Environmental drivers of endemism in the Canary Islands: linking traits to island theory

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Extended abstract

Islands have been very influential in the fields of ecology and evolution. They are frequently described as dynamic because species richness and evolution are especially sensitive to island geological processes, leading to high biodiversity and endemism, which fluctuate through space and time. Islands thus serve as natural laboratories with which to test theories about processes that alter biodiversity. Traditional approaches in island biogeography used species richness to assess island ecological and evolutionary patterns but there is now a movement towards the use of functional traits as they can provide more mechanistic insight. Functional trait ecology has greatly increased our understanding of biodiversity patterns on the mainland and more recent advances are using multiple traits to position species in multi-dimensional space, thus indicating their role in a community. The adoption of multi-trait approaches on islands is part of the growing field of functional island biogeography.

The overarching aim of this thesis was to understand how the abiotic environment influences both the functional and geographical composition of plants endemic to islands (island endemics). This objective was investigated through a series of scientific papers, which are either published or under review, focussing on the flora of the Canary archipelago as a model system.

Firstly, I investigated patterns of endemic richness along topographic gradients. Endemic species typically occur in higher proportions at high elevations and it is theorised that increasing isolation with elevation leads to higher speciation rates (per species). Chapter 4 (which follows Introduction, Literature Review and Methods chapters) investigates the links between topographic isolation and endemism. Here, I extend the theory of isolation by elevation to make predictions at a finer scale, focusing on the isolating influence of small-scale fluctuations in topography in the form of deep barrancos (ravines). I assessed how the depth of barrancos influenced the proportions of species in different endemism categories. Depth did not influence endemism, but elevation did: endemic species were

present in higher proportions at lower elevations within the barrancos. This is opposite to what was expected but suggests that, although barranco depth as a measure of isolation did not influence endemism, the presence of barrancos in general plays a role in shaping patterns of endemism.

Trait-based approaches in island biogeography are still in their very early stages because, as island endemics are typically rare on a global scale, trait data are often severely lacking. Chapter 5 addresses this issue by evaluating the quality of existing plant trait data that are available for Canary Island species in an open access database, as well as comparing recently collected plant trait data from field expeditions with trait data that have been digitised from the literature. The outcome of this revealed a severe lack of trait data for Canary Island native species and lack of overlap between trait data collated from open access databases and traits expressed by island endemics. However, on a more promising note, trait data digitised from the literature can accurately represent what is measured in the field. This means that not all future research may require intensive field expeditions, which can be costly, time-consuming and destructive.

Classic approaches in island biogeography have a strong focus on species richness and the historical lack of functional trait data means that trait variation within and across islands is largely unknown. In Chapter 6, I explore the functional composition of island species and how this relates to island age. I use plant functional trait data to investigate the link between species traits and their environment through the lens of rarity. The rarity of species traits is investigated using the index ‘functional distinctiveness’, defined as the average distance in trait space from the focal species to all other species. Functional distinctiveness of endemic and non-endemic species is analysed with respect to their occupancy in climatically rare habitats. The main result of this analysis is that endemics have an affinity for rare habitats but they are not more distinct in their traits than non-endemic species. Furthermore, as islands increased in age, species occupied fewer rare climates but no change in functional distinctiveness occurred. In other words, I found no link between trait distinctiveness and occupancy of rare climates.

There has been a recent call for the inclusion of functional traits into island research. This thesis endeavours to answer this call by incorporating functional traits into island theory. To summarise the main findings, topography and climate influence the distribution of endemic species on islands, but no clear signal in their traits could be found. Trait data for Canary Island species are still lacking but the viability of some other sources of trait data, besides field data, should be encouraging to future researchers.

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Chapter 1 Introduction

The field of island biogeography has contributed substantially to understanding the origin and maintenance of species diversity (Losos & Ricklefs, 2009). Oceanic islands are isolated ecosystems which we can use to understand evolutionary and biogeographical patterns. They contribute disproportionally to global species richness and are rich in endemic species (Kreft *et al.*, 2008), of which many have evolved in situ (Emerson & Kolm, 2005). Islands comprise over 60% of the documented extinctions (Tershy *et al.*, 2015) and many island species are still endangered (Caujapé-Castells *et al.*, 2010). Studying the evolution and maintenance of insular diversity is therefore important, to aid the conservation of some of the Earth's rarest species.

Current models used in island biogeography emphasise the role of environmental heterogeneity and topographic complexity as influential to speciation (Whittaker *et al.*, 2008), yet treat species as equal, devoid of any biological or ecological characteristics (Brown & Lomolino, 2000; Sukumaran & Knowles, 2018; Schrader *et al.*, 2021). Island endemics show strong relationships with environmental gradients (Steinbauer *et al.*, 2013, 2016; Irl *et al.*, 2015), but, despite being recognised for their 'island syndromes' (Burns, 2019), little is known about how endemic traits vary on islands (Ottaviani *et al.*, 2020). Thus, the incorporation of functional trait research into island biogeography, i.e. functional island biogeography, is long overdue (Schrader *et al.*, 2021). One of the goals of functional island biogeography is to see how the predictions made by island biogeographic models manifest in species' traits and community trait space. This thesis is a step towards that goal.

1.1 Overview of thesis and research aims

This thesis of published works centres on three papers: Chapters 4 and 5, which are published, and Chapter 6 which is in preparation for publication. The overarching aim of these studies is to understand how the abiotic environment influences patterns of endemic species, both geographically and functionally. I investigate how theories and processes related to island biogeography manifest for endemic species in the present day, in terms of their relationship to environmental gradients and their phenotypes, i.e. do we see a signal of these processes in the traits and distributions of endemic species?

Island species can be categorised into groups of varying endemism level and each research project is guided by this framework. These groups are:

- Single-island endemics (SIEs): species occurring on a single island
- Multi-island endemics (MIEs): species occurring on two or more islands
- Archipelago endemics (AEs): all species endemic to an archipelago (SIE + MIE)
- Non-endemic natives (NENs): naturally occurring species that are not endemic

Under this framework I want to discern two things: 1) the distribution of island species in relation to topography and climate, 2) the distribution of island species in functional trait space. Each paper has its own aims, hypotheses and conclusions. Here, I briefly summarise the specific goals of each paper.

Chapter 4 examines how the local topography of islands can influence patterns of endemism. This study specifically looked at the isolating nature of deep barrancos (ravines) on the island of La Palma. Carlquist (1974) hypothesised that topographical variation, such as barrancos, provides more ecological opportunity in lowland areas and that, in the Canary Islands specifically, the presence of barrancos could influence the floristic diversity. Studies that investigate topography often focus on elevational peaks rather than troughs. This chapter explores the depth of barrancos as a potential gradient influencing the distribution of endemic species.

Chapter 5 investigates the availability of plant trait data for Canary Island species and evaluates the utility of scientific floras as a source of trait data. The lack of available trait data for island species is a limiting factor in the pursuit of functional trait research on islands. Recognising what data are available and what data are missing is a necessary step to improve efficiency of future trait data collection. This chapter prefaces the following chapter, which makes use of such data. Chapter 6 compares the functional composition of endemic and non-endemic species through the lens of functional rarity in an attempt to expand the functional aspect of existing island models (MacArthur & Wilson, 1967; Whittaker *et al.*, 2008).

Chapter 2 Literature review

2.1 History, endemism and conservation

Island life captures the fascination of people worldwide, but what is it about islands that makes them so inherently fascinating? It is probably, in part, due to their incredible biodiversity: islands make up about 5% of the Earth's land surface, yet they harbour 20-25% of extant terrestrial plant and vertebrate species (Kreft *et al.*, 2008; Bramwell & Caujapé-Castells, 2011). The reason for this is that, despite being species poor, many of the species on islands are endemic, occurring nowhere else in the world. There are few places on Earth that host such high proportions of endemism, making islands unique in their species composition (Kier *et al.*, 2009; Stuart *et al.*, 2012). Islands are, by definition, isolated—they are enclosed land masses that often lie far from the mainland. The isolation of islands, coupled with their high endemism, means much of Earth's terrestrial biodiversity is condensed and scattered across small pockets of land. It is unsurprising, then, that it was islands and their associated species that caught the attention of both Charles Darwin and Alfred Russel Wallace during their voyages around the globe. For Darwin it was the mockingbirds and finches of the Galapagos, for Wallace it was the birds and insects of the Maluku islands in the Malay Archipelago. The independent discovery, by both naturalists, that variations of a species can be permanent and ever-changing, and that these variations can be linked to survival is what ultimately led to the formulation of the theory of evolution (Darwin & Wallace, 1858). Since the Darwin-Wallace era, oceanic islands have continued to fuel the interests of biologists, and islands are used as a basis for understanding the evolutionary and ecological processes that shape biodiversity. It is even speculated that islands provided the stage for the origins of life (Rosas & Korenaga, 2021).

2.1.1. Oceanic islands as model systems

The species we see on Earth today are just a snapshot in time of the continuously evolving life in a changing ecosystem. Retracing the steps of evolutionary history and understanding ongoing ecological and evolutionary processes is therefore not a straightforward task. Oceanic islands can provide us with a platform for this. Oceanic islands are bits of the Earth's crust that have risen above sea level and are thus disconnected from any large land mass (Gillespie *et al.*, 2009). As such, they are enclosed, discrete ecosystems that act as natural laboratories for ecological and evolutionary research.

