside habitat, Fig. 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. Transect identity nested in road identity was added as a random effect. In order to normalize right-skewed distributions, Rao's Q of SLA, leaf C, leaf N, leaf C:N ratio were square-root transformed; while Rao's Q of LDMC and multi-trait Rao's Q were log-transformed to base *e*. 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). 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.

Results

Species richness patterns

We observed an overall decrease of species richness with elevation with a small peak around 600 m a.s.l. ($F_{1,51.8} = 71.48$, $p < 0.01$; Fig. 2 c). Road plots exhibited overall higher species richness compared to interior plots ($F_{1,52.7} = 26.88$, $p < 0.01$; Fig. 2 c). Species richness differences between road plots and interior plots decreased with elevation (elevation-by-plot type interaction) ($F_{1,52.7} = 3.19$, $p = 0.05$; Fig. 2 c). Species richness showed a hump-shaped relationship with mean temperature of the growing season ($F_{1,51.48} = 67.49$, $p < 0.001$; Online Resource 4) and land surface area ($F_{1,51.02} = 41.92$, $p < 0.001$), a positive relationship with disturbance intensity ($F_{1,69.40} = 8.50$, $p < 0.001$), 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 except for the case of disturbance (temperature: $F_{1,52.68} = 27.27$, $p < 0.001$; precipitation: $F_{1,52.43} = 24.08$, $p < 0.001$; area: $F_{1,52.27} = 26.32$, $p < 0.001$; disturbance: $F_{1,59.0} = 2.78$, $p = 0.1$). The increase in species richness on roadside plots compared to interior vegetation was stronger at intermediate temperatures (temperature-by-plot type interaction; $F_{1,52.46} = 3.23$, $p = 0.048$).

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 N and lead 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 (Fig. 3 a, Table

1). Leaf C showed a flattening increase with elevation, and leaf C:N ratio a mid-elevational peak (Fig. 3 b, c). We observed a significant linear decrease with elevation of the acquisitive traits SLA, leaf Ca and Mg (Fig. 3 d, g, i), while leaf N, P and K had their lowest values at mid-elevations (Fig. 3 e, f, h).

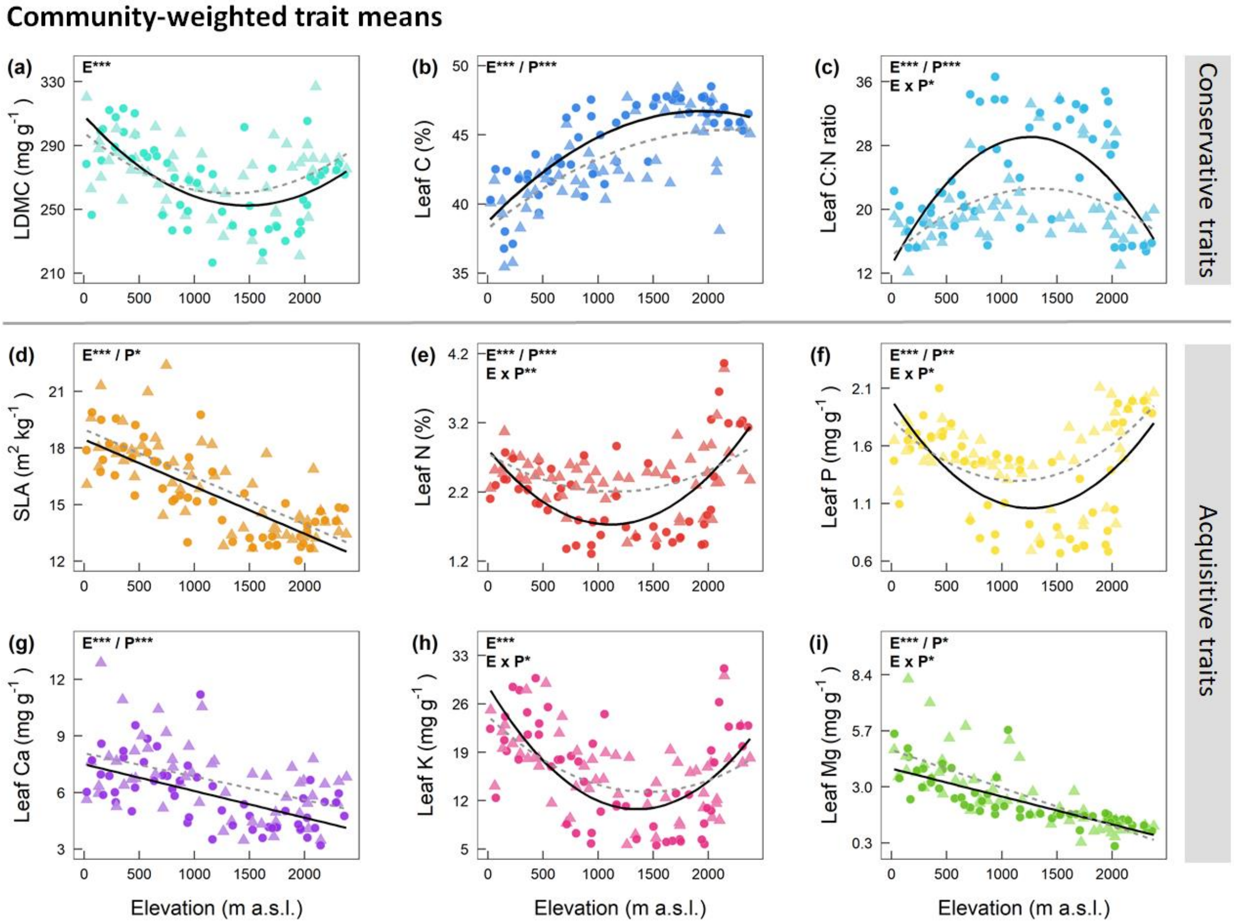

Figure 3. Relationship between elevation and community-weighted means of nine functional leaf traits. Regression lines are based on model predictions. Gray dashed lines and light-colored triangles represent plots next to the roadside (road plots). Black continuous lines and dark-colored circles represent plots away from the road in natural vegetation (interior plots). For LDMC, leaf C, leaf C:N ratio, leaf N and leaf P, 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 x P = elevation-by-plot type interaction). Significance levels < 0.001 = ***, < 0.01 = **, < 0.05 = *.

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 and leaf K (lower leaf C and C:N ratio; higher SLA, leaf N, P, Ca and Mg). The shift was greatest at mid-elevations for leaf C:N ratio, leaf N and leaf P. Leaf Mg had more acquisitive values for roadside than interior plots at low elevations, but the difference disappeared at higher elevations. For leaf K, higher values for road plots were observed only at mid-elevations, but the opposite was true for the low and the high end of the elevational gradient (Table 1).

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

Table 1. Results from the linear mixed-effects models for community-weighted trait means (CWMs) of functional traits and functional trait diversity (Rao's Q) of single traits as well as all traits combined (multi-trait) as response to elevation, plot type (road or interior plot) and their interaction. 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), leaf carbon to nitrogen ration (C:N ratio), leaf nitrogen (leaf N) and leaf phosphorus (leaf P), and for Rao's Q of LDMC, C:N ratio, leaf P and multi-trait, 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 = *.

		Elevation		Plot type		Elevation x plot type	
		df	F	df	F	df	F
LDMC	CWM	49.66	**13.19 *****	48.71	1.51	48.32	2.49
	FD	51.29	**31.75 *****	51.32	**7.59 ****	50.86	0.38
Leaf C	CWM	47.37	**45.70 *****	46.26	**24.07 *****	45.92	0.63
	FD	49.08	**36.50 *****	49.45	**5.97***	49.40	0.44
Leaf C:N	CWM	51.80	**13.83 *****	50.08	**28.65 *****	49.71	**5.01 ***
	FD	49.68	**3.50***	49.53	0.15	49.07	0.60
SLA	CWM	52.24	**54.73 *****	51.50	**6.26 ***	51.12	2.06
	FD	102.31	**71.67 *****	101.98	**6.67 ***	101.98	2.61
Leaf N	CWM	52.41	**11.82 *****	50.37	**16.05 *****	50.04	**5.9 ****
	FD	46.30	0.09	46.51	0.07	46.46	1.93
Leaf P	CWM	50.31	**13.75 *****	49.36	**10.16 ****	48.98	**3.49 ***
	FD	51.72	**24.24 *****	52.73	**23.41 *****	52.28	**4.17***
Leaf Ca	CWM	53.17	**25.99 *****	51.99	**13.48 *****	51.70	0.34
	FD	53.27	**51.36*****	52.74	4.01	52.38	0.02

		Elevation		Plot type		Elevation x plot type	
		df	F	df	F	df	F
Leaf K	CWM	52.26	**16.36 *****	50.47	0.2	50.11	**3.21 ***
	FD	52.25	**43.93 *****	53.64	0.33	53.58	3.13
Leaf Mg	CWM	53.41	**115.64 *****	52.66	**5.44 ***	52.32	**5.59 ***
	FD	53.43	**34.64 *****	52.94	**9.87 ****	52.59	**6.58 ***
Multi-trait	FD	103	**48.41 *****	103	2.25	103	0.22

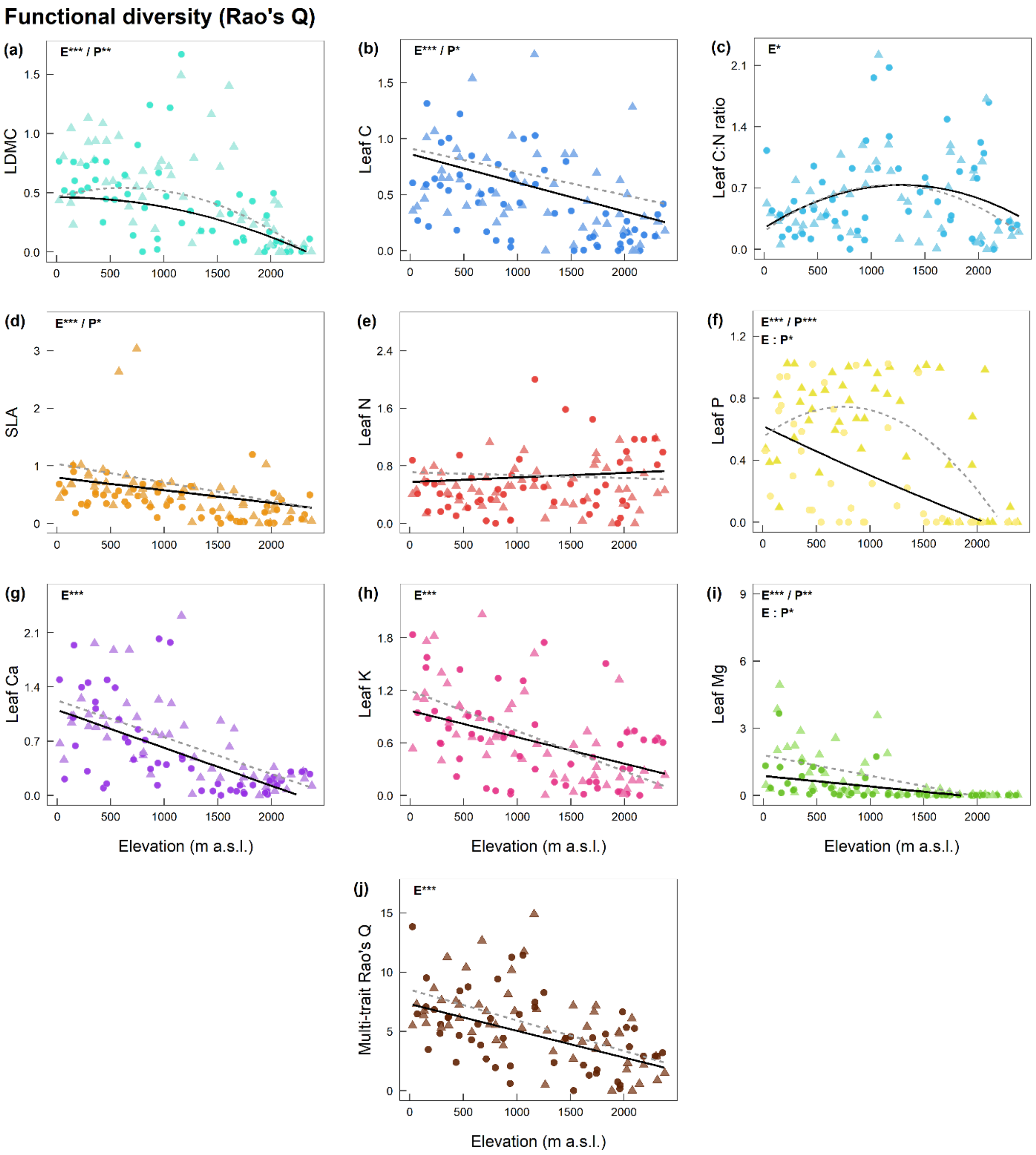

Figure 4. Relationship between elevation and functional diversity (Rao's Q) of nine functional leaf traits and multi-trait functional diversity. Regression lines are based on model predictions. Gray dashed lines and light-colored triangles represent plots next to the roadside (road plots). Black continuous lines and dark-colored circles represent plots away from the road in natural vegetation (interior plots). Significant terms are listed on top of each plot (E = elevation, P = plot type, E x P = elevation-by-plot type interaction). Significance levels < 0.001 = ***, < 0.01 = **, < 0.05 = *.

Discussion

From the set of hypotheses proposed to explain the species richness patterns along the elevational gradient on Tenerife (Fig. 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, the significant changes of functional traits along elevation did not support an effect of available area. We also rejected precipitation as an important driver of the elevational richness pattern, since the trait-elevation relationships did not match our expected patterns for this factor.

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 correlations, 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 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 conservative traits (except for LDMC) increased and community-weighted means of acquisitive traits 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.

In line with our results, a positive correlation between SLA and mean annual temperature was also reported, 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 and Nicolás, 1995).

Following our expectations for community trait responses to temperature, leaf nutrient concentrations decreased with elevation, however for some nutrients (leaf N, P and K, and leaf C:N ratio) 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). Furthermore, the low nutrient values observed in the mid-elevational vegetation belt of Canary Island pine (*Pinus canariensis*) 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). 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 at 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 and Jetz, 2007; Šímová 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 Šímová 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; Šímová 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.

Effect of disturbance on species richness-elevation patterns

Disturbance decreased with elevation and significantly increased species richness. In our study 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 favour species co-existence (Biswas and Mallik, 2010).

The above-described shift towards a conservative growth strategy with increasing elevation did not only support the role of temperature, but also the importance of disturbance in shaping the elevational species richness pattern on Tenerife. As disturbance is known to favour 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 at lower elevations and 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 mean to cope with such temperature fluctuations (Delgado et al., 2007).

In contrast, the observed decrease of functional diversity with elevation did not correspond to our expected elevational increase of functional diversity caused by disturbance. We observed road disturbance to have a positive effect on functional diversity, with higher functional diversity on roadside plots compared to natural vegetation, and at low elevations compared to high elevations. This questions our hypothesis that disturbance acts as a filter favouring acquisitive species. Rather, reduced competition through disturbance might increase heterogeneity in community, allowing acquisitive species to enter the community without excluding conservative species completely. Furthermore, non-native species might be contributing to these patters, 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).

No support for filtering through precipitation

In contrast to our assumptions based on the literature that precipitation peaks at intermediate elevations (1200-1500 m) in Tenerife (AEMET, 2012) and that precipitation favours species richness (McCain and Grytnes, 2010), we observed a linear increase of precipitation with elevation and the number of species decreased with increasing precipitation (see Online Resource 1). 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, drought does 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 in 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 ow 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.

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 community weighted trait means 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; Bello et al., 2017; Chun and Lee, 2018), but of minor importance when analysing 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).