The significance of islands for understanding biodiversity in a testable and predictable manner was first brought to our attention by MacArthur & Wilson (1963, 1967) with their Equilibrium Theory of Island Biogeography (ETIB). The theory proposed that species richness is a function of island size and island isolation (distance from the mainland) and that, eventually, island biotas reach a dynamic equilibrium between processes that alter the number of species: immigration, speciation and extinction. This offered an explanation for island dynamics not just on 'true islands' but for any island-like entity. As such, the ETIB can be applied to many systems such as mountain tops, sometimes referred to as 'sky islands' (Brown, 1971; Robin *et al.*, 2015); trees (Glassman *et al.*, 2017); lakes (Barbour & Brown, 1974; Wagner *et al.*, 2014); caves (Culver *et al.*, 1973); and even hydrothermal vents (Van Dover *et al.*, 2002). Rates of evolution, on the other hand, are higher on more isolated islands, therefore endemism is expected to increase as islands increase in distance from the mainland. The generality and simplicity of the ETIB inspired a paradigm shift in ecological thinking (Kuhn, 1970; Lomolino & Brown, 2009) and has since proven to be highly useful in explaining biodiversity patterns and evolutionary processes in general (Losos & Ricklefs, 2010).

Around a similar time that the ETIB was developed, Sherwin Carlquist (1966) developed a suite of 24 hypotheses, referred to as principles, relating to the dispersal and evolution on islands and how this relates to species establishment and assembly. Although Carlquist's work is arguably more detailed and diverse than what is outlined in the ETIB, it did not accrue anywhere near as much attention. The ETIB was attractive in its simplicity, predictive ability and translatability. Carlquist's principles, on the other hand, were difficult to test empirically. However, much of what Carlquist hypothesised about islands is yet to be disproven, and with the advent of new techniques and increased computing power (e.g. in molecular evolution and systematics) and the increase in available data (e.g. functional traits, species distributions, phylogenies), his work is being revisited (Taylor *et al.*, 2019; König *et al.*, 2021). As Midway & Hodge (2012) eloquently put it: "*while MacArthur and Wilson strove to predict the end of the story, Carlquist set forth to explain the plot*".

The ETIB inspired a great deal of theoretical and empirical work (e.g. Diamond, 1973; Simberloff, 1976; Heaney, 2000; Hubbell, 2001; Losos & Ricklefs, 2010) and has remained almost unchanged since its publication. The theory eventually came under criticism as it treats species and islands as identical (Brown & Lomolino, 2000). Whittaker *et al.* (2008) expanded the theory by including a temporal dimension of oceanic island ontogeny, which they named the General Dynamic Model of oceanic island biogeography (GDM). Oceanic islands have a relatively predictable lifespan, so in addition to island area and isolation, island age can be a useful predictor of biodiversity. The GDM considers the geological lifespan of islands, specifically focusing on islands that are of volcanic origin. These islands emerge lifeless from the ocean and are built up overtime through volcanic activity. This gradually increases the area and elevation of islands until erosion begins to take over as the dominant process, creating complex topographical features. Continued erosion reduces the area and elevation of an island until it reaches submergence, taking with it the biota that assembled there (Whittaker *et al.*, 2008). Biodiversity and speciation peak and wane with this geological lifespan, linking ecological and evolutionary processes with geological ones. Thus, the GDM predicts a hump-shaped relationship with species richness, speciation and island age, with endemism peaking in middle-aged islands. Incorporating oceanic island ontogeny and geology into island theory provided new insights in island research and many aspects of the GDM have received considerable support (Borges & Hortal, 2009; Bunnefeld & Phillimore, 2012; Cameron *et al.*, 2013; Steinbauer *et al.*, 2013; Valente *et al.*, 2014; Otto *et al.*, 2016; Borregaard *et al.*, 2017; Barajas-Barbosa *et al.*, 2020).

Presently, the ETIB and GDM have seen a revival of interest (Fernández-Palacios *et al.*, 2015; Warren *et al.*, 2015; Santos *et al.*, 2016; Patiño *et al.*, 2017) and numerous efforts have been made to improve their predictability and specificity. For instance, present day characteristics of islands may not reflect their past because sea level fluctuations cause significant changes in island area. Incorporating these historic changes in sea level has been shown to have an imprint on current biodiversity patterns on islands (Fernández-Palacios *et al.*, 2016; Weigelt *et al.*, 2016). Furthermore, the influence of ecological interactions and trophic structure has consequences for immigration and extinction probabilities and community development (Gravel *et al.*, 2011; Cirtwill & Stouffer, 2016) and human interference can influence the movement of species (Helmus *et al.*, 2014). There has also been a call for functional traits to be considered as they may be able to offer insights into dispersal and colonisation processes, as well as the evolutionary pathways that species take (Schrader *et al.*, 2021).

2.1.2. Endemism

Both MacArthur & Wilson (1967) and Carlquist (1966, 1974) predicted that endemism would be higher on oceanic islands compared to similar sized continental areas. Although now well accepted, this was quite revolutionary at the time (Midway & Hodge, 2012). Greater proportions of endemic species are found on the largest and most isolated islands (MacArthur & Wilson, 1963, 1967; Whittaker *et al.*, 2017). This is because species richness increases with area (Preston, 1962; MacArthur & Wilson, 1967), while increasing isolation inhibits gene flow driving speciation through allopatry (Coyne & Orr, 2004; Stuessy *et al.*, 2006). The species richness-area relationship on islands is steeper than in non-isolated areas and this pattern is further pronounced when considering endemic richness (Triantis *et al.*, 2008; Whittaker *et al.*, 2017).

Island endemics can be categorised into two groups: neo-endemics and palaeo-endemics (Engler, 1879; Cronk, 1992). Neo-endemics are species that have evolved within the island system. For palaeo-endemics, on the other hand, their speciation event pre-dates island formation (Mansion et al., 2009) and it is the extinction of counterparts on the mainland that renders them endemic. This means palaeo-endemics are isolated at higher taxonomic levels, often residing on long branches of a phylogenetic tree. The prevalence of neo- and palaeo-endemics designates islands as both ‘cradles’ and ‘museums’ of species diversity (Cronk, 1997), whereby they are both centres of origin for species diversity and centres of refuge for persisting species, respectively.

2.1.3. Conservation and threats

Islands are places of unique biodiversity, yet can be vulnerable to extinction. Islands are often considered to be biodiversity hotspots because of their high concentrations of rare and endemic species, contributing significantly to global biodiversity relative to their small area (Whittaker & Fernández-Palacios, 2007). Of the 25 biodiversity hotspots defined by Myers *et al.* (2000), 10 are wholly or partially made up of islands. Due to their small range and inability to escape the island environment, island species are particularly vulnerable to extinction threats, such as land-use change, climate change, introduced species and human invasion (Caujapé-Castells *et al.*, 2010).

A number of characteristics of island species makes them particularly vulnerable to modern day causes of extinction. These characteristics are often termed ‘island syndromes’ (Burns, 2019). Island faunas have evolved in the absence of medium to large quadrupedal predators and island floras have evolved in the absence of medium to large herbivores. This means that island species are often unafraid of predators, or they lack defences to protect themselves, making them easy targets for hunting or grazing by alien invasive species such as cats or humans (Bowen & Vuren, 1997; Courchamp *et al.*, 2003). Indeed, the colonisation of islands by humans has driven many island species to extinction, the most famous being the Mauritian dodo (Cheke & Hume, 2008). The fearlessness of the dodo, coupled with its inability to fly (another island syndrome) meant it was quickly hunted to extinction in the 17th century following the arrival of Europeans to Mauritius. On their arrival, humans also brought with them other animals, including rats, cats, dogs, rabbits and goats, all of which have had devastating impacts on the native island species. Rats and cats have been especially damaging to island bird populations (Courchamp *et al.*, 2003). On the island of Tenerife, Cubas *et al.* (2019) showed that endemic plants were more palatable to introduced herbivores than non-endemics, with up to 67% of the endemic plant species being negatively impacted. Thus, it seems island species may be maladapted for human presence and introduced species, and as there is no quick escape, extinction can occur at an alarming rate (Olson, 1989; Tershy *et al.*, 2015).

2.2. Evolution on islands

In his 1966 paper, Carlquist wrote that: "*The basic mechanisms of evolution on oceanic islands are the same as those on continental islands, and no 'new' laws are needed; yet the direction that evolution takes on islands, and the products that result, are often quite distinctive...*". The abundance of ecological opportunity and their isolated nature makes islands ideal sites for evolution to take place, yet evolutionary potential is constrained by the tough requirements for colonisation and establishment (see next section). These seemingly opposing forces are perhaps the cause of the idiosyncratic nature of evolution on islands that Carlquist describes.

2.2.1. The constraints of island colonisation

Oceanic island evolution often begins from a set of species that have already overcome strong constraints associated with dispersal and colonisation. That is, in order to become established on a new island, species are likely to possess specific traits or phenotypes. The constraints imposed on colonising species caused by the environment are frequently referred to as environmental filters, whereby the environment acts like a sieve, allowing some species to establish while excluding the rest (Keddy, 1992). Recently, however, this concept has been called into question as it may exaggerate the role of the abiotic environment over the biotic one (Kraft *et al.*, 2015; Cadotte & Tucker, 2017). Nevertheless, island communities represent a sample of the mainland source pool with certain taxonomic groups being under- or over-represented, a phenomenon known as taxonomic disharmony (Carlquist, 1974; König *et al.*, 2021). For example, orchids are extremely rare on islands (Taylor *et al.*, 2019), while ferns are prolific (Kreft *et al.*, 2010). For island floras, König *et al.* (2021) found that taxonomic disharmony was driven by both *in situ* evolution and the geographical characteristics of islands.

Species' establishment on islands is firstly limited by their dispersal ability. To reach an oceanic island, species must be able to disperse long distances across the ocean. This is why very remote islands are naturally depauperate in mammals (Carlquist, 1966). Most plants, on the other hand, can disperse via wind suspension, flotation in sea water or by mobile animals (Howe & Smallwood, 1982; Heleno & Vargas, 2015). Thus, dispersal ability may be reflected in the traits of island species, for example, wind dispersal is more likely for plants that have smaller, lighter seeds (Hughes *et al.*, 1994; Westoby *et al.*, 1996). Indeed, the overrepresentation of ferns on islands may be partially dependant on their microscopic spores (Kreft *et al.*, 2010). Consequently, taxonomic groups typically associated with successful dispersal are expected to be overrepresented on islands (Carlquist, 1966). Once species successfully reach an island, the next limitations to establishment are the local abiotic conditions, such as soil or climate, which species must withstand in order to establish a population. Biotic factors are also limiting—islands often have low species richness (Whittaker & Fernández-Palacios, 2007), therefore species that require biotic interaction for survival may be at a disadvantage. For instance, pollinators are essential for many plant species but island interaction networks contain fewer species and therefore fewer links than continental networks (Traveset *et al.*, 2016). Being a good disperser may not suffice if survival is dependent on biotic interactions.