Trait-based approach to interpret elevational species richness patterns

Because abiotic factors and related mechanisms have a predictable effect on functional traits (Diaz et al., 2004; Bruelheide et al., 2018), 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 community-weighted means 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 and 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). For example, filtering through temperature might primarily act upon growth-related traits, while disturbance might additionally select for species with small, but large numbers of 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.

Conclusions

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 multi-trait 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.

Acknowledgments

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Appendices

Online Resource 1 – Data compilation for the studied mechanisms behind the elevational species richness pattern on Tenerife;

Online Resource 2 – Elevational species richness pattern;

Online Resource 3 – Leaf trait sampling and analyses;

Online Resource 4 – Species richness in response to abiotic factors.

Online Resource 1 – *Data compilation for the studied mechanisms behind the elevational species richness pattern on Tenerife*

Climate data: Temperature and precipitation data for each sampling site were obtained from CHELSA (version 1.2, www.chelsa-climate.org), which is a global dataset of interpolated climatic variables with a spatial resolution of 30’’ over a time period of 34 years (1979-2013). Mean temperature and precipitation sum 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.

Surface area of elevational bands: 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 x 90 m at the equator). The surface area for each band (polygon) was calculated with ArcGIS Desktop software (version 10.5, ESRI, Redlands, USA).

Disturbance intensity: Disturbance intensity was recorded for each plot via classes, from 0 to 2, according to the percentage of plot area visually impacted in its vegetation or soil properties (0 = no disturbance, 1 = < 50%, 2 = > 50%). It refers not only to open soil, but also to road construction, fire and animal digging.

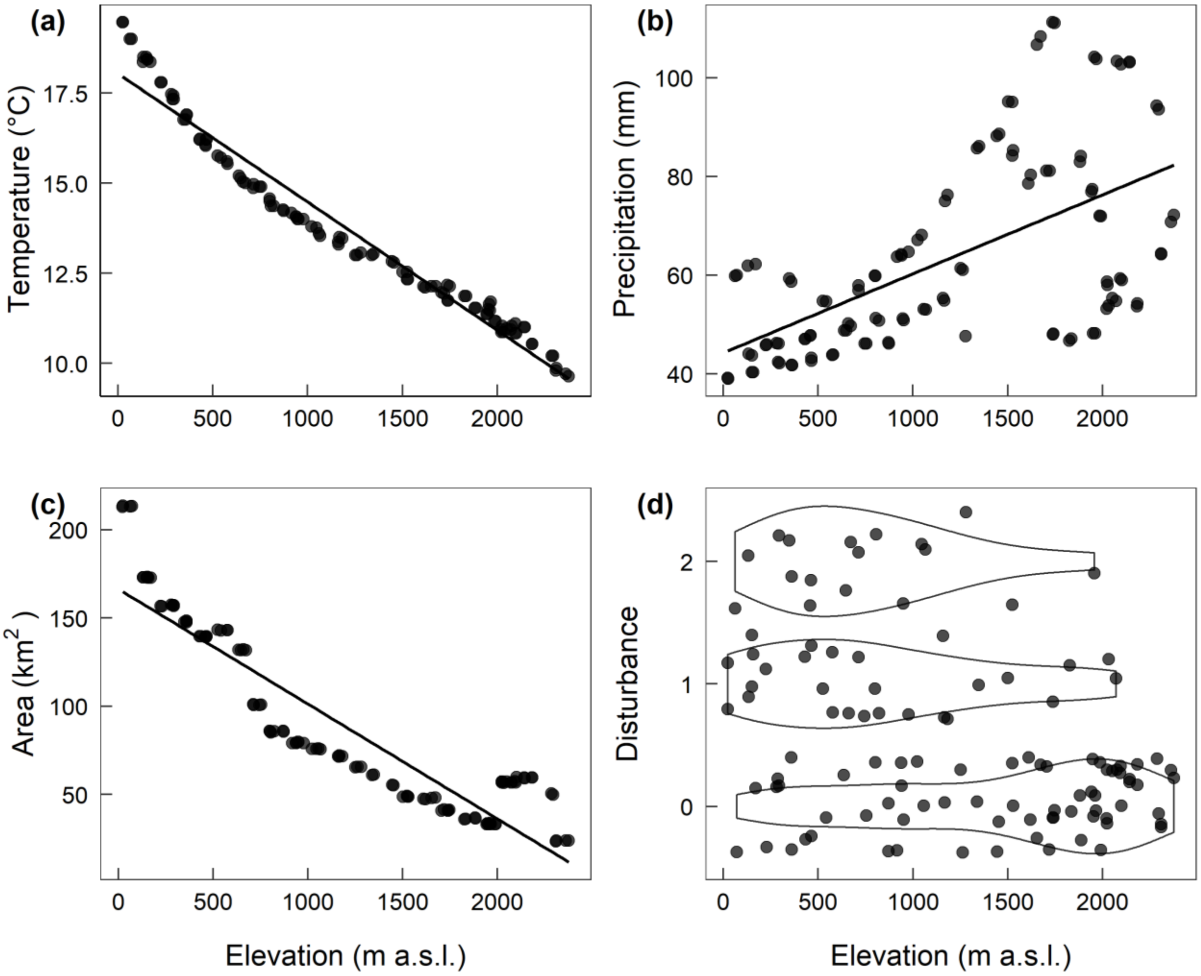

Figure S1. To check if our compiled data on elevational changes of temperature, precipitation, area and disturbance matched the described patterns in the literature, we fitted linear mixed-effects models with each of these variables as the response (except for disturbance, see below) and elevation as fixed predictor. Elevation was scaled to unit variance. Transect nested in road was added as random effect to account for the sampling design. According to our assumptions from the literature, we used the linear term of elevation in the models for temperature of the growing season and land surface area, and the second-order polynomial of elevation for precipitation of the growing season. The precipitation model was also fit with the linear term of elevation, and both models were compared via AIC. For disturbance we calculated the Spearman's rank correlation coefficient between disturbance intensity and elevation. We confirmed the assumed relationships between elevation and (a) mean temperature of the growing season ($F_{1,56.7}$ = 1237.10, $p < 0.01$), (c) land surface area ($F_{1,58.0}$ = 269.64, $p < 0.01$) and (d) disturbance intensity (rho = -0.444, $p < 0.001$). (b) Total precipitation of the growing season, however, increased linearly with elevation instead of showing the expected hump ($F_{1,66.4}$ = 129.06, $p < 0.01$). N = 111 plots sampled along three roads in Tenerife (Fig. 2). Regression lines are based on model predictions.

Online Resource 2 – Vegetation changes along the elevational gradient

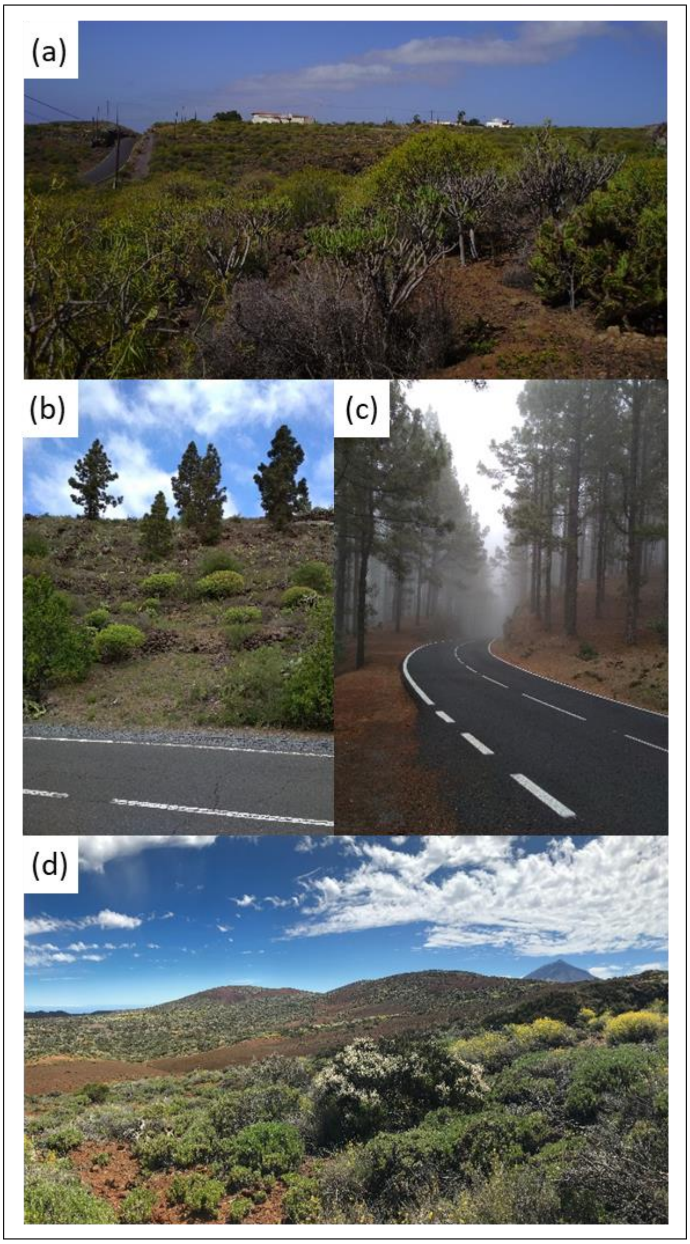

Figure S2. The elevational gradient sampled in Tenerife starts with (a) coastal halophilous vegetation and thermo-sclerophyllous scrub, follows a continuous (b) transition to (c) forests of Canary Island pine (*Pinus canariensis* C. Sm.), and ends at the high elevation plateau of Las Cañadas with (d) high mountain scrub.

Online Resource 3 – Leaf trait sampling and analyses

Table S1. Relative proportion of species cover with trait measurements per plot. Plot ID is comprised by sampling site number (1 = lowest sampling site, 20 = highest sampling site) and plot type (1 = road plot, 2 = interior plot).

Plot ID	Trait coverage		
	Road 1	**Road 2**	**Road 3**
1.1	0.89	0.89	0.92
1.2	0.89	1	0.76
2.1	0.98	0.97	0.95
2.2	0.70	0.98	0.88
3.1	0.93	0.95	0.91
3.2	0.74	0.94	0.97
4.1	0.89	0.97	0.85
4.2	0.57	1	0.96
5.1	0.90	0.96	0.96
5.2	0.84	1	1
6.1	0.95	0.88	0.82
6.2	0.91	1	0.96
7.1	0.93	1	0.89
7.2	0.59	1	0.91
8.1	0.70	0.85	0.96
8.2	0.94	1	0.92
9.1	-	0.94	0.93
9.2	-	1	0.92
10.1	-	0.93	0.91
10.2	-	0.98	1
11.1	1	0.96	0.9
11.2	-	0.99	0.93
12.1	-	1	0.97
12.2	-	0.99	1
13.1	1	0.71	1
13.2	1	1	1
14.1	1	0.87	1
14.2	1	0.99	1
15.1	1	0.91	1
15.2	1	1	1
16.1	1	-	1
16.2	1	-	-
17.1	1	0.90	-
17.2	1	0.99	1
18.1	1	1	1
18.2	1	1	1
19.1	1	1	1
19.2	1	1	-
20.1	1	1	1
20.2	1	1	1

We measured nine eco-morphological and biochemical leaf traits (Table S3.2) which reflect fundamental physiological properties related to plant resource use, growth and life strategies and for which we had clear expectations of how they respond to temperature (Wright et al., 2005), precipitation (Lang et al., 2019) and disturbance (McIntyre et al., 1999; Bernhardt-Römermann et al., 2011). Leaves collected in the field were placed in plastic bags with a moist paper towel, and stored in a cooling box. On the same day, the saturated fresh leaves were weighed (Sartorius MC1 AC210, Sartorius AG, Göttingen, Germany) and scanned with a flatbed scanner at a resolution of 300 dpi. Leaf area was calculated using the software WinFOLIA (Regent Instruments, Quebec, Canada). The samples were subsequently dried for 72 hours at 80 °C in a drying oven, and weighed again to calculate leaf dry matter content (LDMC; Table S3.2) and specific leaf area (SLA; Table S3.2) in accordance with the methods described by Kleyer et al. (2008) and Pérez-Harguindeguy et al. (2013). To determine leaf carbon, nitrogen, phosphorus, calcium, potassium and magnesium contents (leaf C, N, P, Ca, K, Mg; Table S3.2), the samples were ground in an oscillating mill (MM 400, Retsch, Haan, Germany) until they became homogeneous powder. A nitric acid digestion was carried out using 200 mg of leaf powder per sample. The liquefied sample was then used to measure leaf P with a photometric assay using ammonium heptamolybdate ($(NH_4)_6Mo_7O_{24}$) and ascorbic acid ($C_6H_8O_6$) (Pérez-Harguindeguy et al. 2013), and to determine leaf Ca, K and Mg via atomic absorption spectrometry (ContrAA 300 AAS, Analytik Jena, Jena, Germany). Five milligrams of the leaf powder were used to measure leaf C and leaf N gas-chromatographically with the Dumas method (Vario EL Cube, Elementar Analysensysteme, Langenselbold, Germany), from which we further calculated the carbon to nitrogen ratio (leaf C:N ratio).

Leaf samples were analysed within the scope of a larger pool of samples from mountain ranges around the world, which amounted to almost 3000 samples. Therefore, from the total pool of samples, we selected only a subset of samples for laboratory analyses ('calibration samples'), and predicted the trait values for the remaining samples via near-infrared reflectance spectroscopy (NIRS) as described by Foley et al. (1998) and applied for example by Proß et al. (2021). Calibration samples included different families and life-forms to cover a large trait variation (approximately 30 samples from 10 mountain regions). Firstly, leaf powder of all samples was scanned with a stationary NIR spectrometer (MPA, Bruker Optik, Ettlingen, Germany). Each sample was scanned three times and the average spectrum over the three measurements was calculated. Secondly, separate prediction models were created for each trait (Table S3.2) based on the analytical results and reflectance data of the calibration samples using Partial Least Square Regression, after an automated selection of the best spectral pre-treatment (software OPUS version 7.1, Bruker Optik, Ettlingen, Germany). Finally, using these models and the spectroscopy data, trait values for all samples were predicted. Trait values for the same species were averaged, so that we had one value per trait per species.

Within the growth-survival trade-offs described by the leaf economics spectrum, functional traits have been assigned to acquisitive (or fast) and conservative (or slow) growth strategies. Acquisitive strategies involve rapid acquisition and low conservation of resources, and are favoured under high-resource conditions (such as high temperature sites in the lowlands). Conservative strategies involve slower acquisition of resources but longer conservation, and are advantageous in low-resource conditions (such as cold sites at high elevations; Reich 2014; Table S3.2).

Table S2. Traits measured in this study and their position within the leaf economics spectrum. The first group of traits is associated with a conservative growth strategy, typically found at high elevations, while the second group of traits is associated with an acquisitive growth strategy, which is typical for lowlands. The traits are classified as eco-morphological (morph) and leaf biochemical (chem) traits. R^2 and root-mean-square error (RMSE) show the quality of the trait predictions via near-infrared spectroscopy.