2.2.2. Evolutionary processes

Evolution on islands can be described through sequential stages of colonisation, speciation and extinction. The taxon cycle, first formulated by Wilson (1961) but further outlined by Ricklefs & Cox (1972), describes how species evolve on islands through range expansion and contraction. It can be described in four stages: 1) geographical expansion occurs as successful dispersers colonise coastal habitats; 2) niche expansion occurs, which is followed by population differentiation on different islands and then a slowing of expansion; 3) species move inland and become more specialised to the central habitats of the island (e.g. high elevations) and extinction takes over in the lowlands as they are outcompeted by new colonists; 4) high-elevation endemics are highly differentiated due to the extinction of closely related species and are restricted to a single island, persisting as relicts. These endemic species eventually become extinct and are replaced by new lineages as the cycle continues. Wilson (1961) was inspired by his own study system, the ant faunas of Melanesia, which have since shown to be consistent with the taxon cycle hypothesis (Economo & Sarnat, 2012), along with some other systems (Ricklefs & Cox, 1972; Ricklefs & Bermingham, 2002; Jønsson *et al.*, 2014; Otto *et al.*, 2016). Despite this, mechanisms driving the taxon cycle are still not fully understood (Economo & Sarnat, 2012; Santos *et al.*, 2016). Although it is a useful and detailed concept, its complex narrative makes it difficult to test empirically. The taxon cycle helps to explain the flow of species from continents to islands, but implies that islands are evolutionary dead ends, or cul des sacs (Matthews & Triantis, 2021), acting as a sink for dispersing and evolving species. However, growing evidence of back-colonisation of island species to the continent suggests otherwise (Carine *et al.*, 2004; Nicholson *et al.*, 2005; Bellemain & Ricklefs, 2008; Jønsson & Holt, 2015).

Following species establishment, new species are formed through anagenetic or cladogenetic speciation, which can further increase the disharmony on islands (Matthews & Triantis, 2021) and allow species richness to increase despite the limits on colonisation. Gillespie et al. (2008) found that, in the Hawaiian flora and fauna, there are fewer colonisation events than there are species, suggesting speciation can create abundant diversity from just a few successful establishments.

The process of anagenesis leads to the formation of a single species when founder populations accumulate genetic variation through either drift or directional selection (Stuessy *et al.*, 2006). The result is a species that has diverged sufficiently in its genotype from its mainland counterpart to be recognised as a new species. Cladogenetic speciation describes the process of lineage branching, where an ancestral species gives rise to two or more species (Emerson & Patiño, 2018). Speciation though anagenesis has typically received less attention because it does not yield taxonomically diverse lineages (Patiño *et al.*, 2014), yet Stuessy *et al.*

(2006) estimated that about 25% of endemic angiosperms on islands have speciated through anagenesis.

Anagenesis and cladogenesis are concepts that have become central to speciation models in island biogeography, however, these terms have received criticism as their use across biological disciplines can be vague and inconsistent and their definitions have changed through time (Rensch, 1959; Dubois, 2011; Vaux *et al.*, 2016; Emerson & Patiño, 2018). The terms do not provide direct links to the type of evolutionary change that occurs when lineages split, yet when used, radiation is often conflated with adaptive change (Emerson & Patiño, 2018).

2.2.3. Adaptive and non-adaptive radiation

Adaptive radiation is the process of evolutionary divergence of a single lineage into a variety of adaptive forms (Simpson, 1953; Futuyma, 1998; Schluter, 2000; Gavrilets & Losos, 2009). It has been widely studied in island contexts where it appears to be a prominent evolutionary process (Schenk, 2021). Adaptive radiations are accompanied by ecological diversification into vacant niche space (niche differentiation) and are recognized for their exceptional ecological disparity (Losos & Mahler, 2010). Many cases of adaptive radiations on islands were recognised by Carlquist (1966), and many more have been discovered since. Examples include the Hawaiian lobelioids (Givnish *et al.*, 2009) and the *Aeonium* of the Canary Islands (Jorgensen & Olesen, 2001).

Ecological opportunity is a key component in adaptive radiation theory (Simpson, 1953; Schluter, 2000). Wellborn & Langerhans (2015) define ecological opportunity in terms of environmental conditions that, when encountered by a species, cause speciation through divergent selection. They describe this as both niche availability and niche discordance, which refers to the adaptive mismatch of a species' niche-related traits and the ecological conditions of its surroundings (Wellborn & Langerhans, 2015). When a lineage is exposed to ecological opportunity, it is subject to new resources, which, in the absence of competitors, can be evolutionarily exploited (Stroud & Losos, 2016). Thus, ecological opportunity is often considered a pre-requisite for adaptive radiation (Simpson, 1953). This is particularly pertinent for emergent islands that are abundant in untapped resources. Indeed, one of Carlquist (1966) principles states that adaptive radiation is inevitable on an islands where a small number of immigrating species are faced with ecological opportunities.

There is debate as to when a radiation is considered adaptive (Losos & Mahler, 2010). Schluter (2000) argues that a radiation is only adaptive if it improves the ability of a species to utilise the environment to which it is adapting. Specialisation to different niches is thought to be a key element making radiations adaptive (Simpson, 1953; Gittenberger, 1991). Hence, due to their small range and propensity for adaptive radiation, endemic species are often assumed to be specialists (Williams et al., 2009). Studies of ecological networks on islands have revealed mixed support for this: some evidence suggests island endemics are specialists (Rominger *et al.*, 2016), becoming more specialised over time (Trøjelsgaard & Olesen, 2013) but evidence also shows that endemics can be super-generalists (Olesen *et al.*, 2002; Castro-Urgal & Traveset, 2016).

It is now more widely recognised that not all radiations are adaptive (Simoes *et al.*, 2015). Non-adaptive radiation can occur when species become geographically isolated but retain their ancestral niche, resulting in minimal niche differentiation or trait divergence (Gittenberger, 1991; Wiens, 2004). In an environment where selective pressures are relaxed, non-adaptive changes may persist (Carlquist, 1974). The outcome of a non-adaptive radiation is that closely related species will occupy a similar range of habitats in allopatry. Of course, species diverging in allopatry may still incur adaptive changes, but the assumption here is that their speciation is driven by geographical forces rather than ecological ones. Evidence for non-adaptive radiation on islands is limited and generally has received much less attention than adaptive radiation (but see Gittenberger, 1991; Comes *et al.*, 2008; Cameron *et al.*, 2013). However, island archipelagos may in fact be suitable sites for non-adaptive radiations to occur, where a species can occupy the same habitat on different islands, diverging through isolation and genetic drift, rather than being driven by strong selective pressures. The result of this is a new species that is endemic to a single island. This may be the case for some radiating plant lineages in Macaronesia, such as *Limonium*, *Cheirolophus* and *Helianthemum* (Whittaker & Fernández-Palacios, 2007).

It is not guaranteed that species will diversify at all on islands, whether that be adaptively or non-adaptively as some clades have a greater propensity for speciation than others (Carlquist, 1974; Stroud & Losos, 2016). Some clades radiate well irrespective if they are on an island or the mainland (Lovette *et al.*, 2002; Takayama *et al.*, 2018), whereas others appear to radiate specifically in an island context (Genner *et al.*, 2015; Gillespie, 2016). The 'evolvability' (Dawkins, 1989) of a species is therefore another key element for understanding evolution on islands. Speciation is also hindered by geographic space: radiations are linked to island size and cannot occur on islands below a certain area (Losos & Schluter, 2000; Kisel & Barraclough, 2010; Algar & Losos, 2011). Therefore, despite the prevalence of ecological opportunity on islands, it is not so straightforward to explain or predict evolutionary outcomes.

2.2.4. The influence of environmental heterogeneity on endemism patterns on islands

Islands experience multi-scale isolation. At the broader scale, they are physically isolated from the mainland. Within islands, 'mountain top isolation' occurs at high elevations and isolation occurs at even finer scales through variation in topography. Different types of isolation do not necessarily impact endemism in the same way (Flantua *et al.*, 2020). The isolation of islands from the mainland can be selective, hindering the accumulation of biodiversity, while within-island isolation can drive speciation, facilitating an increase in biodiversity. Oceanic islands tend to be very environmentally heterogeneous—they are often high in elevation relative to their area and high levels of erosion make them topographically complex (Whittaker *et al.*, 2008). This creates isolation at fine scales and increases the number of available niches (ecological opportunity) leading to ecological adaptation and speciation, resulting in high proportions of endemic species (Janzen, 1967; Golestani *et al.*, 2012; Steinbauer *et al.*, 2013, 2016; Huang *et al.*, 2017). Indeed, the GDM expects speciation and endemism to peak in middle-aged islands as they reach maximum topographic complexity and environmental heterogeneity (Whittaker *et al.*, 2008).

The importance of environmental heterogeneity on islands has consequences for the distribution and habitat affinities of endemic species. Endemics have high richness at high elevations (Steinbauer et al., 2013, 2016) and coastal habitats have been found to support many endemic species, for example in the Balearic islands (Buira *et al.*, 2020). This means endemics are often associated with stressful or extreme habitats, particularly those that are steep and rocky (Dullinger *et al.*, 2000; Lavergne *et al.*, 2004; Casazza *et al.*, 2005; Von Gaisberg & Stierstorfer, 2005; Buira *et al.*, 2020), which are common in mountainous and coastal areas.