Growth strategy	Trait	Abbreviation	Unit	Trait type	Formula	r^2	RMSE
Conservative	Leaf dry matter content	LDMC	mg g^{-1}	morph	Leaf dry mass / leaf fresh mass	86.64	35.50
	Leaf carbon content	Leaf C	%	chem	Percentage of leaf dry mass	85.36	1.35
	Carbon:nitrogen ratio	Leaf C:N ratio	g g^{-1}	chem	Leaf C / leaf N	-	-
Acquisitive	Specific leaf area	SLA	mm^2 mg^{-1}	morph	Fresh leaf area / leaf dry mass	88.09	20.60
	Leaf nitrogen content	Leaf N	%	chem	Percentage of leaf dry mass	93.39	0.23
	Leaf phosphorus content	Leaf P	mg g^{-1}	chem	P / leaf dry mass	60.58	0.36
	Leaf calcium content	Leaf Ca	mg g^{-1}	chem	Ca / leaf dry mass	70.66	3.41
	Leaf potassium content	Leaf K	mg g^{-1}	chem	K / leaf dry mass	70.70	6.25
	Leaf magnesium content	Leaf Mg	mg g^{-1}	chem	Mg / leaf dry mass	85.87	0.97

Online Resource 4 – Species richness in response to abiotic factors

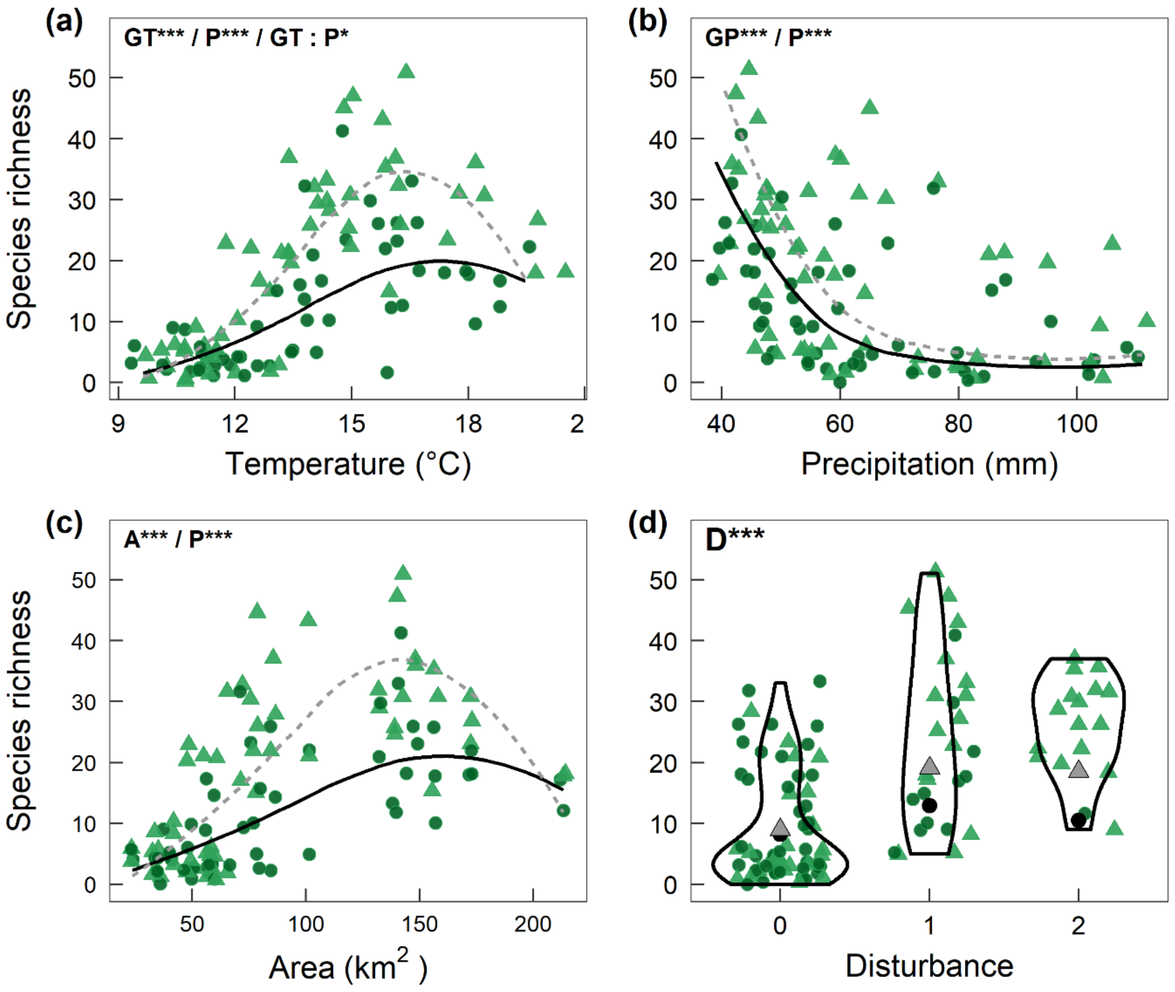

Figure S3. Species richness showed a hump-shaped relationship with (a) mean temperature of the growing season and (c) land surface area, (d) a positive relationship with disturbance intensity, and (b) an exponentially decreasing relationship with precipitation of the growing season. Roadside plots had significantly higher species richness except for the case of disturbance (Table S4.3). The increase in species richness on roadside plots compared to interior vegetation was stronger at intermediate temperatures (temperature-by-plot type interaction). Grey dashed lines and light-coloured triangles represent plots next to the roadside (road plots). Black continuous lines and dark-coloured circles represent plots away from the road in natural vegetation (interior plots). Significant terms are listed on top of each plot (E = elevation, GT = mean temperature of growing season, GP = total precipitation of growing season, A = land surface area, D = disturbance intensity, P = plot type (roadside vs interior plot). Significance levels < 0.001 = ***, < 0.01 = **, < 0.05 = *.

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CHAPTER 4

Contrasting patterns of intraspecific trait variability in native and non-native plant species along an elevational gradient on Tenerife, Canary Islands

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ANNALS OF BOTANY
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SPECIAL ISSUE ON INTRASPECIFIC VARIATION IN PLANT FUNCTIONAL TRAITS

Contrasting patterns of intraspecific trait variability in native and non-native plant species along an elevational gradient on Tenerife, Canary Islands

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- **Background and Aims** Non-native plant species are not restricted to lowlands, but increasingly are invading high elevations. While for both native and non-native species we expected variability of plant functional traits due to the changing environmental conditions along elevational gradients, we additionally assumed that non-native species are characterized by a more acquisitive growth strategy, as traits reflecting such a strategy have been found to correlate with invasion success. Furthermore, the typical lowland introduction of non-native species coming from multiple origins should lead to higher trait variability within populations of non-native species specifically at low elevations, and they might therefore occupy a larger total trait space.
- **Methods** Along an elevational gradient ranging from 55 to 1925 m a.s.l. on Tenerife, we collected leaves from eight replicate individuals in eight evenly distributed populations of five native and six non-native forb species. In each population, we measured ten eco-morphological and leaf biochemical traits and calculated trait variability within each population and the total trait space occupied by native and non-native species.
- **Key Results** We found both positive (e.g. leaf dry matter content) and negative (e.g. leaf N) correlations with elevation for native species, but only few responses for non-native species. For non-native species, within-population variability of leaf dry matter content and specific leaf area decreased with elevation, but increased for native species. The total trait space occupied by all non-native species was smaller than and a subset of that of native species.
- **Conclusions** We found little evidence that intraspecific trait variability is associated with the success of non-native species to spread towards higher elevations. Instead, for non-native species, our results indicate that intermediate trait values that meet the requirements of various conditions are favourable across the changing environmental conditions along elevational gradients. As a consequence, this might prevent non-native species from overcoming abruptly changing environmental conditions, such as when crossing the treeline.

Key words: Intraspecific trait variation, phenotypic plasticity, plant functional traits, functional diversity, elevation gradient, altitudinal gradient, alien, exotic, invasion success, forbs, near-infrared spectroscopy.

INTRODUCTION

Biological invasions are a focal topic in nature conservation, because the ‘invasive’ species among the non-native ones cause ecological damages and threaten native biodiversity (Vilà *et al.*, 2011; Simberloff *et al.*, 2013). The transportation of non-native species into new regions and their ability to successfully establish themselves and spread under a range of novel environmental conditions might be enabled by a high variability in functional traits of such species (Davidson *et al.*, 2011; Matesanz *et al.*, 2012; Colautti and Barrett, 2013). However, as yet, only a few studies have explicitly compared the intraspecific trait variability of native and non-native species along environmental gradients (e.g. Alexander *et al.*, 2009; Canessa *et al.*, 2018).

While most terrestrial ecosystems are affected by biological invasions, mountains represent a rare exception in that only recently non-native plant species have been documented to expand there, and only a small proportion of these become dominant (Becker *et al.*, 2005; Pauchard *et al.*, 2009; Alexander *et al.*, 2016). Two main mechanisms are likely to prevent plant invasions in harsh environments such as high-elevation sites: propagule limitation and biotic resistance from resident species (Zefferman *et al.*, 2015). However, increasing human influence in mountain areas enhances propagule transportation and disturbance frequency and intensity, all supporting the invasion of non-native species at high elevations. Regarding the invasion capacity of non-native species, invasion success along elevational gradients has been linked to high phenotypic plasticity (e.g. Ansari and Daehler, 2010), and genetic adaption to local environmental conditions (e.g. Monty and Mahy, 2009; Haider *et al.*, 2012). The recent increase of mountain invasions is cause for particular concern due to the ecosystem services these regions provide and the role they play in preserving biodiversity (Nagy and Grabherr, 2009; Pauchard *et al.*, 2009). Concomitantly, these incipient invasions can provide a basis for understanding how non-native plant species expand into these high-elevation regions (Alexander *et al.*, 2011).

Elevational gradients represent a combination of various changing environmental factors, including colder climate, decreasing soil depth and less fertile soil, but also reduced human disturbance due to difficult terrain (Körner, 2003). Non-native species are in most cases introduced in and adapted to human-disturbed habitats at low elevations (Pauchard *et al.*, 2009; Lembrechts *et al.*, 2016) and are likely to have higher intraspecific trait variability in these areas due to receiving germinules from a wide variety of population and geographical backgrounds (Alexander *et al.*, 2011). Related to this, non-native species often exhibit acquisitive growth strategies involving rapid accumulation of biomass (Dawson *et al.*, 2012), larger leaf-area allocation (e.g. higher specific leaf area (SLA); van Kleunen *et al.*, 2010), higher leaf nitrogen and lower leaf carbon content (Henn *et al.*, 2019), and increased nitrogen and phosphorus use efficiency (Drenovsky *et al.*, 2008; Funk, 2008). In contrast, the long-term community assembly of native species might have led to an elevational distribution of species according to their trait suitability for the respective habitat. Thus, native plant species at high elevations typically possess functional traits suited to persist under lower temperatures, a shorter growing season and other elevation-related factors (Körner, 1989, 2003; Read *et al.*, 2014; Rosbakh *et al.*, 2015; Bucher *et al*., 2016, 2018, 2020). Typical traits for plant species exposed to these conditions include an increased leaf dry matter content (LDMC), which is concurrent with a decrease in SLA, and increased leaf nitrogen and phosphorus contents, reflecting an overall more conservative growth strategy (Körner, 1989, 2003; Dubuis *et al.*, 2013). Due to the long-term evolution of native species populations along elevational gradients, we might expect that the basis of intraspecific trait variability are genetic adaptations to the specific local environmental conditions. Additionally, long-term evolution under less favourable environmental conditions is expected to result in high similarity of plant individuals and thus reduced trait variability within populations (‘environmental filtering’; Ordoñez *et al.*, 2009).

In mountain regions, non-native species predominantly spread along and establish in roadside habitats (Seipel *et al.*, 2012; Haider *et al.*, 2018). Therefore, traits of non-native species in mountain areas are not only a response to the environmental gradients described above, but also a result of the specific conditions of ruderal roadside habitats. In particular, such specific suites of traits are favoured that relate to short generation times or high dispersal rates; while clonality, a long lifespan and shade tolerance are important for colonization of adjacent more natural, non-roadside areas (McDougall *et al.*, 2018).

Intraspecific trait variability, irrespective of its source being identified as phenotypic plasticity, genetic differentiation or both, has been found to support the invasion processes of non-native plants in a variety of ways. For instance, Asteraceae forb species non-native to Europe or North America showed similar elevational clines of seed mass and plant height along elevational gradients in their native and introduced ranges, possibly caused by local adaptation (Alexander *et al.*, 2009). In a glasshouse study with the herbaceous species *Polygonum cespitosum*, which is invasive in North America, seeds from populations distributed across a wide geographical range were planted in a variety of light and moisture treatments (Matesanz *et al.*, 2012). The authors described that individuals from all populations varied in growth, fitness and leaf traits across the different experimental conditions (i.e. displaying high phenotypic plasticity in all populations). Furthermore, intraspecific variability of SLA, leaf chlorophyll concentration and the root-to-shoot biomass ratio of non-native species in a tropical forest had a significant positive correlation with the range that species were able to occupy along a light gradient (Canessa *et al.*, 2018). Based on such findings, it can be assumed that high intraspecific trait variability resulting from both phenotypic plasticity and genetic differentiation might also support the upward spread of non-native species along elevational gradients.

To compare intraspecific trait variability between native and non-native plant species, we conducted a field study along a gradient spanning almost 2000 m in elevation on Tenerife, Canary Islands. Because mountain roads are the primary pathway for non-native species to spread towards higher elevations (Seipel *et al.*, 2012; Haider *et al.*, 2018), we focused on roadside habitats. In our study area on Tenerife, roadside habitats were characterized by more open dry conditions compared to adjacent more natural areas. By contrast, roadside and non-roadside habitats did not differ in terms of soil temperature and showed the same magnitude of temperature decrease with increasing elevation (own data; unpublished), the latter forming the main environmental gradient in our study. For 11 native and non-native species, ecomorphological and leaf biochemical traits characterizing the position of a plant in the leaf economics spectrum from acquisitive to conservative growth strategies (Wright *et al.*, 2004; Reich, 2014) were measured in 83 populations along the elevational gradient, and intraspecific trait variability was calculated and compared within as well as between populations of native and non-native species. Our aim was to investigate the magnitude of trait variability, irrespective of it arising from plastic responses to the environment or from genetic differentiation, which from a functional point of view is not of primary interest. Rather, we intend to give a general idea of non-native species’ capacity to cope with the steep environmental gradients in mountain areas (compare Milla *et al.*, 2009; Albert *et al.*, 2010).

We tested the following three hypotheses as visualized in Fig. 1:

H1: With increasing elevation, acquisitive growth strategies (e.g. high SLA, high leaf nitrogen content) are increasingly replaced by conservative growth strategies (e.g. high LDMC, high leaf carbon to nitrogen ratio). The change of traits with elevation is equally strong within non-native species and native species (identical slope of the red line in Fig. 1). However, on average, non-native species follow a more acquisitive growth strategy compared to native species (higher intercept for native species in Fig. 1).

H2: Across the elevational gradient, within-population trait variability is lower for native compared to non-native species. For native species, we expect the amount of within-population trait variability to remain constant across elevations because these populations are the results of long-lasting environmental filtering processes that in their intensity should not vary with elevation (vertical blue arrows with constant length in Fig. 1A). By contrast,

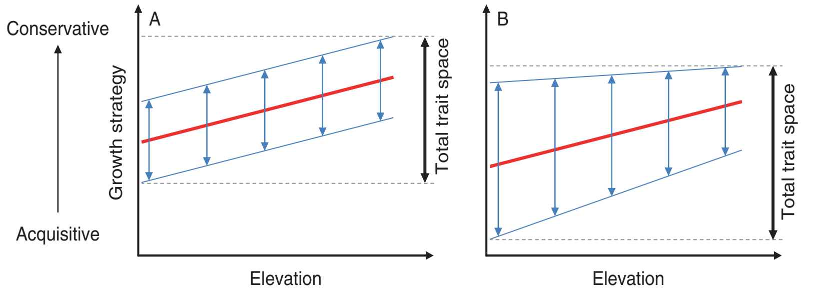

FIG. 1. Expectations for changes in growth strategy and within-population trait variability with elevation, and total trait space occupied by (A) native and (B) non-native species. For both native and non-native species we expected acquisitive growth strategies to be replaced by conservative growth strategies with increasing elevation (bold red line; Hypothesis 1). Trait variability within populations (vertical blue arrows) was expected to be constant along the elevational gradient for native species, but to decrease with elevation for non-native species (Hypothesis 2). As a consequence, the total trait space occupied (bold vertical black arrows) was assumed to be larger for non-native species (Hypothesis 3).

non-native species are expected to display high within-population trait variability in the more favourable parts of the elevational gradient and comparatively lower within-population trait variability in adverse parts (vertical blue arrows with decreasing length in Fig. 1B).