The complexity of these habitats means the ecological conditions vary a lot within a small area, thus species need only disperse small distances to compensate for changes in climate (Hobohm et al., 2014). This, coupled with the fact that islands have milder climates, which are less seasonal than comparable areas on the mainland (Weigelt et al., 2013), makes persistence of endemics in these habitats more likely. This allows year-round growing seasons for many island plants and is one of the reasons used to explain the tendency for herbaceous plants to become woody on islands (Carlquist, 1974). This phenomenon, often termed ‘insular’ or ‘secondary’ woodiness is yet another island syndrome and has been documented for many island taxa (Böhle *et al.*, 1996; Francisco-Ortega *et al.*, 1997b; Baldwin, 2007; Lens *et al.*, 2013; Nürk *et al.*, 2019).

The ecological and evolutionary processes described thus far are consistent across islands and have resulted in numerous instances of convergent evolution (Burns *et al.*, 2012; Mahler *et al.*, 2013; Burns, 2019), whereby island colonisers evolve similar phenotypes, despite being in completely different geographic locations and arising from different source pools. These processes are what lead to many of the aforementioned island syndromes (Burns, 2019).

2.3. Functional island biogeography – a new avenue for island research

Functional island biogeography is an emerging discipline: it merges the fields of functional ecology and island biogeography with the aim of understanding how island processes are mediated by functional traits (Schrader *et al.*, 2021). A functional trait is a morphological, physiological or behavioural feature of an organism that contributes to its performance (Violle *et al.*, 2007). The variation and value of functional traits, i.e. functional trait diversity (herein shortened to 'functional diversity'), can reveal important information about ecological and evolutionary processes (Kraft *et al.*, 2015). There is controversy around the term 'functional' in association with species traits as not all traits are clearly associated with a function (Volaire *et al.*, 2020). Throughout this thesis, I will use the term 'functional traits' in keeping with the majority of the literature whilst recognising that not all traits are 'functional'.

The use of functional traits allows for a more quantitative approach in ecology, whereby species are situated along a continuum rather than being treated as discrete entities (McGill *et al.*, 2006; Violle & Jiang, 2009; Violle *et al.*, 2014). This has led to a shift from taxonomic-based approaches to functional trait-based approaches in community ecology. The use of functional traits has been particularly pertinent in plant ecology, where it has long been recognised that plant characteristics are linked to environmental conditions (Schimper, 1898). Consistent global trends have been found between plant traits and the environment, as well as correlations and trade-offs between different traits (Wright *et al.*, 2004; Chave *et al.*, 2009; Reich, 2014; Díaz *et al.*, 2016; Kong *et al.*, 2019). However, the trait-environment relationship at the global scale does not necessarily explain patterns at finer scales (Moore *et al.*, 2018). Plant trait combinations found on islands tend to differ from those in non-insular environments (Ottaviani *et al.*, 2020) and recent evidence shows that island monocots are functionally more distinct than those from the continent (Veron *et al.*, 2021). Today, it remains largely unknown how island biogeography influences the functional composition of species within islands.

2.3.1. Quantifying functional diversity

Functional diversity can be quantified by measuring the spread of species in n-dimensional trait space (Petchey & Gaston, 2006). This is what Rosenfeld (2002) referred to as the 'functional niche' and is analogous to Hutchinson's niche (Hutchinson, 1957), with the axes representing functional traits instead of environmental gradients. Single-trait measurements are insufficient for understanding community-level functioning as species contribute differently depending on the trait being measured. For instance, they may be specialist on one trait but generalist on another (Poisot *et al.*, 2011). Calculating functional diversity requires information on multiple, non-covariant traits—Mouillot *et al.* (2021) estimate an optimal number between three and six. Species that possess unique or distinct trait combinations will sit in the peripheries of trait space (Grenié *et al.*, 2017; Violle *et al.*, 2017), indicating the use of novel areas of niche space. Species that possess common trait combinations will not expand trait space, but instead be more tightly packed in some existing areas of trait space, suggesting finer partitioning in resource use (Pigot *et al.*, 2016). Thus, depending on whether they add different trait syndromes or not, the addition of novel species to an assemblage could add new functions and increase functional diversity (Jarzyna & Jetz, 2016), or keep the functional diversity more or less the same but generate functional redundancy (Rosenfeld, 2002; Petchey & Gaston, 2006).

Analysing a species' position in trait space can provide clues as to the processes involved in community assembly. Counterintuitively, interspecific competition has been used to explain both clustering and overdispersion in trait space (D'Andrea *et al.*, 2020). In order for species to coexist, interspecific competition is reduced by niche differentiation. In trait space, this manifests as large differences in trait values (i.e. overdispersion) among species (Kraft *et al.*, 2008; Kraft & Ackerly, 2010; Götzenberger *et al.*, 2012), with many being quite distinct (Kondratyeva *et al.*, 2019). On the other hand, competition can also produce clustering in trait space as strong similarity among species might facilitate co-existence through coevolution (Aarssen, 1983; Scheffer & van Nes, 2006). Making conclusions about trait space composition is therefore not simple, theoretically or empirically.

Functional diversity has many facets, including richness, rarity, redundancy, originality, evenness and divergence; work to quantify and reconcile these is ongoing (Mason *et al.*, 2005; Petchey & Gaston, 2006; Mouchet *et al.*, 2010; Pavoine *et al.*, 2017; Violle *et al.*, 2017; Kondratyeva *et al.*, 2019). One of these facets, functional rarity, is concerned with the rarity of species' traits. As a general concept, rarity has been considered by ecologists to be an important factor in the study of biodiversity for decades (Gaston, 1994). Rarity can be defined by geographic range, abundance or habitat breadth, and this can overlap with other properties of an organism, such as endemism (Kruckeberg & Rabinowitz, 1985). Functional rarity adds to the different facets of rarity, originally outlined by Rabinowitz (1981), by incorporating the rarity of species' traits or trait combinations (Violle *et al.*, 2017) and can be described as a sliding scale from 'distinct' to 'redundant' (Kondratyeva *et al.*, 2019). Quite simply, a species is considered functionally rare if there is a low probability of encountering its traits (Kondratyeva *et al.*, 2019). As the concepts of rarity and endemism overlap, and because island endemics are often noted for their distinct features, investigating patterns of functional rarity on islands should shed light on predicted evolutionary and ecological outcomes on islands.

2.3.2. The functional composition of islands

Functional island biogeography has the potential to bring a fresh perspective to observable patterns of biodiversity in island systems. A limitation of the existing island models (ETIB and GDM) is that they treat species as functionally equivalent, focusing solely on species richness (Brown & Lomolino, 2000; Schrader *et al.*, 2021). Indeed, evidence points towards a linear relationship between species richness and functional diversity (Biswas & Mallik, 2011; Mouillot *et al.*, 2011; Whittaker *et al.*, 2014; Karadimou *et al.*, 2016), however, this is not always the case (Stuart-Smith *et al.*, 2013; Mazel *et al.*, 2014; Karadimou *et al.*, 2016). Considering that species richness and functional richness can tell us different things, incorporating functional traits into island theory will add another dimension for predicting and visualising evolutionary outcomes on islands.

Based on existing models, functional trait composition on islands should be quite predictable (García-Verdugo *et al.*, 2020; Ottaviani *et al.*, 2020). Species colonising the same island must pass through the same dispersal and environmental filters and be subject to similar levels of isolation, therefore they likely experience similar evolutionary trajectories. Thus, the evolutionary processes on islands, particularly adaptive radiations, should result in predictable changes in the composition of functional trait space (Schrader *et al.*, 2021). A recent study by García-Verdugo *et al.* (2020) found evidence of parallel differentiation of a woody plant complex, *Periploca laevigata*, in the Mediterranean and Macaronesia, particularly towards larger leaves. Functional trait composition should also vary with island biogeography variables, i.e. area, age, isolation and environmental heterogeneity, as is expected of species richness and speciation (Whittaker *et al.*, 2008; Schrader *et al.*, 2021). Negoita *et al.* (2016) looked at dispersal mode of island plants in the Gulf of Maine, USA and found spatial isolation to be the strongest driver of trait variation, whereas island area and elevation had weak effects.

Comparing the trait space of endemic and non-endemic species might reveal clues as to how evolutionary processes on islands manifest. Many endemic species have evolved in isolation on islands (Stuessy *et al.*, 2006), whereas non-endemic native species have arrived via colonisation. If evolutionary change occurs through increased specialisation, endemics may occupy smaller areas of trait space compared to non-endemics, as specialisation has been associated with a loss of function (Poisot *et al.*, 2011; Forister *et al.*, 2012). Additionally, endemics may possess extreme combinations of functional traits, sitting in the peripheries of trait space (Mouillot *et al.*, 2011). An alternative argument is that endemics exhibit more generalist properties. Endemics are globally rare, appearing to be specialists on large scales, but they often have high local abundances and may act as generalists at the regional scale (Hughes, 2000; Williams *et al.*, 2009; Mykrä & Heino, 2017; Braga & Diniz). In fact, reduced functional diversity on islands may actually encourage the evolution of generalist traits (Armbruster & Baldwin, 1998; Olesen & Jordano, 2002). It could be that island endemics are non-specialists which would expand their niche if given the opportunity. In other words, island species may be capable of using more resources, which are currently unavailable to them due to the reduced variability of resources on islands and the physical isolation of islands preventing their spread (MacArthur & Wilson, 1967). If island endemics are more generalist than specialist, then an alternative configuration of trait space might be expected, i.e. one where endemics have a wider spread.