H3: Overall, the group of non-native species covers a larger trait space compared to the group of native species (longer vertical black arrow for non-native species in Fig. 1).

MATERIAL AND METHODS

Study area

The field study was carried out on Tenerife, Spain. With c. 2000 km^2 Tenerife is the largest island in the Canary archipelago and is located off the African coast at 28.28°N, 16.15°W. The centre of the island is dominated by the volcanic cone of Pico del Teide, which rises to 3718 m a.s.l. North-east trade winds divide the island into two climatically different parts: the temperate and moist northern half and the more arid south (Fernández-Palacios, 1992) where our studied elevational gradient was located. The natural vegetation along the southern slope begins with coastal and thermophilous scrub in the areas up to 1000 m a.s.l., transitions to forests of Canary pine (*Pinus canariensis*) up to 2000 m a.s.l. which are followed by high mountain scrub on the central plateau of Las Cañadas from 2000 to 2500 m a.s.l. The alpine regions close to the summit are only inhabited by a few specialized plant species. While the coastal regions of the island are densely settled, the extent of human influence and the resulting disturbance decreases with increasing elevation and is lowest above 1000 m a.s.l. (Otto *et al.*, 2014).

Sampling design and study species

Sampling was conducted during the growing season from April to May 2018 along three roads which ran from the coast to the central plateau (Fig. 2). The three roads are paved over the entire length of the gradient, are open to traffic throughout the year, and receive similar amounts of traffic (Arévalo *et al.*, 2010). As this project was conducted within the framework of the Mountain Invasion Research Network (MIREN; Kueffer *et al.*, 2014), we used a subset of the permanent plots established in 2008 according to the standardized protocol of the global MIREN survey (Arévalo *et al.*, 2010; Seipel *et al.*, 2012; Haider *et al.*, 2018). The plots have a size of 50 × 2 m, with the long side parallel and directly adjacent to the road. To avoid a bias in sampling date, we began in the lowest plots of all roads and moved up the elevational gradient over the course of the fieldwork, following the phenology of the different vegetation belts described above (Fig. 2). The majority of sampled individuals of all species were either flowering or fruiting, supporting our intention to measure leaves only of fully developed plants (Supplementary Data, Table S1).

Eleven forb species that exhibited sufficient abundance and large elevational ranges were sampled (Table 1). All species were present in the majority of the plots in 2008 when the first vegetation survey of our permanent plots was made (Arévalo *et al.*, 2010). With the exception of *Calendula arvensis* and *Volutaria canariensis*, which belong to the family Asteraceae, all sampled species belong to different plant families (Table 1). Forbs were selected because they are the only growth form of which native as well as non-native species occur along large parts of the elevational gradient. However, an intrinsic limitation of our study system is that native forb species generally occupy narrower elevational bands, reaching lower maximal elevations compared to non-native species. This restriction needs to be considered when interpreting differences between the groups of native and non-native species.

Species were assigned a floristic status (native or non-native) based on the ‘Lista de especies silvestres de Canarias’ (Acebes Ginovés *et al.*, 2010), and where the information from that source was ambiguous, other published studies from Tenerife were consulted in addition (Arévalo *et al.*, 2005; Haider *et al.*, 2010). Within the group of non-native species, only *Eschscholzia californica* is classified as an invasive species on Tenerife (Acebes Ginovés *et al.*, 2010; Table 1). Among the native species, *Bituminaria bituminosa* and *Rumex vesicarius* also occur as non-native species outside their native range (Dawson *et al.*, 2012; Table 1). A coarse analysis (not shown) revealed that the studied non-native species have larger climate niches compared to the studied native species, supporting our

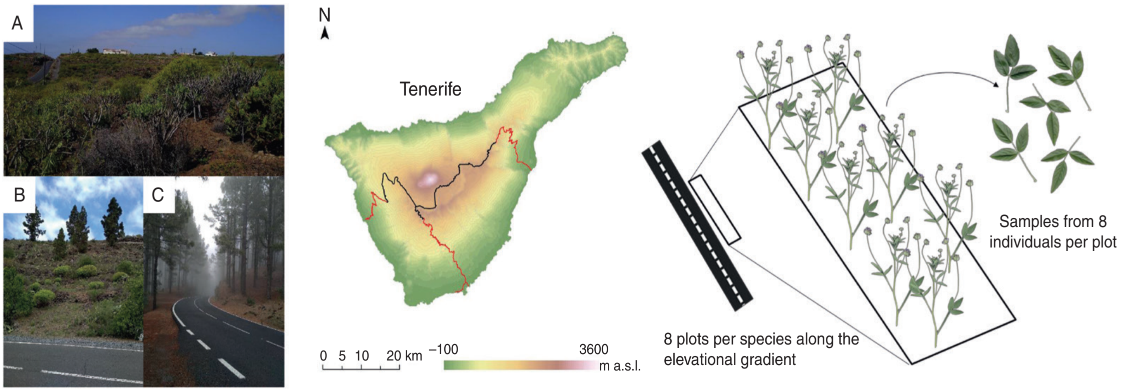

FIG. 2. Map of the island of Tenerife, with the three roads used for sampling. The roads start in the vegetation zone of coastal and thermophilous scrub (A), follow a continuous transition (B) to forests of Canary pine (C), and end on the central high-elevation plateau with high mountain scrub. Red parts indicate the actual extent of each road where samples were taken. In each plot, we sampled and measured leaves from eight individuals per species.

TABLE 1. *Overview of the study species, their taxonomic family, floristic status on Tenerife (based on Arévalo et al., 2005; Acebes Ginovés et al., 2010; Haider et al., 2010), invasiveness and the elevational range in which they were sampled. For non-native species, '+' means that the species is considered invasive in the sense of rapidly spreading and causing ecological harm, and '–' means that the species is introduced, but not considered harmful (yet) (based on Acebes Ginovés et al., 2010). For native species, we applied the approach of Dawson et al. (2012) and counted the number of global regions mentioned in the 'Global compendium of weeds' (Randall, 2017) which are not part of the species' natural range*

Species	Family	Floristic status	Invasiveness	Elevational range (m)
Bituminaria bituminosa	Fabaceae	Native	1	340–1140
Fagonia cretica	Zygophyllaceae	Native	0	55–505
Forsskaolea angustifolia	Urticaceae	Native	0	55–1005
Rumex vesicarius	Polygonaceae	Native	1	130–405
Volutaria canariensis	Asteraceae	Native	0	55–440
Calendula arvensis	Asteraceae	Non-native	–	405–1020
Erodium cicutarium	Geraniaceae	Non-native	–	340–1925
Eschscholzia californica	Papaveraceae	Non-native	+	875–1635
Hirschfeldia incana	Brassicaceae	Non-native	–	340–1425
Malva parviflora	Malvaceae	Non-native	–	130–1140
Silene vulgaris	Caryophyllaceae	Non-native	–	755–1900

assumption of larger trait variability for non-native species (Hypothesis 3).

While *C. arvensis*, *Erodium cicutarium*, *Es. californica*, *R. vesicarius* and *V. canariensis* are annual or biennial plants, the other species are perennial (Muer *et al.*, 2016). We aimed to sample each of the 11 species in eight plots covering the whole species' elevational range. This could be realized for most species and in the case of *Forsskaolea angustifolia* even be overachieved with ten plots sampled, while the sampling goal could not be met for *Malva parviflora* or *R. vesicarius* (five plots), or *V. canariense* (seven plots). In each plot and for each species, eight individuals (representing one population) were measured and 10–50 leaves per individual (depending on leaf size) were collected for further analyses. Overall, 83 populations were sampled in 29 different plots, resulting in 664 individual leaf samples.

Trait measurements

Leaves collected in the field were placed in zip-lock bags with a moist tissue inside, and stored in a cooling bag. On the same day, the saturated fresh leaves were weighed (Sartorius MC1 AC210, Sartorius AG, Göttingen, Germany) and scanned with a flatbed scanner at a resolution of 300 dpi. Leaf area was calculated using the software WinFOLIA (Regent Instruments, Quebec, Canada). The samples were subsequently dried for 72 h at 80 °C in a drying oven, and weighed again to calculate LDMC (leaf dry mass divided by leaf fresh mass; Table 2) and SLA (fresh leaf area divided by leaf dry mass; Table 2) in accordance with the methods described by Kleyer *et al.* (2008) and Pérez-Harguindeguy *et al.* (2013).

To determine leaf carbon, nitrogen, phosphorus, calcium, potassium and magnesium contents (leaf C, N, P, Ca, K, Mg; Table 2), the samples were ground in an oscillating mill (MM 400, Retsch, Haan, Germany) until they became homogeneous powder.

A nitric acid digestion was carried out using 200 mg of leaf powder per sample. The liquefied sample was then used to measure leaf P with a photometric assay using ammonium heptamolybdate ($(NH_4)_6Mo_7O_{24}$) and ascorbic acid ($C_6H_8O_6$) (Pérez-Harguindeguy *et al.*, 2013), and to determine leaf Ca, K and Mg via atomic absorption spectrometry (ContrAA

Table 2. *Traits measured in this study and their position within the leaf economics spectrum. The first group of traits is associated with a conservative growth strategy, typically found at high elevations, while the second group of traits is associated with an acquisitive growth strategy, which is typical for lowlands. The traits are classified as eco-morphological (morph) and leaf biochemical (chem) traits.* R^2 *and root-mean-square error (RMSE) show the quality of the trait predictions via near-infrared spectroscopy. Trait means for the eco-morphological and leaf biochemical traits for each species are given in Supplementary Data Table S3.*

Growth strategy	Trait	Abbreviation	Unit	Trait type	Formula	r^2	RMSE
Conservative	Leaf dry matter content	LDMC	mg g^{-1}	morph	Leaf dry mass/leaf fresh mass	90.23	0.02
	Leaf carbon content	Leaf C	%	chem	Percentage of total dry mass	80.50	2.91
	Carbon:nitrogen ratio	Leaf C:N ratio	Non-dimensional	chem	Leaf C/leaf N	60.40	5.44
Acquisitive	Plant height	Height	cm	morph	–	–	–
	Specific leaf area	SLA	cm^{-2} g^{-1}	morph	Fresh leaf area/leaf dry mass	84.85	25.1
	Leaf nitrogen content	Leaf N	%z	chem	Percentage of total dry mass	88.10	0.37
	Leaf phosphorus content	Leaf P	µmol g^{-1}	chem	P/leaf dry mass	49.02	7.22
	Leaf calcium content	Leaf Ca	µmol g^{-1}	chem	Ca/leaf dry mass	82.36	54.3
	Leaf potassium content	Leaf K	µmol g^{-1}	chem	K/leaf dry mass	62.01	146
	Leaf magnesium content	Leaf Mg	µmol g^{-1}	chem	Mg/leaf dry mass	81.22	61

300 AAS, Analytik Jena, Jena, Germany). Five milligrams of the leaf powder was used to measure leaf C and leaf N gas-chromatographically with the Dumas method (Vario EL Cube, Elementar Analysensysteme, Langenselbold, Germany), from which we further calculated the carbon to nitrogen ratio (leaf C:N ratio).

Due to the high number of leaf samples, we selected only a subset for the laboratory analyses listed above ('calibration samples'), and predicted the trait values for the remaining samples via near-infrared reflectance spectroscopy (NIRS) as described by Foley *et al.* (1998). For the calibration samples, one individual from each plot and species was randomly selected, giving a total of 83 samples. First, leaf powder of all samples was scanned with a stationary NIR spectrometer (MPA, Bruker Optik, Ettlingen, Germany). Each sample was scanned three times and the average spectrum over the three measurements was calculated. Second, separate prediction models were created for each trait (LDMC, SLA and leaf biochemical traits; Table 2) based on the analytical results and reflectance data of the calibration samples (software OPUS version 7.1, Bruker Optik). Finally, using these models and the spectroscopy data, trait values for all samples could be predicted. The quality of the prediction models ranged from $r^2 = 0.49$ (leaf P) to $r^2 = 0.90$ (LDMC; Table 2). Although using predictions with only moderate coefficient of determination runs the risk of increased β-errors, namely failing to detect an existing relationship, we included them in the further analyses because this conservative approach does not increase the risk of false positive results.

In total, ten eco-morphological and leaf biochemical traits were analysed (Table 2).

Statistical analysis

All statistical analyses were carried out in R version 3.5.0 (R Core Team, 2018). To test our hypothesis on intraspecific trait changes along the elevational gradient (Hypothesis 1), we first conducted a redundancy analysis (rda function in the vegan package; Oksanen *et al.*, 2018) to investigate whether elevation, floristic status (native or non-native) and their interaction significantly affected the trait combinations (only including plant individuals with values for all traits; $n = 420$). Second, to explore the individual responses of the different traits, we fitted linear mixed-effects models using trait values from all measured individuals as separate data points ($n = 664$). These models were fitted with each of the ten eco-morphological and leaf biochemical traits as the response variable (Table 2), and elevation, floristic status (native or non-native) and their interaction as fixed effects. Species identity and plot were included in the models as crossed random factors.

To verify whether there was an important influence of phylogeny in the ten eco-morphological and leaf biochemical traits (Table 2) and floristic status (native or non-native), we tested for a phylogenetic signal in these. We constructed a phylogenetic tree for the 11 studied species with the function phylo.maker in the R package V.PhyloMaker (Jin and Qian, 2019), and calculated Blomberg's K and Pagel's λ for each trait and floristic status with the function phylosig (package phytools; Revell, 2012) (cf. Supplementary Data, Table S2 for more details on the methods and results). We did not find a phylogenetic signal either for the traits or for floristic status. This means that there is no relationship between the trait values and the phylogeny of our studied species, and that the non-native species were phylogenetically not more similar or distant to each other compared to the sampled native species (cf. Münkemüller *et al.*, 2012; Table S2). Therefore, we did not include a phylogenetic correction in the models described above and in all further analyses.

To test whether within-population trait variability changes with elevation (Hypothesis 2), we calculated Rao's quadratic entropy (Rao's Q; Rao, 1982; Botta-Dukát, 2005) for each population ($n = 83$), using the equation in the FD package (Laliberté and Legendre, 2010):

$$\textit{Within-population trait variability} = \sum\nolimits_{(i=1)}^{(N-1)} \sum\nolimits_{(j=i+1)}^{N} p_i p_j d_{ij}$$

In contrast to the usual method for calculating Rao's Q of plant communities, where the species' trait distances are weighted by its relative abundance in the community, the within-population trait variability corresponds to the sum of all pairwise functional distances between individuals weighted by their relative abundances in the population. Therefore, N here equals the number of individuals in a population (with few exceptions, $N = 8$), p_i and p_j are the relative abundances of individuals i and j (the abundance of each individual is equal to one), and d_{ij} is the trait distance between individuals i and j in a population. Thus, eqn (1) measures the mean functional distance between randomly chosen individuals in a population. The calculation of within-population trait variability was done for each trait separately and for all traits combined, using the FD package (R package FD; Laliberté *et al.*, 2014) and scaling trait values to unit variance. We then fitted linear mixed-effects models with the within-population trait variability as the response variable, and elevation, floristic status (native or non-native) and their interaction as fixed effects. As for the previous models, species identity was included as a random factor.

All mixed-effects models were fitted with the function lmer in the R package lmerTest (Kuznetsova *et al.*, 2017), and *P*-values were calculated from *F*-statistics of type III sum of squares with the Satterthwaite approximation to estimate the denominator degrees of freedom.

Where interactions in any of the models yielded no significant results, the models were simplified by removing the interaction term and refitted.

To test our third hypothesis on how native and non-native species differ in their total trait space, we first performed a principal component analysis (PCA) including the ten eco-morphological and leaf biochemical traits scaled prior to the analysis. Second, we calculated functional richness (FRic) across all native and across all non-native species individuals with both single- and multitrait approaches (R package FD; Laliberté *et al.*, 2014). For the case of single traits, the functional richness of each trait corresponds to the trait range, calculated as Euclidean distance. For the case of multitrait analysis, functional richness is the minimum convex hull volume of the observations of the ten traits included for each of the two groups of species (native and non-native, respectively) distributed in a ten-dimensional trait space (Villéger *et al.*, 2008). The multitrait space (convex hull volume) is analogous to Hutchinson's multidimensional niche concept, with each functional trait corresponding to a different dimension occupied by species or individuals according to their trait values (Rosenfeld, 2002).

Because the PCA displayed the gradient from conservative to acquisitive traits, we also used it to test if the location of the centroid of native and non-native species differed along the PCA axes (Hypothesis 1), using the envfit function in the vegan package (Oksanen *et al.*, 2018).

RESULTS

Elevational trait patterns

The redundancy analysis (RDA; total inertia: 8.69; proportion explained by constrained eigenvalues: 0.455; proportion explained by unconstrained eigenvalues: 0.545) showed that elevation had a significant effect on the trait combinations ($F = 20.24$, $P < 0.001$). Separate mixed-effects models revealed that across all sampled individuals, leaf N and the leaf cation contents decreased significantly with increasing elevation (Fig. 3), while leaf C and leaf C:N ratio increased significantly with elevation (Table 3; Fig. 3B, C). However, except for leaf C (~3 % overall increase) and leaf Ca (~40 % overall decrease), these responses were mainly driven by trait changes in native species, for which leaf N, leaf K and leaf Mg decreased by about 40 % and leaf C:N ratio increased by about 70 % with increasing elevation. In contrast, for non-native species, these traits remained rather constant along the elevational gradient. For LDMC and plant height we did not find a significant main effect of elevation across native and non-native species. While both traits increased with elevation for native species (~12 % for LDMC and >100 % for plant height; Fig. 3A, D), they (slightly) decreased for non-native species (~3 % and 30 %, respectively). There were no significant changes in SLA and leaf P along the elevational gradient. We did not detect any differences between the species' mean trait values for native compared to non-native species (Table 3; Supplementary Data Table S3).

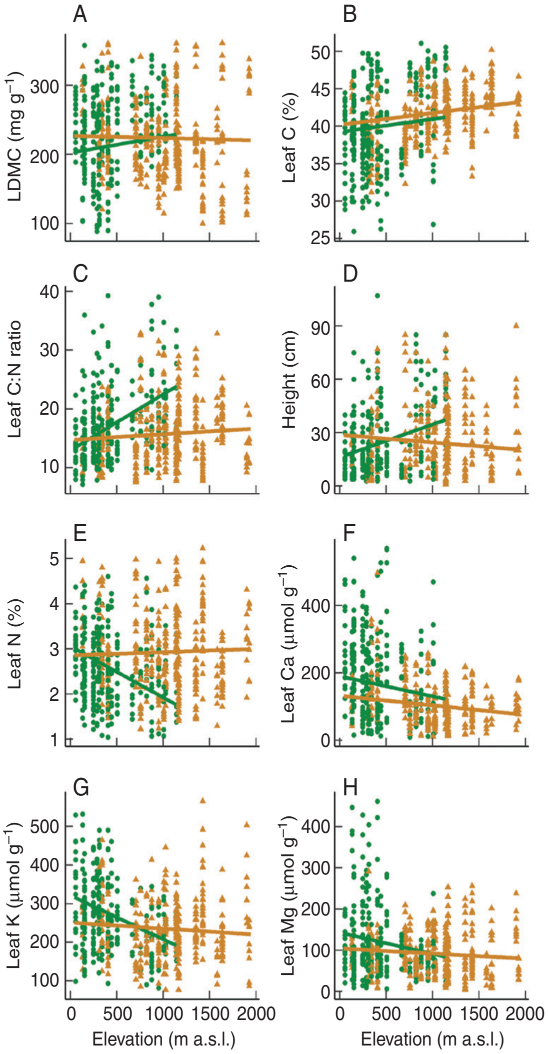

FIG. 3. Significant trait changes along the elevational gradient for 11 native and non-native forb species ($n = 664$). Traits are sorted by their association with either conservative (A–C) or acquisitive growth strategy (D–H). Regression lines are based on model predictions (Table 3). Green lines and points represent native species, while orange lines and triangles represent non-native species.

The differing responses to elevation of native and non-native species were also reflected in the RDA, revealing a significant interacting effect of elevation and floristic status ($F = 12.89$, $P < 0.001$). Removal of the interaction resulted in a higher Akaike's information criterion value (953 vs. 942 including the interaction), i.e. in a lower explanatory power of the model.

Within-population trait variability

Along the elevational gradient, the change of within-population trait variability (calculated as Rao's Q) of LDMC, leaf C:N ratio and SLA differed significantly between native and non-native species (Table 4). The within-population trait variability increased for native species by 300 % (LDMC; Fig. 4A), 800 % (leaf C:N ratio; Fig. 4B) and 80 % (SLA; Fig. 4C). For non-native species it decreased (by 95 % for LDMC and by 70 % for SLA; Fig. 4A, C) or remained constant (leaf C:N ratio; Fig. 4B). All other traits measured did not display any changes of within-population variability along the elevational gradient (Table 4). Within-population variability of LDMC was about 70 % higher for native than for non-native species, but we did not find any other significant differences in within-population trait variability between the groups of native and non-native species.

Total trait space

In the PCA including the ten eco-morphological and leaf bio-chemical traits (Table 2), the first axis was mainly associated with leaf C:N ratio (negatively), and leaf K and leaf P (positively), and explained 31.8 % of the observed variance (Fig. 5). The second axis of the PCA explained 22.7 % of the trait variability and was mainly associated with leaf Ca (positively) and

TABLE 3. *Results from the linear mixed-effects models for traits of all individuals sampled as a response to elevation and floristic status (native or non-native). Traits are ordered by their association with either a conservative or acquisitive growth strategy (Table 2).* F-*values and* P-*values, taken from type III sum of squares with the Satterthwaite approximation to estimate the denominator degrees of freedom (d.f.), are indicated in bold text when significant* (P < *0.05). If the interaction was not significant, the model was refitted without the interaction*

	Fixed effects								
	Elevation			Floristic status			Elevation × floristic status		
Response traits	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
LDMC	49.61	1.22	0.275	9.79	0.42	0.53	490.78	**4.65**	**0.031**
Leaf C	41.67	**7.27**	**0.010**	9.28	0.15	0.71			
Leaf C:N ratio	51.50	**18.18**	**<0.001**	29.57	1.04	0.32	331.38	**20.73**	**<0.001**
Height	56.46	3.86	0.054	12.26	1.89	0.19	384.97	**16.73**	**< 0.001**
SLA	36.95	2.23	0.144	9.11	0.00	0.96			
Leaf N	59.45	**9.06**	**0.004**	19.36	0.45	0.51	369.90	**19.06**	**<0.001**
Leaf P	52.53	2.59	0.114	9.35	0.00	1.00			
Leaf Ca	42.53	**4.77**	**0.035**	9.59	0.88	0.37			
Leaf K	45.26	**10.22**	**0.003**	16.25	3.72	0.07	388.33	**11.16**	**<0.001**
Leaf Mg	85.48	**13.33**	**<0.001**	10.19	0.89	0.37	212.44	**5.91**	**0.016**

TABLE 4. *Results from the linear mixed-effects models for within-population trait variability (measured as Rao's Q) of each trait and all traits combined (convex hull volume), using elevation, floristic status (native or non-native) and their interaction as fixed effects. Traits are ordered by their association with either acquisitive or conservative growth strategies.* F-*values and* P-*values, taken from type III sum of squares with the Satterthwaite approximation to estimate the denominator degrees of freedom (d.f.), are indicated in bold text when significant* (P < *0.05). When the interaction was not significant, the model was refitted without the interaction*

	Fixed effects								
	Elevation			Floristic status			Elevation × floristic status		
Response traits	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
LDMC	63.41	3.64	0.061	34.40	**4.75**	**0.036**	63.41	**23.23**	**<0.001**
Leaf C	78.06	0.00	0.966	11.74	3.87	0.073			
Leaf C:N ratio	44.15	**14.65**	**<0.001**	23.74	0.41	0.528	44.15	**14.05**	**0.001**
Height	74.99	0.04	0.835	11.82	0.13	0.723			
SLA	70.83	0.47	0.494	30.99	0.12	0.729	70.83	**5.04**	**0.028**
Leaf N	79.84	1.97	0.164	10.02	0.11	0.744			
Leaf P	73.76	0.14	0.711	9.33	1.48	0.254			
Leaf Ca	78.00	0.01	0.923	13.17	2.64	0.128			
Leaf K	63.15	0.02	0.899	15.28	0.15	0.702			
Leaf Mg	74.71	0.56	0.456	9.47	0.76	0.404			
Convex hull volume	72.00	1.73	0.192	72.00	0.01	0.934			

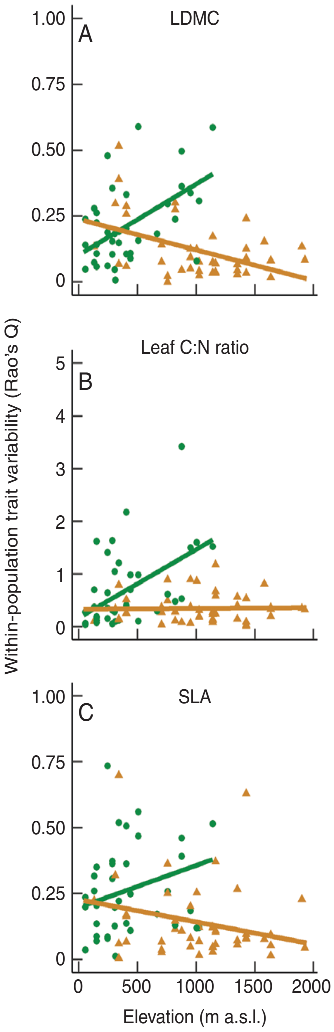

FIG. 4. Significant elevational change of within-population trait variability (n = 83) as measured by Rao's Q for LDMC (A), leaf C:N ratio (B) and SLA (C). Regression lines are based on model predictions (Table 4). Green lines and points represent native species, while orange lines and triangles represent non-native species.

plant height (negatively). The leaf economics spectrum (Wright *et al.*, 2004; Reich, 2014) was linked to the first PCA axis, with traits reflecting a conservative growth strategy (high LDMC and leaf C:N ratio) and traits reflecting an acquisitive growth strategy (high SLA, leaf N and leaf P) pointing in opposite directions. Fitting floristic status (native or non-native) to the PCA showed that the position of the centroids of both species groups along the first axis did not differ ($P = 0.784$, $r^2 = 0.0002$), and thus that non-native species were not characterized by a more acquisitive growth strategy compared to native species. Also the linear mixed-effects models for separate traits did not show any differences between the species groups (Table 3).

The total trait space (calculated as functional richness) of native species was between ~20 % (height, leaf Ca) and 200 % (leaf P) larger than that of non-native species for seven out of ten traits, and 300 % larger in the multitrait analysis (Supplementary Data, Table S4). In contrast, the total trait space of LDMC, leaf N and leaf K was up to 12 % larger for non-native compared to native species. In line with the smaller convex hull volume (multitrait functional richness) of non-native species, the trait space visualized in the PCA was smaller for non-native species and a subset of the native species' trait space. Specifically along the second axis (associated with leaf Ca), native species were more dispersed.

While the trait space of most species was strongly overlapping, *R. vesicarius* had the largest expansion along the first PCA axis and *F. angustifolia* the largest along the second axis (Supplementary Data, Fig. S1).

DISCUSSION

To understand the fairly recent phenomenon of plant invasions in mountain areas (Pauchard *et al.*, 2009; Alexander *et al.*, 2016) and how these introduced species manage to reach high elevations, we compared intraspecific trait variability of 11 native and non-native plant species by measuring functional traits from several populations per species along an elevational gradient on Tenerife. We found that non-native and native species differed in their trait response to elevation. Native species responded to elevation in the majority (8 out of 10) of the traits measured. In contrast, non-native species only barely showed trait changes in response to the varying local conditions along the elevational gradient. Surprisingly, for native species, we did not find any indications for environmental filtering with increasing elevation. Only for non-native species did within-population trait variability of LDMC and SLA decrease along the elevational gradient. For our studied species, non-native species occupied a subset of the total trait space occupied by native species.

Elevational trait patterns

We expected acquisitive growth strategies to be increasingly replaced by conservative growth strategies with increasing elevation (Hypothesis 1). Accordingly, leaf C and leaf Ca showed positive and negative correlations, respectively, with elevation for both native and non-native species. In addition, this hypothesis was confirmed for native plant species, which exhibited further trait shifts with elevation, such as increasing LDMC and leaf C:N ratio, but decreasing leaf mineral nutrients (N, K, Mg), as also described by several studies in different regions and for different life-forms (Cordell *et al.*, 1998; Wright *et al.*, 2004; Dubuis *et al.*, 2013; Liu *et al.*, 2016; Pfennigwerth *et al.*, 2017). The results thus support the general idea that species occurring along environmental gradients exhibit at the less benign end of the gradient shifts in traits towards the 'slow-return' of the leaf economics spectrum, with low carbon fixation rates and nutrient contents, associated with longer leaf lifespans and thicker, denser leaves (Reich *et al.*, 2003). These 'slow' or conservative traits are particularly advantageous under low-resource conditions, such as high-elevation areas, because resource conservation confers these plants with the ability to better cope with stress, which can increase their survival chances. Interestingly, although the

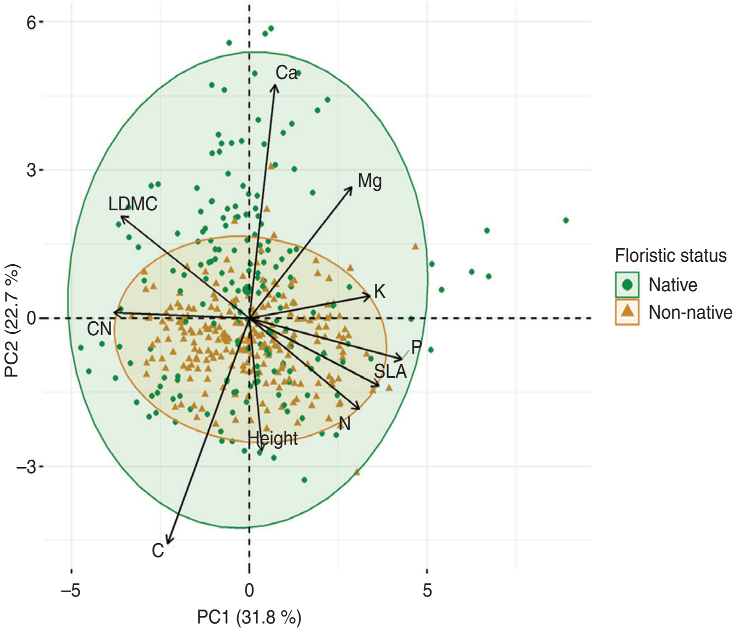

Fig. 5. PCA indicating the total trait space of the two groups of native and non-native species (Table 1), based on ten eco-morphological and leaf biochemical traits (Table 2). Per cent values show the variance explained by PC1 and PC2. The ellipses are 95 % confidence ellipses. Larger symbols correspond to the ellipse centroids.

native species studied here did not reach such high elevations as the non-native species, their trait shift towards a more conservative growth strategy was more pronounced compared to the non-native species, which did not show a clear response to elevation. Therefore, our results only partly support our hypothesis, namely that both native and non-native species display trait changes along the elevational gradient, but not that the magnitude of trait changes is similar. While non-native species have been observed to respond to changes in environmental conditions in a meta-analysis (Davidson *et al.*, 2011), several other studies show the opposite. Individual studies (e.g. Brock *et al.*, 2005; Murphy *et al.*, 2016) and a meta-analysis by Palacio-López and Gianoli (2011) failed to find non-native species to be more plastic than native species. Brock *et al.* (2005) and Murphy *et al.* (2016) both came to the conclusion that trait values related to fitness, such as seed mass, or resource capture, such as SLA, might be more important for invasion success than overall trait plasticity.