2.3.3. Functional island biogeography—the next step

Given the perceived uniqueness of island endemics, the use of functional traits in island research seems like a logical step towards understanding the outcomes of evolutionary processes and how this relates to the environmental conditions on islands. Despite the calls for the incorporation of trait-based methods into island research (Patiño *et al.*, 2017; Ottaviani *et al.*, 2020; Schrader *et al.*, 2021), functional island biogeography is still in its infancy and our understanding of how and why traits vary within and across islands remains limited (Ottaviani *et al.*, 2020). Part of the reason for this is that, although many archipelagos have thorough species inventories, there remains a significant lack of trait data for island species, especially island endemics. Measuring species traits on site is probably the most reliable way to obtain trait measurements, but with the recognition that fieldwork is not always possible, or even necessary, functional trait data consolidated in repositories (e.g. the TRY database for plants; Kattge *et al.*, 2020) and trait data from herbarium specimens and scientific floras (e.g. the GIFT database, Weigelt *et al.*, 2020) are frequently used in lieu of *in situ* measured traits. However, the validity of this approach is rarely checked and calls for more rigorous examination.

Incorporating functional traits into island research has been acknowledged by many as a direction worth pursuing (Santos *et al.*, 2016; Patiño *et al.*, 2017; Keppel *et al.*, 2018; Ottaviani *et al.*, 2020; Schrader *et al.*, 2021). Not only can functional traits provide new insights to existing hypotheses about islands, such as convergent evolution and island syndromes (García-Verdugo *et al.*, 2020), the island rule (Biddick *et al.*, 2019) and those derived from the ETIB and GDM (MacArthur & Wilson, 1967; Whittaker *et al.*, 2008), they can also help us to understand the role of islands as biodiversity refugia and endemism hotspots, the conservation of which should be based on a deep ecological and evolutionary understanding of their functioning (Keppel *et al.*, 2018).

2.4 The Canary Islands

This thesis uses the flora of the Canary Islands as a study system. The Canary Islands are an archipelago of volcanic origin located west of the Moroccan coastline in Africa, consisting of seven major islands: El Hierro, La Palma, La Gomera, Tenerife, Gran Canaria, Fuerteventura and Lanzarote (**Figure 2-1**). Presently, all islands (apart from La Gomera) are volcanically active (Fernández-Palacios *et al.*, 2011), with the most recent eruption being that of the Cumbre Vieja on La Palma in September to December 2021 (Carracedo *et al.*, 2022). Mega-landslides have eroded and destroyed parts of some islands and this is particularly evident in the most volcanically active islands of El Hierro, La Palma and Tenerife (Masson *et al.*, 2002; Whelan & Kelletat, 2003). Volcanic activity and landslides contribute to the ongoing erosion and geological evolution of the islands, meaning that each island is composed of both new and older terrain.

There is considerable variation in elevation, climate and environmental heterogeneity across the islands, which has led to high habitat diversity and, consequently, floristic diversity (Fernández-Palacios *et al.*, 2004; Fernández-Palacios & Whittaker, 2008; Barajas-Barbosa *et al.*, 2020). The north-east trade winds generate a precipitation gradient from the north-east to the south-west, which creates cloudbanks or a ‘sea of clouds’ on the wind-facing slopes (del Arco Aguilar *et al.*, 2010). This is particularly evident on Tenerife, which reaches the highest elevation of 3718m (Fernández-Palacios *et al.*, 2004). In general, the climate is described as subtropical Mediterranean, but this can vary quite drastically within islands, from warm and dry conditions in coastal areas, to relatively temperate conditions in mountainous areas, to cold and dry conditions at the highest elevations (del Arco Aguilar *et al.*, 2010). The variation in climate within and between islands can be linked to changes in topographic complexity and variation—the easternmost islands of Fuerteventura and Lanzarote are older and more eroded than the western islands, which are steep and rugged. Strong climatic gradients have led to distinct vegetation zones in the form of elevational belts (Fernández-Palacios & de Nicolás, 1995).

Plants are an excellent study group on islands: they are species-rich compared to other taxonomic groups, due to their greater propensity for long distance dispersal and they have a high incidence of adaptive radiation (Schenk, 2021). High-elevation islands, such as the Canary Islands host a high diversity of endemic plant species (Whittaker & Fernández-Palacios, 2007; Kreft *et al.*, 2008). Approximately one third of the Canarian flora is endemic (Arechavaleta *et al.*, 2009) and there are numerous cases of adaptive radiation, including *Argyranthemum* (Francisco-Ortega *et al.*, 1997a), *Aeonium* (Jorgensen & Olesen, 2001), *Echium* (Böhle *et al.*, 1996; Mansion *et al.*, 2009), *Micromeria* (Puppo *et al.*, 2015) and *Sonchus* (Kim *et al.*, 1996).

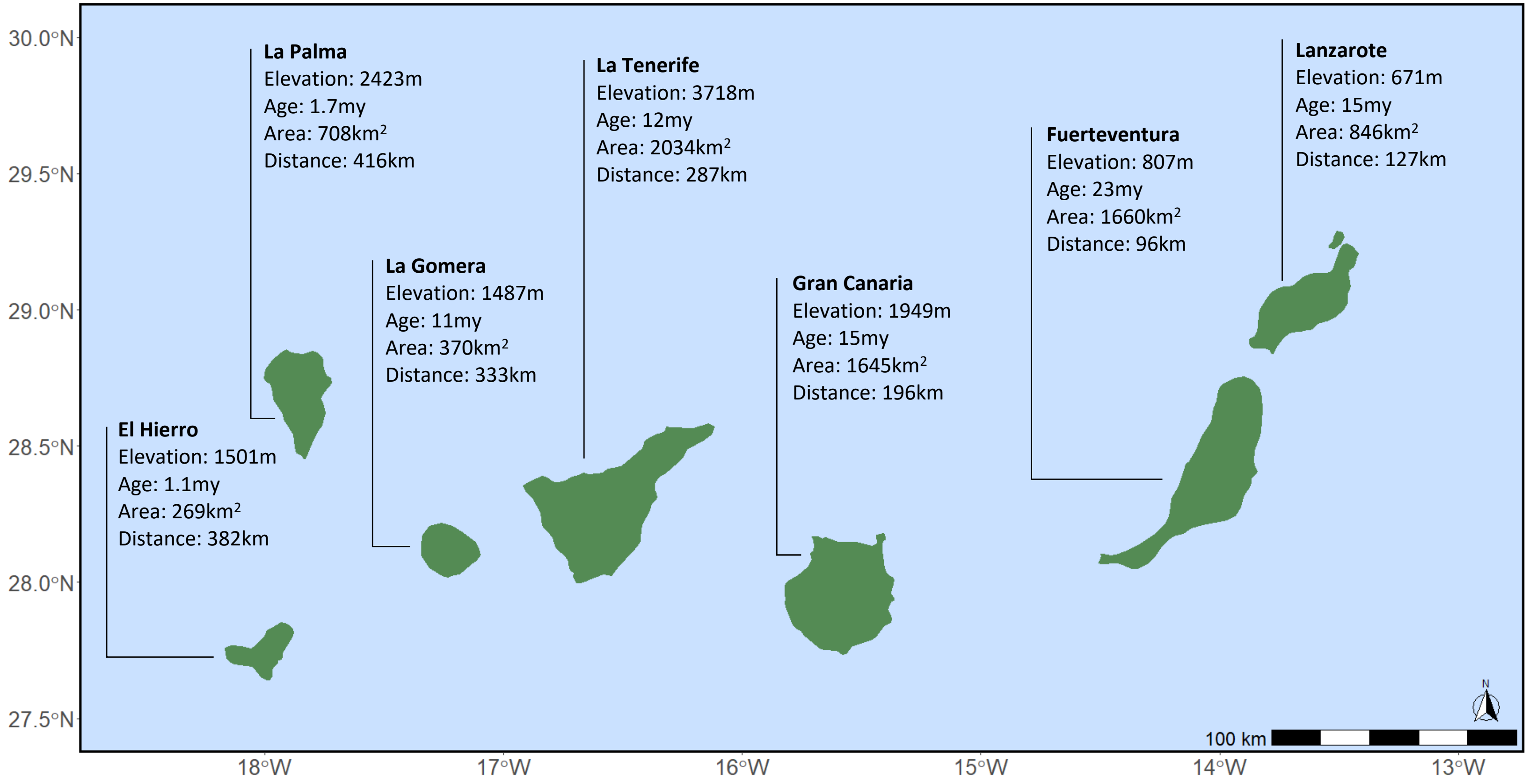

Figure 2-1 Map of the Canary Islands. The Canary Islands are located 96km from the Moroccan coastline in north-west Africa (Google Earth). Each island is labelled with descriptors of elevation (metres above sea level), age (million years), area and distance from Africa. Ages are the oldest determined age for each island obtained from van den Bogaard (2013). Other descriptors were obtained from Steinbauer & Beierkuhnlein (2010).

Chapter 3 Methods

The methods used for each study are described in their individual chapters. This chapter provides additional information about the trait data collected in the field, as well as clarifying my contributions and those of my collaborators.

The trait data used in this thesis were collected as part of a wider goal to have field-sourced plant trait data for all native species in the Canary Islands. I collected plant trait data alongside my collaborator, Dagmar Hanz (PhD student at Goethe University Frankfurt), from the island of La Palma in 2019. These data were used in conjunction with data collected from Tenerife in 2016-17 by another collaborator, Paola Barajas (PhD student at the time at University of Gottingen). From La Palma, I collected data for 75 species. From Tenerife, my collaborators collected data for 447 species. As the Tenerife field season took place first, many of the native species were sampled there. Thus, species sampled from La Palma were mostly single-island endemics, with some additional native non-endemics that were not present on Tenerife. The long-term goal for this working group is to eventually have field-sourced plant trait data for multiple traits for all endemic species in the Canary Islands.

3.1 Sample collection and trait measurements

For plant trait measurements, I followed the handbook by Pérez-Harguindeguy et al. (2013), which outlines best practices for measuring plant traits. **Table 3-1** defines each trait and provides detail about how it was measured. The traits chosen reflect the leaf economic spectrum and the global spectrum of plant form and function (Wright *et al.*, 2004; Díaz *et al.*, 2016).