Traffic along the road can result in constant seed dispersal and thus mixture between different plant populations along the gradient, which further inhibits the expression of trends in traits at the local level by a homogenization effect (Haider *et al.*, 2012). These factors could further explain the weak to absent trait response to the gradient for non-native species. This is in contrast to the native species, which are assumed to disperse from locally adapted populations inside the natural habitats along the elevational gradient and thus do exhibit shifts in traits as described above. Roads acting as a corridor for non-native species' dispersal can aid their movement to upper elevations by bringing in individuals from different backgrounds (and thus contributing to within-population variability), but at the same time preventing an expected shift in trait values with elevation.

For the studied eco-morphological and leaf biochemical traits, we did not observe non-native species to follow on average a more acquisitive growth strategy compared to native species, which contrasts with several studies that found them to exhibit higher SLA (van Kleunen *et al.*, 2010), leaf N (Drenovsky *et al.*, 2008) and P use efficiency (Funk, 2008). In contrast, Funk and Vitousek (2007) found invasive species to out-perform native ones under low nutrient conditions by resource conservation traits. In accordance with our results, when comparing non-native and native forb species in different fertilization treatments, Scharfy *et al.* (2011) observed almost no differences between the two groups. Scharfy *et al.* (2011) concluded that the difference between the fertilization treatments they used might not have been significant enough to give non-native species a clear advantage. Similarly, the roadside habitats in our study might not have been sufficiently nutrient-rich to induce non-native species trait values that are clearly differentiated from those of the native species.

Within-population trait variability

We hypothesized that native species display overall lower, but constant, within-population trait variability across the elevational gradient when compared to non-native species, while non-native species should display high within-population trait variability in suitable parts and comparatively lower variability in adverse parts of the elevational gradient.

While in our study within-population trait variability of native and non-native species did not differ *per se*, we found significant differences in the direction of change of within-population trait variability of LDMC, leaf C:N ratio and SLA along the elevational gradient between the two species groups. The decrease of within-population trait variability for LDMC and SLA for non-native species concurs with our expectation that these species display decreasing within-population trait variability as they expand into higher elevations where environmental conditions become less suitable. Similarly, Lang *et al.* (2019) also found a significant response of within-population trait variability for SLA along a gradient from dry to moister conditions in Mongolian rangelands, but with trait variability peaking at intermediate moisture conditions.

In our study, higher levels of within-population trait variability of non-native species at lower elevations might be explained by repeated introductions from multiple source populations to the coastal regions (Arteaga *et al.*, 2009; Haider *et al.*, 2010; Alexander *et al.*, 2011). The changing environmental conditions with increasing elevation (lower temperatures and lower nutrient availability) gradually restrict the range of suitable trait characteristics, resulting in lower functional diversity in non-native populations at higher elevations. This trait filter could be another factor in the comparatively slow expansion of non-native species into mountain ecosystems, next to lower propagule pressure, lower disturbance and less benign environmental conditions when compared to the lowlands (Pauchard *et al.*, 2009). However, with our study design we cannot conclude whether filtering of locally adapted genotypes is the actual mechanism underlying the within-population trait variability observed, which could only be inferred from experimental or genetic analyses.

For native species, we found for most traits no change of within-population trait variability along the elevational gradient. Similarly, Lang *et al.* (2019) detected changes of within-population trait variability only for a subset of their traits measured along a precipitation gradient, indicating that not all traits respond to the same environmental gradient, which in our case was considered to be a temperature gradient. In contrast to our expectation of climate filtering towards higher elevations, within-population trait variability of LDMC, leaf C:N ratio and SLA for native species increased with elevation. A possible explanation might be that biotic interactions in the form of hierarchical fitness differences cause this surprising result: Although soil moisture is low across the whole elevational gradient (<10 vol.%), it might be a more limiting resource at lower elevations where the evaporational demand is higher and soil nutrient supply is greater. It has been shown that competition for a single resource might not lead to trait overdispersion as a result of limiting similarity, but to trait clustering and thus lower trait variability (Mayfield and Levine, 2010; Gallien, 2017). Additionally, as our sampled native species populations did not reach higher than 1140 m a.s.l., while non-native species were found as high as 1925 m a.s.l., it is likely that the effect of the climate filter towards higher elevations could only be captured in our study for non-native species.

Total trait space

Our third hypothesis was that the group of non-native species is more variable than the group of native species. However, multidimensional analysis including ten eco-morphological and leaf biochemical traits across all individuals revealed that non-native species occupied a subset of the total trait space occupied by native species. Mainly two species were responsible for the larger native species' trait space: *R. vesicarius* along the first axis and *F. angustifolia* along the second axis of a PCA (Supplementary Data, Fig. S1). In the case of *R. vesicarius*, an agricultural analysis found high concentrations of numerous mineral nutrients including K, Ca and Mg for this species (Kambhar, 2014), in addition to large intraspecific trait variability being reported for several congeneric species (e.g. *Rumex crispus*; Hume and Cavers, 1982) which might indicate the high trait variability potential inherent to the genus.

Furthermore, the trait range across all non-native species was smaller than for native species for most of the traits considered. This was surprising, because the non-native flora specifically at low elevations results from multiple introductions from different source regions for each of the species (Alexander *et al.*, 2011), and other studies found higher intraspecific trait variability also within single non-native species (e.g. Alexander *et al.*, 2009; Davidson *et al.*, 2011; Canessa *et al.*, 2018). However, our results are similar to those of Scharfy *et al.* (2011), who also found no differences in intraspecific trait variability between non-native and native forb species. Also, Murphy *et al.* (2016) found no significant correlation between intraspecific trait variability of leaf and growth traits and the global invasion success of different *Rosa* species in a glasshouse experiment. The lack of consensus indicates that intraspecific trait variability might be strongly dependent on the studied species, measured traits and other local factors (e.g. Kichenin *et al.*, 2013; Bucher *et al*., 2016, 2019). For our case, some of the studied species were highly variable regarding specific traits (*R. vesicarius* and *F. angustifolia* extended the native species' trait space especially regarding leaf biochemical traits, such as leaf Ca and leaf K), while SLA surprisingly did not show any response to elevation.

The observed large total trait space of native species recorded along the elevational gradient might be interpreted as the ability of native species to exhibit high fitness homeostasis under different resource availabilities, as observed in a meta-analysis (Davidson *et al.*, 2011). The combination of strong responses of native species to elevation and their large trait space indicates that these species, being present there for longer time, are locally adapted to the specific conditions of each site along the elevational gradient, while still maintaining high trait variability across the whole gradient. The fact that the sampled native species responded strongly to the elevational gradient despite being restricted to narrow elevational bands reinforces this conclusion.

The results presented here give new insights into the role traits and intraspecific trait variability play in allowing range expansions of non-native species towards high elevations. In contrast to other studies (Alexander *et al.*, 2009; Davidson *et al.*, 2011), we found only few differences in trait variability between native and non-native species. Thus, there is little evidence that intraspecific trait variability is associated with the success of non-native species to spread towards higher elevations. Rather, it seems that being able to express a certain set of traits is more useful for the successful upwards spread of non-native species than having larger intraspecific trait variability than native species, similar to the conclusions Murphy *et al.* (2016) drew in their study. This also concurs with a meta-analysis carried out by Dawson *et al.* (2012), who found that a high plasticity of resource-capture traits was not correlated to the global distribution range of species, and that this success was rather correlated with the ability to rapidly increase biomass in suitable conditions. Similarly, Helm *et al.* (2019) found no evidence that intraspecific trait variability supported the recolonization success of typical species of Mediterranean steppe communities.

Along elevational gradients, environmental filters gradually restrict the functional suitability of non-native species. This might make it increasingly difficult for non-native species to propagate through the different vegetation types along the gradient and bridge the gap between abruptly changing habitat types, for example crossing the treeline or percolating away from the road into natural plant communities.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Fig. S1: PCA showing the total trait space occupied by each of the 11 native and non-native species studied. Table S1: Relationship between the phenological status of sampled individuals and sampling elevation. Table S2: Testing for phylogenetic signal in eco-morphological and leaf biochemical traits and in floristic status. Table S3: Mean and standard deviation for each trait and species. Table S4: Functional richness of eco-morphological and leaf biochemical traits for the two groups of native and non-native species.

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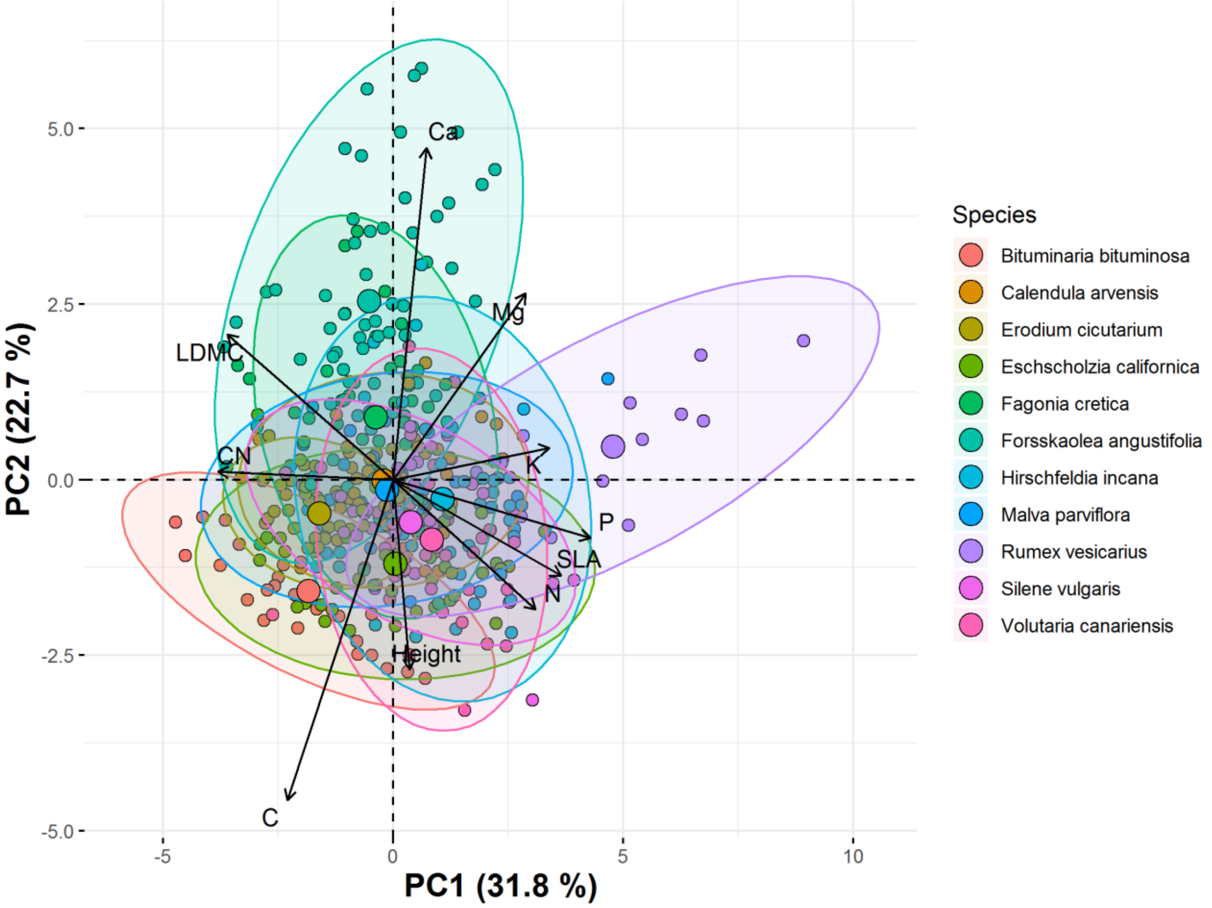
Figure S1. Principal Component Analysis (PCA) indicating the total trait space of the 11 native (*Bituminaria bituminosa*, *Fagonia cretica*, *Forsskaolea angustifolia*, *Rumex vesicarius*, *Volutaria canariensis)* and non-native species studied (*Calendula arvensis*, *Erodium cicutarium Eschscholzia californica*, *Hirschfeldia incana*, *Malva parviflora*, *Silene vulgaris*; Table 1), based on 10 eco-morphological and leaf biochemical traits (LDMC, leaf C, leaf C:N ratio, plant height, SLA, leaf N, leaf P, leaf Ca, leaf K, leaf Mg; Supplementary Data, Table S2).



Notes: Sample size for the PCA was n=420 individuals. Different colors show the different species and their respective 95 % confidence ellipses. Larger symbols correspond to the ellipse centroids. Black vectors indicate the plant traits contributions. Explained variation described by axis 1 was 31.8 % and 22.7 % by the second axis.

Table S1. Results from generalized linear mixed-effects models (glmer in R package lmerTest) for phenological status as a response of elevation of the sampling location.

Response	**Estimate**	**s.e.**	***Z***	***P***
Vegetative	0.0696	0.2372	0.293	0.769
Budding	0.3062	0.1954	1.567	0.117
Flowering	0.2469	0.1225	2.016	**0.044**
Fruiting	-0.3338	0.1355	-2.463	**0.014**

Notes: The phenological status of every sampled individual was recorded in the field: vegetative when no reproductive organs were present, budding when one or more buds were present, flowering when one or more fully opened flowers were present and fruiting when one or more fully-grown fruits were present. The observations of each phenological status were converted into four binary vectors, where “1” denoted that the individual exhibited the respective phenological status. For each of the four vectors, a model was fitted with phenological status as a response, elevation of the sampling location as predictor and species as random effect. The results show that the number of flowering individuals increased significantly with elevation, while the number of fruiting individuals significantly decreased with elevation.

Table S2. Testing for phylogenetic signal in ten eco-morphological and leaf biochemical traits and floristic status (native or non-native). Blomberg's *K* and Pagel's λ were calculated with the function phylosig (package phytools, Revell 2012). No phylogenetic signal for any of the traits was found for either of the metrics; i.e. there are no relationships between the trait values and the phylogeny of our studied species.

Trait	**Blomberg's *K***	***P***	**Pagel's λ**	***P***
LDMC	1.110	0.054	1.337	0.057
Leaf C	1.031	0.132	1.227	0.347
Leaf C:N ratio	0.979	0.331	1.204	0.704
Height	0.881	0.618	0.000	1.000
SLA	1.016	0.184	1.094	0.500
Leaf N	0.970	0.275	0.000	1.000
Leaf P	0.837	0.529	0.000	1.000
Leaf Ca	0.971	0.293	0.716	0.790
Leaf K	0.907	0.440	0.000	1.000
Leaf Mg	1.028	0.185	1.149	0.439
Floristic status	0.691	0.603	0.000	1.000

Notes: We constructed a phylogenetic tree for our 11 studied species with the function phylo.maker in the R package V.PhyloMaker (Jin and Qian, 2019). The mega-tree used as a backbone phylogeny in V.PhyloMaker (GBOTB.extended.tre) is an updated version of the phylogeny from Smith and Brown's (2018) phylogeny for seed plants and Zanne *et al.'s* (2014) phylogeny for pteridophytes. It is based on genetic data from GenBank (http://www.ncbi.nlm.nih.gov/genbank) and phylogenetic data from the Open Tree of Life project (https://tree.opentreeoflife.org/about/synthesis-release/v9.1), and is the largest (74'533 species) and most up-to-date time-calibrated species-level phylogeny of vascular plants.

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Table S3. Mean value and standard deviation for each trait and species sampled along an elevational gradient on Tenerife. Values were predicted with near-infrared reflectance spectroscopy (NIRS) as described by Foley *et al.* (1998) (see manuscript for more details). Floristic status on Tenerife is based on Acebes Ginovés *et al*. (2010), with additional information from Arévalo *et al*. (2005) and Haider *et al*. (2010).

Species	**Floristic status**	**LDMC (mg g^{-1})**	**Leaf C (%)**	**Leaf C:N ratio**	**Height (cm)**	**SLA (cm² g^{-1})**	**Leaf N (%)**	**Leaf P (µmol g^{-1})**	**Leaf Ca (µmol g^{-1})**	**Leaf K (µmol g^{-1})**	**Leaf Mg (µmol g^{-1})**
Bituminaria bituminosa	Native	234 (±35)	47 (±2)	19 (±6)	44 (±23)	12 (±2)	3 (±1)	7 (±2)	66 (±41)	217 (±71)	58 (±21)
Fagonia cretica	Native	237 (±40)	39 (±3)	18 (±6)	14 (±10)	12 (±2)	2 (±1)	11 (±3)	258 (±93)	217 (±67)	76 (±33)
Forsskaolea angustifolia	Native	288 (±28)	35 (±3)	17 (±7)	14 (±10)	13 (±2)	2 (±1)	6 (±2)	291 (±124)	260 (±85)	144 (±59)
Rumex vesicarius	Native	119 (±27)	35 (±3)	14 (±4)	16 (±8)	24 (±2)	3 (±1)	18 (±7)	122 (±62)	396 (±70)	269 (±94)
Volutaria canariense	Native	196 (±40)	43 (±4)	15 (±5)	30 (±19)	16 (±2)	3 (±1)	13 (±1)	120 (±69)	295 (±72)	65 (±31)
Calendula arvensis	Non-native	220 (±26)	40 (±3)	16 (±5)	18 (±9)	15 (±2)	3 (±1)	11 (±2)	86 (±44)	237 (±66)	104 (±35)
Erodium cicutarium	Non-native	321 (±27)	44 (±1)	17 (±5)	7 (±5)	13 (±1)	3 (±1)	11 (±1)	90 (±35)	185 (±54)	39 (±21)
Eschscholzia californica	Non-native	199 (±32)	44 (±3)	17 (±5)	33 (±13)	15 (±1)	3 (±1)	8 (±3)	67 (±44)	263 (±99)	60 (±37)
Hirschfeldia incana	Non-native	182 (±36)	38 (±3)	13 (±5)	37 (±21)	14 (±2)	3 (±1)	12 (±3)	177 (±86)	237 (±63)	93 (±44)
Malva parviflora	Non-native	261 (±37)	42 (±3)	13 (±3)	15 (±9)	13 (±2)	3 (±1)	10 (±3)	118 (±42)	238 (±85)	95 (±48)
Silene vulgaris	Non-native	168 (±35)	42 (±2)	18 (±6)	43 (±18)	18 (±3)	3 (±1)	10 (±3)	99 (±53)	237 (±82)	156 (±42)

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Table S4. Functional richness (FRic) of different traits for the groups of native and non-native species.

Status	LDMC	Leaf C	Leaf C:N ratio	Height	SLA	Leaf N
Native	4.52	5.52	5.67	5.41	6.06	4.22
Non-native	4.54	4.17	4.48	4.63	4.08	4.75

Status	Leaf P	Leaf Ca	Leaf K	Leaf Mg	Convex hull volume
Native	8.72	5.20	5.17	6.40	70.42
Non-native	4.16	4.52	5.61	4.04	23.21

Notes: In the case of single traits, FRic of each trait corresponds to the trait range, calculated as Euclidean distance. For the case of multi-trait analysis, FRic is the minimum convex hull volume of the observations of the ten traits included for each of the two groups of species (native and non-native) distributed in a ten-dimensional trait space (Villéger *et al.*, 2008).

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CHAPTER 5

Synthesis

Mountain ecosystems are important biodiversity hotspots vulnerable to global change. The elevational gradients along mountain slopes encompass several steep environmental gradients over short geographical distances, giving rise to distinct vegetation belts. Despite the long interest in vegetation changes along elevational gradients, there are still knowledge gaps regarding the patterns and the abiotic drivers of plant diversity. In this thesis, I tackled different questions regarding changes of plant species richness, functional composition and functional diversity along elevational gradients. The effects of different environmental drivers and their interactions on these diversity aspects were also investigated. Here, I summarize the key findings across the different chapters of my thesis (Fig. 1), discuss how they integrate into the current state of knowledge about other mountain systems and other environmental gradients, their transferability and future perspectives.

Summary of results

In chapter 2, most chemical soil properties varied as expected along the elevational gradient: soil cation concentrations, cation exchange capacity (CEC) and pH decreased with increasing elevation. Temperature had the strongest effect on the analyzed vegetation characteristics. Temperature had a positive effect on species richness and favored communities with a more acquisitive strategy (higher specific leaf area, SLA, and leaf nitrogen, leaf N, and lower leaf carbon to phosphorous ratio, leaf C:P ratio). The impact of road disturbance was evident in a larger number of species found on the roadside compared to far away from the road. However, no road effects on functional composition or diversity of the plant communities were detected. While soil chemical properties did not affect species richness, soil cations had a positive effect on specific leaf area, thus, resulting in more acquisitive communities. Functional diversity of the traits considered was not affected by any of the environmental factors analyzed.

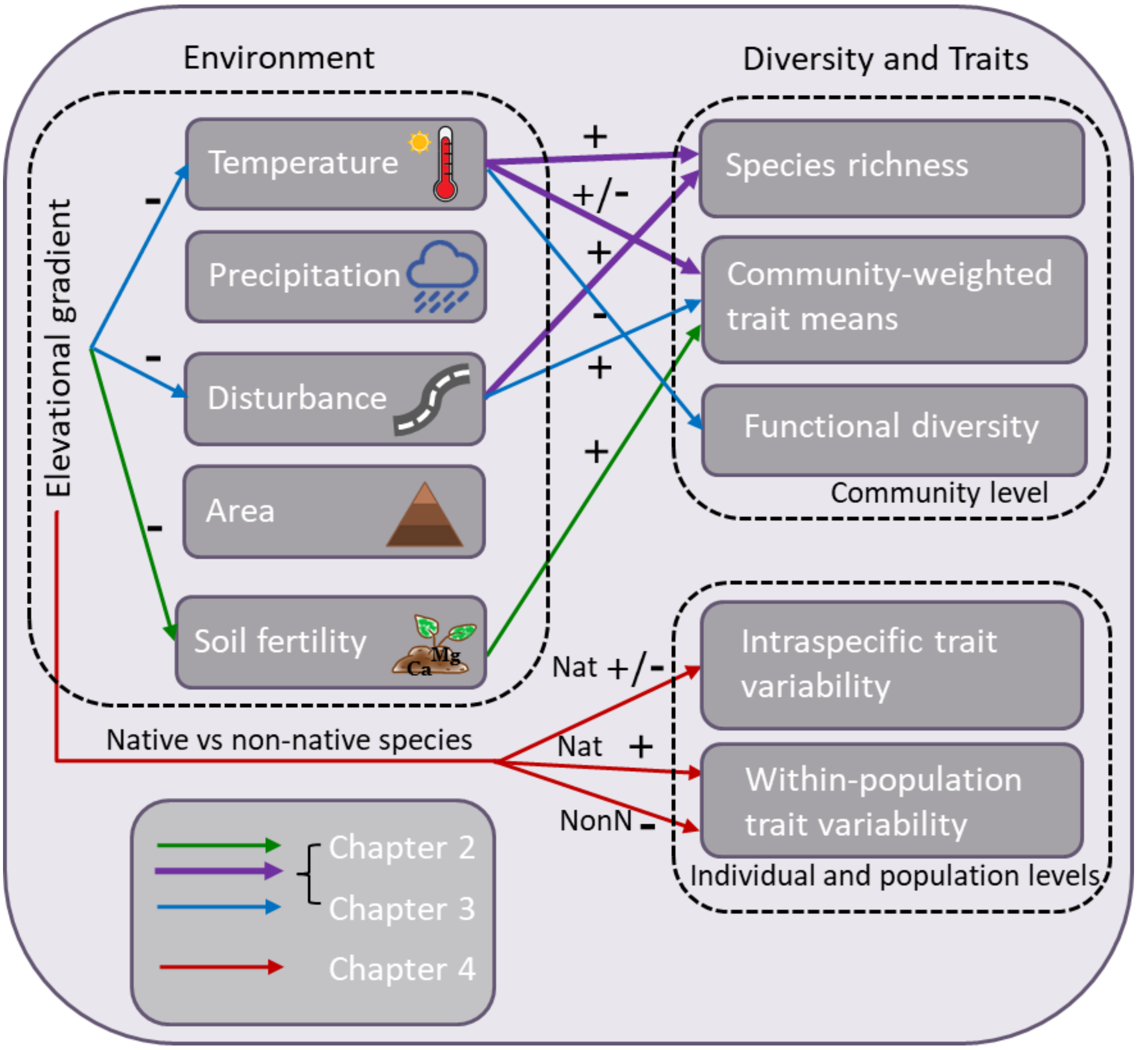

Figure 1. Overview of the main results discussed in this chapter. Predictors and responses are linked by colored arrows; purple arrows mean that the relationship was found on chapters 2 and 3. '-' and '+' signs mean negative and positive relationships, respectively. '+/-' means a positive effect on conservative traits and negative a effect on acquisitive traits. Temperature, precipitation, disturbance, area and soil fertility are environmental variables analyzed along the elevational gradient. Species richness, community-weighted trait means and functional diversity were analyzed at the community level; while intraspecific trait variability and within-population trait variability were analyzed at the individual and population levels, respectively.

In chapter 3, I found that species richness was positively correlated with temperature, land surface area of the elevational band and disturbance. The analysis of patterns of community-weighted trait means (CWMs) and functional diversity revealed that filtering through temperature was the only mechanism for which I could confirm most of the mechanism-specific hypotheses about elevational trait changes. CWMs of most traits indicated shifts from acquisitive to conservative growth strategies, and functional diversity decreased along the elevational gradient. The expected effect of disturbance on growth strategies was also supported by the fact that roadside communities were overall more acquisitive than less disturbed communities away from the road.

In chapter 4, I found that non-native species were overall less variable than native species. With increasing elevation, individuals from native species exhibited denser leaves (higher LDMC), with higher leaf carbon content and lower leaf nutrient content, according to the expectations from the leaf economics spectrum (with slow resource-processing species expected under more stressful conditions), while non-native species showed almost no response to elevation. In contrast, when considering the within-population trait variability along the elevational gradient, non-native species populations at higher elevations showed lower variability for LDMC and SLA, indicating that environmental filtering selects for intermediate trait values in non-native species that meet the requirements of various conditions. Surprisingly, within-population trait variability of native species increased with elevation for LDMC, leaf C:N ratio and SLA.

Discussion

Trait patterns along elevational gradients: individual, population and community levels

The leaf economics spectrum (LES) describes ecological plant strategies based on consistent correlations between leaf traits related to resource allocation (Díaz et al., 2016; I. J. Wright et al., 2004). It reflects a gradient from slow (conservative) to fast (acquisitive) strategies in terms of investment and use of nutrients and other resources (Reich, 2014). Traits related to resource use and investment include specific leaf area (SLA), leaf dry matter content (LDMC) and leaf nutrients. The acquisitive-conservative plant strategies’ continuum is related to gradients of available resources and/or environmental stress (I. J. Wright et al., 2002), such as elevational gradients. Lowlands present less stressful conditions in terms of climate and resources, and therefore trait syndromes associated with acquisitive communities (fast resource acquisition, metabolism and growth) prevail. With increasing elevation and stress, trait values associated to conservative strategies (with protection against freezing, high solar radiation and wind, and also resource conservation) become dominant. Such trait-environment relationships have been shown for the intraspecific (e.g. Bucher et al., 2016; Read et al., 2014) and community levels (e.g., Bruelheide et al., 2018; Schellenberger Costa et al., 2017; Ding et al. 2019). Along the elevational gradient of Tenerife, I observed patterns consistent with tradeoffs between acquisitive and conservative strategies of resource acquisition and investment. The results presented in chapters 3 and 4 support the expectations from the LES. Along an elevational gradient of increasing climatic harshness, most of the leaf traits, acquisitive traits decreased while conservative traits increased for both community-weighted means (Chapter 3) and individual trait measurements (intraspecific trait responses for native species, Chapter 4).

In Chapter 4, I found that non-native herbaceous species exhibited almost no change in traits from low to high elevations. Thus, the patterns of within-species trait variation for non-native species differed from both those for native species and those for the community-level changes presented in Chapter 3. Trait-environment relationships at different levels of organization have different underlying components. At the intraspecific level, trait changes result from species phenotypic plasticity or genetic adaptation to the environmental gradients (Albert et al., 2011), while at the community level, trait changes reflect the combination of intra- and interspecific variation (due to species turnover; de Bello et al., 2011). To this date, there are few studies that compared community and species responses measured in the same study system and plots and simultaneously measured intraspecific trait variability of multiple species along the same elevational gradient (but see Kichenin et al., 2013; Roos et al., 2019; Zuo et al., 2017). Studies that did so, decomposed the intra- and interspecific effects on the community by calculating CWMs using trait values measured at each community for each species *versus* trait values averaged across all communities per species. They have shown that, even though intraspecific trait variation explains a substantial part of the community responses, interspecific trait variation has a larger contribution (Kichenin et al., 2013; Roos et al., 2019; Zuo et al., 2017). Furthermore, because directional changes in community trait mean values result from the sum of species responses and species turnover, species-specific responses might change in completely different directions (as shown by Anderegg et al., 2018; Bucher et al., 2016; Kichenin et al., 2013). In this thesis, changes in community-weighted trait mean values are mainly consistent with the changes of native species, and non-native species differ substantially from the community trends. The low influence of non-native species on the community patterns is likely due to the lower number of non-native species and their typically low dominance compared to native species (Arteaga et al., 2009).

Regarding the lack of a response to elevation by non-native species, this might be explained by the fact that non-native species have been introduced relatively recently along the elevational gradient, and possibly multiple times, without having had enough time to adapt to local environmental conditions (Alexander et al., 2011). Native species, in contrast, have a long residence time, are locally adapted to the specific conditions of each site along the elevational gradient (Read et al., 2014). Additionally, the role of roads as a corridor for non-native species' spread along the elevational gradient can aid in constant seed dispersal and mixing of populations, resulting in homogenization (Arévalo et al., 2010; Haider et al., 2012) and no overall trait response of non-native species along the gradient. Further research including more non-native species, genetic components and reproductive traits might help to elucidate this question.