During my field expedition on La Palma, trait measurements were taken from species that had not already been sampled from Tenerife (mostly La Palma endemics). Identification of plants is much easier during the flowering season; therefore, sampling took place during March-April. Sampling was opportunistic as the aim was to obtain samples from all endemic species on La Palma, some of which are very rare and hard to find. However, specimens of the same species were taken from different locations where possible. Only healthy adult plants were measured and five individuals were sampled per species. When a plant specimen was identified, plant height and chlorophyll content were measured first, before the individual was disturbed. Stems and leaves were sampled from each plant. Where possible, secondary stem samples were cut to minimise disturbance. A minimum of 10 and a maximum of 100 leaves were collected per individual plant (**Table 3-1**). Seeds were also collected but were not present on all individuals. Leaf and stem samples were sprayed with water to keep them hydrated and stored in plastic bags at a cool temperature for 24-72 hours before the remaining traits were measured in the lab. Pérez-Harguindeguy et al. (2013) recommend storing plant samples for no more than 24 hours, but due to limited access to the lab on La Palma, it was not always possible to process samples quickly.

Table 3-1 Standardised measurements for plant traits based on the handbook by Pérez-Harguindeguy et al. (2013).

Trait	Measurement
Plant height	The distance between the upper boundary of the main photosynthetic tissues (excluding inflorescences) and the ground. Therefore, it is the height of the foliage. This was measured on a live specimen using a tape measure.
Chlorophyll content	A chlorophyll meter (SPAD) was used to measure chlorophyll content of five fresh leaves (still attached) from each individual.
Leaf area (LA)	The one sided surface area of a fresh leaf (without petiole). Approximately 10 leaves per individual were scanned using an A4 scanner and the surface area calculated using image processing software (ImageJ).
Leaf thickness (L_{th})	Thickness was measured using a calliper, which was placed at approximately the centre of each leaf, avoiding veins. Three leaves were measured per individual.
Leaf dry matter content (LDMC)	The oven-dry mass of a leaf, divided by its fresh mass. The leaves were dried in an incubator at 80°C for at least 24 hours until dry weight was constant. 10-100 leaves per individual.
Specific leaf area (SLA)	One-sided surface area of a fresh leaf (LA) divided by its oven-dry mass. See LDMC for dry mass measurement. 10-100 leaves per individual.
Stem specific density (SSD)	Oven-dry mass per unit of fresh stem volume. The volume of the stem is determined by measuring its total length and its diameter. Stems were cut to a maximum length of 10cm. Stem diameter was measured at three points along the stem. Stems were dried in an incubator at 80°C for at least 24 hours, until dry mass was constant.
Seed mass	Oven-dry mass of an individual seed measured using a precision scale. Approximately 10-100 mature seeds were measured per individual.

Chapter 4 The effect of small-scale topography on patterns of endemism within islands

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4.1 Statement of contribution of joint authorship

I planned the project, conducted field work, analysed the data, wrote and compiled the manuscript and prepared the figures and tables. Negin Katal and Caroline Löwer contributed to project planning and field work. Richard Field, Adam Algar and Manuel Steinbauer supervised and assisted with compiling the manuscript. Carl Beierkuhnlein and Severin Irl assisted with plant identification and commented on the final manuscript.

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4.2 Abstract

Topography influences evolutionary and ecological processes by isolating populations and by enhancing habitat diversity. While the effects of large-scale topography on patterns of species richness and endemism are increasingly well documented, the direct effect of local topography on endemism is less understood. This study compares different aspects of topographic isolation, namely the isolating effect of deep barrancos (ravines) and the effect of increasing isolation with elevation in influencing patterns of plant endemism within a topographically diverse oceanic island (La Palma, Canary Islands, Spain). We collected plant presence–absence data from 75 plots in 8 barrancos on the northern coast of La Palma, spanning an elevation gradient from 95 to 674m a.s.l. Using mixed-effects models, we assessed the effect of barranco depth and elevation on the percentage of single-island endemics, multi-island endemics and archipelago endemics. We found that percent endemism was not significantly correlated with barranco depth, and correlated negatively with elevation within barrancos (rather than the expected positive relationship). The topographic barriers associated with the deep island barrancos thus appear insufficient to drive speciation through isolation in oceanic island plants. The decrease in endemism with elevation contradicts findings by previous broader-scale studies and it may reflect local influences, such as high habitat heterogeneity at low elevations.

Keywords: Isolation, barranco, ravine, La Palma, topography, endemism, elevation, islands.

4.3 Introduction

Topography is a key factor influencing the evolutionary and ecological processes that generate and maintain the diversity of life on Earth (Irl *et al.*, 2015; Tukiainen *et al.*, 2017; Godinho & da Silva, 2018). It influences species diversity via two main mechanisms. First, topographic complexity drives local variation in climate across a small area through alterations in slope, elevation and cold-air drainage (Dobrowski

2011), increasing the co-occurrence of species with different climatic tolerances (Lenoir et al. 2013). This contributes to habitat diversity, which positively correlates with species diversity (Kohn and Walsh 1994, Hortal et al. 2009, Tews et al. 2004). Secondly, topography causes isolation, acting as a dispersal barrier between populations (Janzen 1967). Topography may restrict species physically, for example by riverine barriers (Moraes et al. 2016). But species can also be restricted by their physiological tolerances, for example to low temperatures at high elevations. Topographic barriers limit gene flow through isolation, which leads to divergence, providing the conditions required for allopatry (Coyne and Orr 2004). Additionally, the isolation provided by topographic structures can create refugia for many species by supporting relict populations and protecting them from the spread of competing species (Harrison and Noss 2017). The ability of species to track their climate niche during climatic changes further decreases the extinction risk of species in topographically diverse areas (Sandel et al. 2011). Climatic fluctuations can lead to repeated isolation and reconnection and may act as a ‘species pump’ (Gillespie and Roderick 2014, Steinbauer et al. 2016). Topography thus positively influences species richness and endemism by enhancing evolutionary processes as well as by preventing extinction. As a result, areas with larger variation in elevation are thought to have higher speciation and endemism rates (Godinho and da Silva 2018).

The effect of large-scale topography, such as mountain ranges, on patterns of species richness, speciation rates and endemism, are increasingly well documented (Thomas et al. 2008, Steinbauer et al. 2012, Verboom et al. 2015, Steinbauer et al. 2016, Xing and Ree 2017), but the direct effect of local topography, such as steep-sided barrancos or ravines, is less well understood. In contrast to mountains, deep valleys or barrancos are only rarely discussed as barriers to gene flow (Janzen 1967, Ghalambor 2006, Steinbauer et al. 2016) and few studies have considered barranco beds as isolated habitats which are themselves separated from each other by dispersal barriers, creating divergence between resident populations (Zhao and Gong 2015). Barrancos (or ravines) are deep gorges with steep-sides and very narrow beds. They can harbour different, often milder, climates from their surroundings, while the barranco walls may represent extreme environments, which are rocky, extremely steep and severely lacking in soil. This means that species at the bottoms of barrancos could be physically and ecologically isolated from equivalent environments (other barranco bottoms). If populations located on highland areas separated by lowland are considered to be disconnected, then, by analogy, a population within a deep barranco may be disconnected from a population in another barranco, depending on the connectivity of the lowland environment. If some barrancos are isolated habitats, then they may have the potential to harbour relatively high levels of endemism. This is true of the valleys in the Hengduan Mountain Region of China: they host a high diversity of plant species, of which 37% are endemic, and some species are endemic to specific valleys (Zhao and Gong 2015). This mechanism is taxon dependent, whereby more vagile species are less affected.

Barrancos can differ from each other as well as from the surrounding landscape. The environments within barrancos may become more similar to their surroundings as barrancos become shallower and less steep. Thus, topographically different barranco forms may possess very different ecological characteristics, and different degrees of isolation. As well as being more isolated, deeper barrancos (i.e. with increasing elevational difference between the barranco ridge and the barranco floor) have higher habitat heterogeneity within a small area, from the shady, relatively moist barranco bed to the steep, rocky, sun/wind exposed cliffs. Habitat heterogeneity is a well-known factor governing diversity and speciation (MacArthur and Wilson 1967, Stein et al. 2014).

Oceanic islands provide informative systems for studying the effect of topography on endemism because of their disproportionately large numbers of endemic species, many of which have evolved *in situ* (Whittaker and Fernández-Palacios 2007). Oceanic islands tend to have long topographic and climatic gradients relative to their size, which have been linked to endemic species richness (Irl et al. 2015). Substantial volcanic activity means that many high-elevation oceanic islands are topographically complex, with lava flows, land slips and high rates of erosion carving out deep, steep-sided barrancos, and the barranco mouths are often separated by high cliffs.

Here, we analyse the effect of small-scale topography on patterns of endemic species richness in a set of barrancos on the island of La Palma (Canary Islands). La Palma is a highly suitable study site in this context because, within a small area, the topography varies drastically (Carracedo et al. 2002, Irl and Beierkuhnlein 2011) and the Caldera de Taburiente volcano complex possesses, on its outer flanks, many similar, adjacent barrancos of varying depths. Past sea-level fluctuations mean that these barrancos were once extended when the sea level was lower: with rising sea level, the open ends of the barrancos at the coast became disconnected from similar habitats, creating large cliffs and perhaps hindering dispersal between barrancos at lower elevations.

We investigate **percent endemism**, defined as the percentage of native species that are endemic (following Steinbauer *et al.*, 2016), within different barrancos and assess its relationship with elevation and barranco depth. We use percent endemism instead of endemic richness to control for overall species richness. We focus mainly on endemism defined at the archipelago level (archipelago endemics, or AEs), but also differentiate between single-island endemics (SIEs – species that are endemic to La Palma) and multi-island endemics (MIEs – species which are endemic to the archipelago and found on at least one island other than La Palma; MIE + SIE = AE). We contrast two competing effects of topography-driven isolation on evolutionary dynamics, as follows. First, in line with recent findings (Steinbauer et al. 2016) at a larger scale (grain size), we may expect an increase in percent endemism with elevation (above sea level) of the barranco floor due to increasing isolation leading to higher speciation rates on the island and the archipelago as a whole. This predicts that (1) the floors of deeper barrancos will have lower speciation rates and lower percent endemism because they are at lower elevations. Alternatively, the isolating effect of deep barrancos may favour specialist or endemic species adapted to unique environments, whilst enhancing the survival of relict species. This would predict (2) higher percent endemism in deeper barrancos.

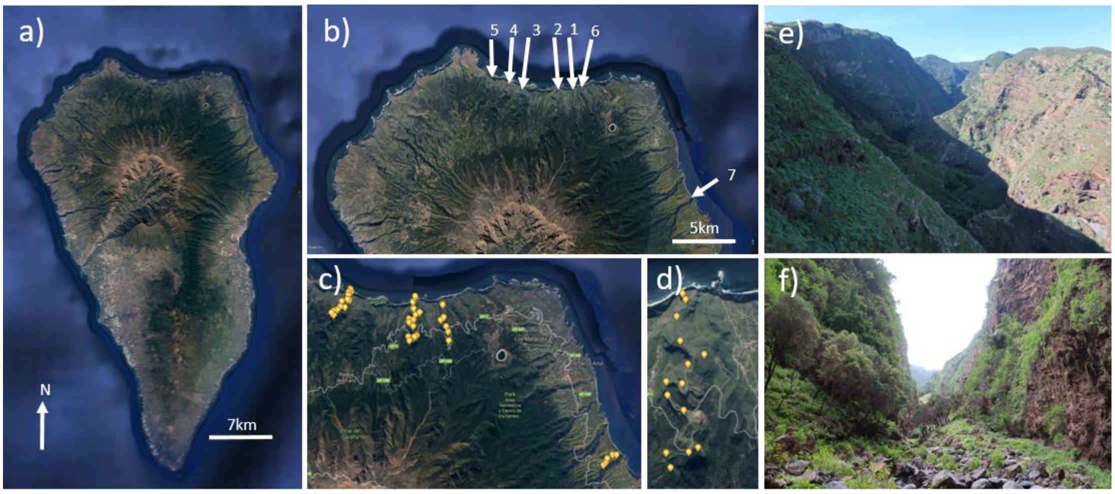

Figure 4-1 Maps of La Palma and the study area. a) Map of La Palma Island. b) View of the northern part of the island with the location of the barrancos labelled with their ID. Plot locations are shown for some of the barrancos in c). As an example, the plot spacing in barranco 2 is shown in d). Orientation (north) is the same in all panels. Images obtained from Google Earth Pro v 7.3.1.4507 (14/12/2015) 28°42’48.18”N, 17°54’20.81”W. Images of two different barrancos are shown in e) and f). Photo credit: Vanessa Cutts and Caroline Löwer.

4.4 Materials and Methods

4.4.1 Study area

La Palma is located within the Canary Islands archipelago (**Figure 4-1**). It is 708 km^2 in area and its highest elevation is 2426 m a.s.l. (Irl and Beierkuhnlein 2011). The climate is mild and stable all year round but, spatially, it changes quite drastically between the north-east and south-west of the island because the trade winds approach from the north-east (Irl and Beierkuhnlein 2011). The northern part of the island is approximately 1.8 million years old and topographically complex, which is due to high levels of erosion that have formed many deep barrancos (Carracedo et al. 2002, Iohnson 2008). In contrast, the southern part of the island is much younger and subject to more recent volcanic eruptions, so the barrancos are less developed. For these reasons, our sample sites were located in the northern and north-eastern part of the island where there is a set of barrancos of varying depths, which possess similar climates and have lush vegetation on their beds. There is an abundance of endemic species on the island, most of which are well documented (Muer et al. 2016). The island contains approximately 115 vascular plant species endemic to the archipelago (AEs), 371 native non-endemics and 238 exotics. Of the archipelago endemics, 40 are single-island endemics and 75 are multi-island endemics (Muer et al. 2016). It should be noted that there are no recorded SIEs that are endemic to a single barranco, though one species, *Echium bethencourtii*, is known to be endemic to the barranco floors of the study area.

Data Collection

Species presence–absence data were recorded in 75 plots across 7 different barrancos. We attempted to sample barrancos only in the north of the island, but as many were too difficult to access on foot, we included an additional barranco in the north east (barranco 7, **Figure 4-1b**). The number of plots varied between barrancos due to the difficulties of access (see **Table 4-1**). Within each barranco, 2m x 11m plots were placed along a transect following the barranco bed and were placed on alternate sides of the barranco where possible (**Figure 4-2**). The length of the transect depended on the accessibility of the barranco: transects were sometimes cut short, usually because of large cliff faces eroded by waterfalls. Once we determined the length of the transect, we then set out plots that were evenly spaced. Plots were situated just above the barranco floor. We avoided the riverbed so as to exclude the disturbances associated with occasional river flows (the barrancos are dry most of the time). From the coast inwards, the barranco floors follow an increasing elevational gradient; thus, across all barrancos, we were able to sample an elevation gradient from 95m to 674m. Elevation was recorded at each plot using a handheld GPS (Garmin Oregon® 600). Most species were identified in the field, but for those about which there was any doubt we collected specimens and identified them within three days, with the help of experts. There were 5 individuals for which we could not get an accurate ID, so we removed these from the data set (this made no detectable change to our results). Species were categorised as SIE (single-island endemic), MIE (multi-island endemic) and AE (archipelago endemic, i.e. either SIE or MIE) using (Muer et al. 2016). Species richness and percent endemism (pAE, pSIE and pMIE) were calculated for each plot and each barranco (**Table 4-1**).

Barranco metrics

Barranco depth was calculated as the difference between the barranco floor and the lowest ridge using the elevation profile in Google Earth. This was calculated in four different ways. First, we calculated depth as a single average measurement for each barranco, by measuring depth at 10 evenly spaced points along the barranco, starting at the coast and ending at approximately 600m in elevation (as this is the highest elevation we could reach with our plots) and taking the median value. We refer to this as average barranco depth. Second, because our plots span different ranges in each barranco, we calculated average depth using only the area of the barranco that was sampled by the plots. Again, we measured depth at 10 evenly spaced points along the barranco, but this time only between the first and last plots in each barranco, and used the median value. We refer to this as average sample depth. Thirdly, we measured depth at each individual plot and refer to this as plot depth. Finally, we used the maximum depth value for each barranco. Maximum depth was obtained by using the highest depth value for each barranco that was calculated from any of the above measurements. Thus, we have four measurements for barranco depth: average barranco depth, average sample depth, plot depth and maximum depth (**Figure 4-2**).

As an alternative measure of isolation, we quantify barranco shape using the height to width ratio (HWR), where higher HWR indicates narrower or steeper-sided barrancos, which we assume are more isolated. The HWR was calculated using the following formula adapted from Bull and McFadden (1977):

$$HWR = \ log_{10}\left(\frac{arh}{2dr}\right)$$

where arh = average height of both ridges and dr = the distance between the left and right ridges. These parameters were calculated using elevation profiles in Google Earth. Cross-sections were placed at 10 points along each barranco to get a topographical profile and the measurements were extracted and an average value calculated for each barranco. Narrow, deep barrancos have high HWR values whereas broad, shallow barrancos have low values. Post-field work, we were able to calculate barranco depth at every plot, except barranco 3 where GPS coordinates are missing. HWR was scaled before further analysis. HWR was highly correlated with barranco depth (*r*=0.98, *P*<0 .001) indicating that the barrancos are all very similar with respect to how shape relates to depth, so we do not consider it further.

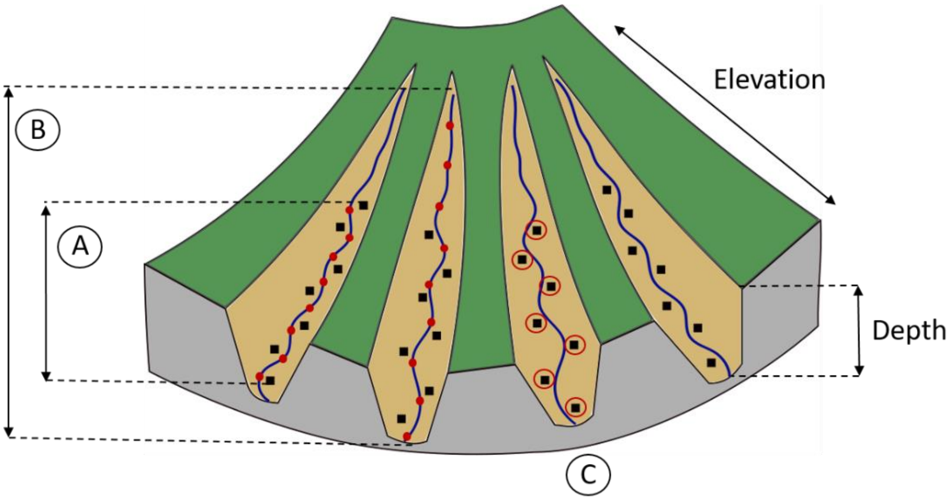

Figure 4-2 Schematic diagram depicting four barrancos situated on the flanks of the volcano. Black squares represent plots and the blue lines represent the floor of the barranco (which is now dry). Red dots and circles indicate where depth measurements were taken. Cases A-C illustrate the different depth measurements: A) average sample depth, where depth was measured at intervals between the first and last plot and an average taken, B) average barranco depth, where the depth was measured at intervals across the entire barranco and averaged, 3) plot depth, where the exact depth at each plot was considered. Maximum depth for each barranco was calculated as the maximum depth found from each of the other three depth measurements. The barranco on the right shows the elevation and depth gradients.