In Chapters 3 and 4, I found that functional diversity decreased with increasing elevation at the community level and also at the population level for non-native species. However, functional diversity increased for native species. This contrast between the findings for community-level functional diversity and within-population level for native species should be discussed in the light of the two different levels of organization being considered. At the community level, functional diversity was assessed across several different species, representing the average difference in functional traits between any two random species selected from the community (Botta-Dukát, 2005). At this level, changes of functional diversity are strongly influenced by species turnover and interspecific trait variation, and do not provide information about how individual species respond. In contrast, within-population trait variability estimates the average trait difference between different individuals of the same species. Here, responses of functional diversity are specific to each species' evolutionary history and ecological strategy. Therefore, it is not surprising that community-level changes of functional diversity are different from those of specific species or small subsets of species from the community. Furthermore, as the sampled native species populations did not reach higher than 1140 m a.s.l. (compared to the studies' total elevational range of 2353 m), it is possible that the effect of environmental filtering towards higher elevations is not important for these specific native species occurring at the lower half of the elevational gradient. The limiting resource for the populations of these species might be water availability, and therefore, the filtering effect happens from intermediate to low elevations.

Altogether, the results suggest that introductions and spread of non-native species into native communities can have important effects on the way communities respond to environmental changes. Plant invaders are more likely to have a larger effect over common species compared to rare species due to niche overlap between invaders and common species, and the fact that rare species are occupying specialized niches (Powell et al., 2011). As mountain invasions become more frequent and non-native species are likely to become a more dominant part of plant communities, community trait patterns along elevation might disappear or change direction. Such changes of the dominant strategy of the communities will affect their ability to respond to environmental changes, and might also result in changes of ecosystem functions (and services) such as nutrient cycling (Ehrenfeld, 2003) and pollination (Traveset & Richardson, 2006). Therefore, the recent increase of non-native species observed in mountain regions and their complex effects on native communities must be taken into account for better predicting how the novel communities and ecosystems will respond to global change.

Elevational drivers of plant species diversity and functional traits

Chapters 2 and 3 investigated the drivers of different vegetation characteristics along the elevational gradient in Tenerife. A positive effect of temperature was observed both on species richness and traits related to an acquisitive strategy. The findings give further support to the key role of temperature, often coupled with precipitation, in explaining patterns of species richness and functional traits along elevational gradients, as has been described in previous studies (Irl et al., 2015; Odland & Birks, 2006; Peters et al., 2016; Rosbakh et al., 2015). Climate is indeed one of the most important drivers of global patterns of species diversity (Hawkins et al., 2003; Kreft & Jetz, 2007). Similarly, large-scale biogeographic studies of trait changes also emphasize the importance of temperature (Šímová et al., 2017). Energy hypotheses which try to explain the mechanistic role of temperature in determining species richness patterns include the productivity hypothesis (stating that diversity is limited by the amount of solar energy and water availability; Wright, 1983) and the metabolic hypothesis (stating that an organisms' physiological requirements and the ambient energy are the most limiting factors; Terborgh, 1973). The second explanation, also called climatic tolerance hypothesis (Šímová et al., 2011; Terborgh, 1973), proposes that temperature extremes act as a barriers (filters) on species distribution and diversity. The consistent effects of temperature as a filter on species richness and functional traits found in this thesis give further support to the climatic tolerance hypothesis.

The effect of soil in Chapter 2 was only detected for SLA. Surprisingly, no effect on species richness was found. Global studies using traits from large databases have observed a joint effect of soil and climate to be important in explaining trait variation at the interspecific (Joswig et al., 2021; Ordoñez et al., 2009) and community levels (Bruelheide et al., 2018). Ordoñez et al. (2009) found that leaf economics traits depend on soil properties, especially soil nutrient supply. However, only the total amount of nutrients in the soil were measured, which might not be sufficient to capture the effect of soil on functional traits. Temperature is a large-scale filter that selects species from the regional species pool (de Bello et al., 2013). Therefore, it is powerful in explaining species richness variation across larger environmental gradients (Bruelheide et al., 2018). In order to explain local scale variation in species richness and community characteristics, factors such as soil properties come into play. Additionally, high resolution microclimatic data has been shown to give us even further insight into how plant individuals and communities are affected by temperature (Lembrechts et al., 2019, 2020), for example, in the context of anthropogenic disturbances and climate change.

Next to natural environmental factors, anthropogenic disturbance is also an important driver of mountain diversity (Midolo et al., 2021; Peters et al., 2019). I expected disturbance to increase both species richness and acquisitiveness in the communities. In Chapters 2 and 3, road disturbance affected species richness in a positive way. Even though communities at the road verge harbored more species than the communities away from the road in the study region (Chapters 2 and 3), an increase in acquisitiveness on roadside communities was only detected in Chapter 3. In Chapter 2, where the relative effects of different abiotic drivers were analyzed simultaneously, roadside communities were not found to be more (or less) acquisitive than communities far away from the road. This apparent contradiction might be resolved if the potential drivers are considered separately. Disturbance along roadsides leads to spatial heterogeneity and creates empty space for new species to establish. This road effect on species richness is rather independent of temperature. The new species (either introduced or native species) are favored by the release from competition and the increase in resources, and thus, tend to follow more acquisitive strategies (Forman & Alexander, 1998). However, the increase in acquisitiveness on roadside communities found on Chapter 3, seems to be better captured in Chapter 2 by the higher temperature and soil cations on roadside compared to communities more distant from the road. This reemphasizes the importance of using high resolution soil and climatic data on studies diversity-environment relationships.

The effect of non-native species on native species richness or trait patterns along the elevational gradient was not evaluated explicitly in the chapters of this thesis. However, in a supplementary analysis, I found that non-native species contributed significantly to an increase in species richness and more so on the roadside. Hence, it is reasonable to say that the increase in species richness on roadside plots was mainly due to non-native species which were especially promoted by disturbance. Non-native species which become successful invaders tend to be ruderal species, shifting the community traits towards more acquisitive strategies (Funk & Vitousek, 2007; Jauni et al., 2015). A study by Powell et al. (2011) found that common species are more affected by non-native species via their effect on species abundance at small scales. The common species might, therefore, go extinct at the community without reflecting in a decrease of species richness at the regional scale. In conclusion, while species richness might not be affected profoundly at the regional scale, community traits still might change drastically.

Conclusion, limitations and future perspectives

The research work presented here contributes to the current understanding of the drivers of plant diversity along elevational gradients, by looking at multiple ecological scales (individual, population and community scales), dimensions of diversity (taxonomic and functional) and non-native species. The findings emphasize the need for including information on local site conditions that are available at fine spatial resolution, e.g. soil temperature (Lembrechts et al., 2021) and soil characteristics. Including microsite conditions improves our understanding of the drivers of mountain diversity patterns and help model projections for future climate effects on community structure and ecosystem functions (Lembrechts et al., 2019). Distinguishing the mechanisms and drivers behind vegetation patterns along elevational gradients is especially important for predicting how mountain ecosystems are responding to climate change and other anthropogenic threats such as land use change and plant invasions. As the relationship between environmental drivers such as temperature and soil characteristics can be expected to change in future climate scenarios, trait patterns might be affected in complex ways. Many of the traits studied here are related to ecosystems functions of the different communities occurring along the elevational gradient on Tenerife, and these will also be affected. Especially in the communities in high mountain areas, changes in nutrient cycling and energy exchange are expected.

Even though this thesis contributes to the question of how different abiotic drivers affect species diversity patterns on mountains, there are limitations to be acknowledged. Firstly, there is a limitation in geographical extent as the different studies were conducted in one specific study region, the oceanic island of Tenerife. Therefore, one must be cautious when extrapolating some of the results from this thesis which might reflect peculiarities of the elevational gradient of mount Teide. Indeed, Tenerife has a particular climate related to the tradewinds and the temperature inversion which creates a humid layer of clouds at ca. 1200 m a.s.l. (Fernández-Palacios, 1992). In this layer, the vegetation is dominated by Canary pine (*Pinus canariensis*), and some of the trait patterns found in Chapter 3 have been discussed in the light of the dominance of this coniferous species. Similarly, soil effects on vegetation characteristics have to be taken into account, given the particular soil types of volcanic origin and their interaction with precipitation patterns.

Secondly, I decided to focus on leaf traits from the LES, as they summarize growth strategies and how communities respond to environmental gradients (Díaz et al., 2016; I. J. Wright et al., 2004). Thus, other sets of traits which can also responsible for community assembly on mountains *via* biotic interactions (root or defense traits) or reproduction (dispersal syndrome and distance), were not included. Especially at low elevations, plant-plant as well as plant-herbivore interactions can be an important driver of trait patterns and community composition (Lynn et al., 2019; Pellissier et al., 2012). In this context, the analysis of plant metabolites is a promising way to investigate the importance of biotic interactions along elevational gradients. The analysis of metabolites has been suggested to be a more direct way to understand the mechanisms behind organisms' responses to environmental changes than traditional functional traits (Walker et al., 2022). Relating metabolites to leaf functional traits might be a key step to understanding the underlying physiological mechanisms behind species diversity patterns along environmental gradients.

Patterns of plant functional traits have been studied globally, and shown to be useful indicators of changes in communities' life history strategies along environmental gradients and predictors of community assembly (Bruelheide et al., 2018; Ordoñez et al., 2009). Functional traits affect the performance of individuals and, therefore, their chance to belong to a community (Violle et al., 2007). Only species with the appropriate functional traits can reach and establish under the particular biotic and abiotic conditions of a site (de Bello et al., 2013). It was shown in chapter 3 how they can be applied to test different hypotheses regarding the mechanisms behind species richness patterns. With data from mountain regions across the world, this approach can be further applied to investigate large scale biogeographical patterns. Patterns of trait variation with elevation can be expected to be similar across mountain regions. The same expectation of a shift from more acquisitive to conservative growth strategies is expected as conditions get harsher with increasing elevation. In contrast, as certain environmental gradients might differ in different mountain regions, such as precipitation, soil characteristics and disturbance regimes, local differences on trait patterns might occur. Testing mechanism-specific hypotheses for elevational patterns of both community-weighted means and functional diversity can help to distinguish between correlational and mechanistic relationships between species richness and environmental variables. I propose that the trait-based framework presented here can be fruitfully applied to better understand species richness patterns in other regions and across other types of environmental gradients.

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APPENDICES

Authors' contributions

Chapter 2

ARB, LF and SH conceived the ideas; ARB conducted the fieldwork and collected the vegetation data with help from SH and JRA; ARB and LF conducted the chemical soil and leaf analysis, respectively; ARB, SH and LF analyzed the data. ARB and LF led the writing with important contributions from SH. All authors revised drafts of the manuscript, and approved the final version. My overall contribution was 60%.

Chapter 3

ARB, SH, CR and PK conceived the ideas; ARB conducted the fieldwork and collected the data with help from SH, ST, JRA and MAPM?; ARB analyzed the data with assistance from SH and PK. ARB led the writing with important contributions from SH, CR, JA and PK. All authors revised several drafts of the manuscript, and approved the final version. My overall contribution was 70%.

Chapter 4

SH, CR, ARB and PK conceived the study. ARB and PK conducted the fieldwork and collected the vegetation data. PK conducted the laboratory analysis and calibration models with assistance from ARB. ARB and PK carried out statistical analyses and produced the graphs, with input from SH and HB. ARB wrote the first draft of the manuscript, with input from SH, HB and PK. All authors contributed to writing and reviewing of the manuscript. My overall contribution was 40%, my intellectual contribution was 60%.

Curriculum vitae

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Professional experience

Feb 2022 – present	**Scientific employee** Martin Luther University Halle-Wittenberg (Halle, Germany) Researcher on the project “TRACE – Trait-environment interactions driving elevational range expansions under climate change”.
Oct 2017 – Sep 2021	**Scientific employee** Martin Luther University of Halle-Wittenberg (Halle, Germany) Researcher on the project “Using plant functional traits to reveal mechanisms behind species richness patterns along elevation gradients”.
Aug 2014 – Jul 2015	**Biologist** PROSUL (Florianópolis, Brazil) Environmental impact assessment for the licensing of highways, dams and power lines.
Mar 2013 – Jul 2014	**Research assistant** Federal University of Rio Grande do Sul (Porto Alegre, Brazil) Field and lab work for the project 'Functional attributes of the grassland vegetation of Rio Grande do Sul'.
May 2012 – Aug 2012	**Volunteer Research Assistant** University of New Mexico / Sevilleta Long Term Ecological Research, (Socorro, USA) Field work in desert, grassland, forest and aquatic habitats in the Sevilleta National Wildlife Refuge.

Education

Oct 2017 – present	**Ph.D. in Ecology** Martin Luther University of Halle-Wittenberg and German Centre for Integrative Biodiversity Research (iDiv) (Leipzig, Germany) Thesis title: Plant taxonomic and functional diversity along elevational gradients and their abiotic drivers. Supervisor: Dr. Sylvia Haider Co-supervisor: Prof. Dr. Christine Römermann
Sep 2015 – Aug 2017	**M.Sc. International Master in Applied Ecology** University of East Anglia (UK), University of Kiel (Germany) and University of Poitiers (France).

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Mar 2010 – Sep 2014	**B.Sc. Biology** Federal University of Rio Grande do Sul (Porto Alegre, Brazil) Thesis title: Ecological succession after land abandonment in a forest-grassland ecotone in the Pampa biome. Supervisor: Prof. Gerhard Overbeck

Participation in courses and workshops

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Jun 2019	SoilTemp network meeting (University of Antwerp, Belgium)
Feb 2019	Working at the Science-Policy Interface German Centre for Integrative Biodiversity Research (iDiv) (Jena, Berlin, Germany)
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Oct 2017 – present	Co-supervision of 2 research internships, 1 master thesis and 2 bachelor theses.

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Sep 2015 – Aug 2017	Full scholarship from the European Commission for completion of the International Master in Applied Ecology program.
Jan 2012 – Dec 2012	Full scholarship from the Brazilian Agency of Scientific Development through the Science Without Borders exchange program for studying at the Rensselaer Polytechnic Institute, Troy (United States).

Publications and conference contributions

Publications

Publications in international peer-reviewed journals

Ratier Backes, A., Frey, L., Arévalo, J.R., Haider, S. 2021. Effects of soil properties, temperature and disturbance on diversity and functional composition of plant communities along a steep elevational gradient on Tenerife. *Frontiers in Ecology and Evolution*, 9, 758160.

Kühn, P., **Ratier Backes, A.,** Römermann, C., Bruelheide, H., Haider, S. 2021. Contrasting patterns of intra-specific trait variability in native and non-native plant species along an elevational gradient on Tenerife, Canary Islands. *Annals of Botany*, 127(4), 565-576.

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Lembrechts, J.J., …, **Ratier Backes, A.** et al. 2019. Comparing temperature data sources for use in species distribution models: From in-situ logging to remote sensing. *Global Ecology and Biogeography*, 28(11), 1578-1596.

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Conferences and invited talks

Ratier Backes, A., Römermann, C., Alexander, J.M., Arévalo, J.R., Keil, P., Padrón-Mederos, M.A., Trogisch, S., Haider, S. "An overall decreasing plant species richness-elevation relationship in Tenerife: functional traits as tools to reveal underlying mechanisms" (Conference poster). *Ecological Society (GfÖ) Conference*, Münster, Germany. September 2019.

Kühn, P., **Ratier Backes, A.,** Römermann, C., Bruelheide, H., Haider, S. "Contrasting patterns of intra-specific trait variability in native and non-native plant species along an elevational gradient on Tenerife, Canary Islands." (Conference poster). *Ecological Society (GfÖ) Conference*, Münster, Germany. September 2019.

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Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „Plant taxonomic and functional diversity along elevational gradients and their abiotic drivers“ eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe. Die vorliegende Doktorarbeit wurde bis zu diesem Zeitpunkt weder bei der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt.

Amanda Ratier Backes, Halle (Saale), 28.02.2022