Statistical Analysis

We tested the hypothesised effects of barranco depth and elevation on pAE, pMIE, pSIE and species richness using four generalised linear mixed-effects models . As the data were proportions, we used binomial family errors, except for the species richness model, which uses count data, where we used Poisson errors. We tested each barranco depth metric separately in the models. The influence of elevation on percent endemism was calculated for all barrancos combined, so, here, the sampling unit is the barranco. Therefore, each plot represents a pseudoreplicate within each barranco. For this reason, we used barranco as a random effect, allowing the intercept to vary. Depth and elevation were scaled and included as predictor variables in the models. For the plot depth measurement, barranco 3 was also removed as no GPS points were available for this barranco to accurately calculate depth for the plots. Pearson's product moment correlation (r) was used to check the correlation between plot depth and elevation within each barranco.

As the number of plots varied between each barranco, we wanted to be sure that this would not affect our results. Therefore, as the minimum number of plots in a barranco was 6, we ran the above analysis using only 6 plots per barranco (for barrancos with more than 6 plots, we randomly sampled sets of 6 from the available ones). See S2 in the supporting information. All analyses were performed using R version 3.4.2 (R Core Team 2017). Mixed effects models were performed using the R package 'lme4' (Bates et al. 2015). The amount of variation accounted for by the predictor variables was quantified using pseudo-R^2 as calculated using the function r.squaredGLMM in the R package 'MuMIn', which returns a revised statistic based on Nakagawa & Schielzeth (2013).

4.5 Results

Overall, we recorded 180 species in the 75 plots, of which 67 were endemic to the Canary Islands (AE; 10 SIE and 57 MIE), 105 were native but not endemic, and 8 were exotic. The total number of native plant species on La Palma is 486. Therefore, we captured a considerable proportion of the entire flora in a small sampled area of the spatially rare habitat at the bottom of isolated barrancos.

Average barranco depth ranged from 56m to 299m, average sampled depth ranged from 37m to 299m, maximum depth ranged from 73m to 422m and the HWR ranged from 1.84 to 2.54 (**Table 4-1**). We found a positive correlation between plot depth and elevation in barranco 1 (r=0.77, P= 0.001), 2 (r=0.58, P=0.39), 4 (r= 0.91, P<0.001) and 7 (r=0.89, P=0.001) (**Figure 4-3**).

Table 4-1 Characteristics of each barranco in ascending order of percent endemism. Barranco ID corresponds to the barranco ID in **Figure 4-1**. HWR = height to width ratio, SR = total species richness, which comprises: AE = archipelago endemics (further split into multi-island endemics [MIE] and single-island endemics [SIE]), NEN = non-endemic natives, Exo = exotics. Percent endemism was here calculated at the barranco level, as 100*AE/(AE+NEN).

Barranco ID	No. of plots	Average barranco depth (m)	Average sample depth (m)	Maximum depth (m)	Elevation range sampled (m)	HWR	SR	AE	MIE	SIE	NEN	Exo	Percent endemism
6	6	141	135	193	181	2.16	52	14	11	3	35	3	29
5	6	132	178	215	91	2.14	33	9	7	2	22	2	29
3	10	269	299	390	174	2.48	91	34	28	6	52	6	40
1	14	210	211	353	305	2.30	109	43	34	9	62	4	41
2	13	219	233	306	414	2.34	93	37	29	8	53	3	41
7	9	160	166	228	84	2.27	68	29	24	5	35	4	45
4	14	299	275	422	206	2.54	88	44	36	8	41	3	52

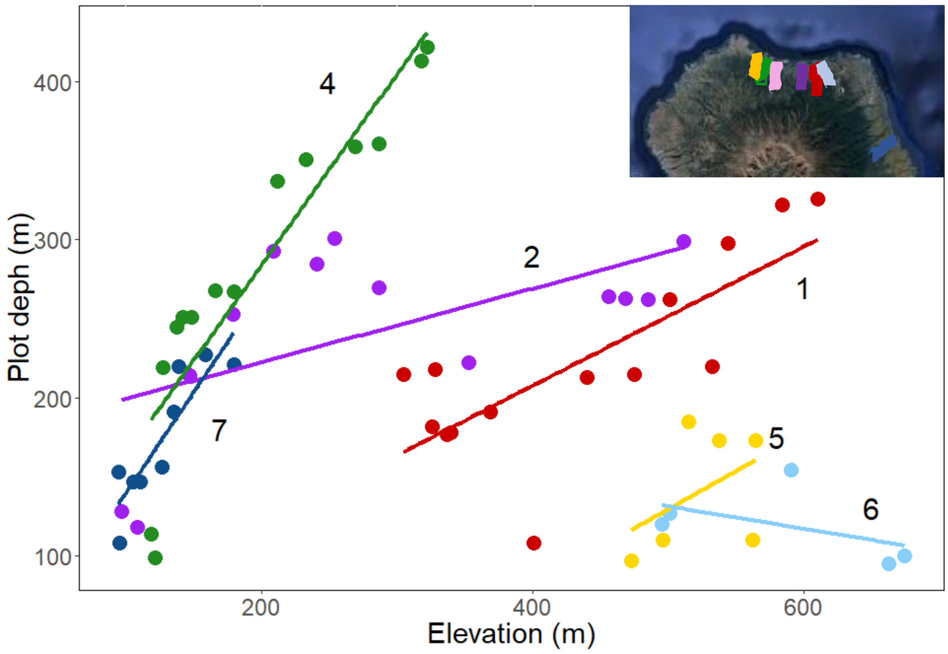

Figure 4-3 Significant positive correlations were found between plot depth and elevation for barranco 1 (*P*=0.001, *r*=0.77), 2 (*P*=0.039, *r*=0.58), 4 (*P*<0.001, *r*=0.91) and 7 (*P*=0.001, *r*=0.89). Each line is labelled with the corresponding barranco ID, which is synonymous with barranco ID in **Table 4-1**. Barranco 3 is not included in the scatter plot due to missing GPS points. The map in the top right corner show the location of the barrancos: colours match the correspond lines on the graph.

We did not find a significant increase in pAE, pMIE or pSIE with increasing barranco depth (**Table 4-2**, **Figure 4-4**). This was true for all depth measurements (average barranco depth, average sample depth, plot depth and maximum depth), with one exception: pMIE increased significantly with plot depth (slope=-0.27±0.11, *P*=0.018, R^2=0.055). Using plot depth in the models lowered the AIC values compared with models using alternative depth measurements.

We found a significant decrease in pAE and pMIE with elevation, while the decrease for pSIE was not significant (**Table 4-3**, **Figure 4-5**). When assessed individually with models, the relationship between pAE and elevation was significantly negative for barrancos 4 (slope=-0.007±0.003, *P*=0.012, R^2=0.44), 6 (slope=-0.004±0.002, *P*=0.045, R^2=0.69) and 7 (slope=-0.021±0.002, *P*<0.001, R^2=0.92). The remaining barrancos showed no significant relationship (**Figure 4-6**). Species richness models showed a significant decrease in species richness with elevation, but no significant relationship with depth (**Figure 4-7**). When barrancos were modelled separately, the negative relationship with elevation was significant for barrancos 2 (slope=-0.002±0.0004, P=0.002, R^2=0.59) and 6 (slope=-0.008±0.001, P=0.005, R^2=0.90).

We used binomial family errors for the pAE, pMIE and pSIE generalized linear mixed-effects models because the response variables were proportions. As this accounts for the differences in species richness, the resulting R^2 values are extremely low due to the higher weighting of plots with high species richness. Using a linear mixed effects model with a Gaussian distribution produced higher R^2 values; we report these results in the supporting information (4.11.S1).

Table 4-4 Model outputs from generalised linear mixed effects models. Barranco was included as a random factor (intercept) in all models. pAE = percentage of archipelago endemics, pMIE = percentage of multi-island endemics, pSIE = percentage of single-island endemics, SR = species richness.

Model	**Slope**				**Intercept**	***P***	R^2	**AIC**
	Elevation	***P***	**Depth**	***P***				
pAE ~ elevation + average valley depth	-0.27±0.08	<0.001***	0.11±0.09	0.216	-0.46±0.07	<0.001***	0.034	326.1
pAE ~ elevation + average sample depth	-0.03±0.08	<0.001***	0.01±0.09	0.898	-0.46±0.08	<0.001***	0.032	327.5
pAE ~ elevation + plot depth	-0.17±0.28	0.550	-0.25±0.23	0.243	-0.50±0.22	<0.022*	0.064	265.6
pAE ~ elevation + maximum depth	-0.28±0.07	<0.001***	0.10±0.08	0.237	-0.47±0.07	<0.001***	0.034	326.2
pMIE ~ elevation + average valley depth	-0.32-±0.09	<0.001***	0.04±0.10	0.663	-1.04±0.08	<0.001***	0.040	302.0
pMIE ~ elevation + average sample depth	-0.35±0.09	<0.001***	-0.04±0.11	0.694	-1.03±0.09	<0.001***	0.038	302.0
pMIE ~ elevation + plot depth	-0.25±0.13	0.064	-0.27±0.11	0.018*	-1.01±0.14	<0.001***	0.055	244.6
pMIE ~ elevation + maximum depth	-0.33±0.09	<0.001***	0.03±0.10	0.754	-1.04±0.09	<0.001***	0.040	302.1
pSIE ~ elevation + average valley depth	-0.03±0.12	0.813	0.17±0.16	0.275	-2.03±0.14	<0.001***	0.023	221.3
pSIE ~ elevation + average sample depth	-0.04±0.12	0.710	0.12±0.16	0.436	-2.03±0.14	<0.001***	0.020	221.9
pSIE ~ elevation + plot depth	-0.13±0.12	0.293	0.13±0.12	0.276	-2.01±0.15	<0.001***	0.024	184.0
pSIE ~ elevation + maximum depth	-0.04±0.12	0.707	0.18±0.15	0.249	-2.03±0.13	<0.001***	0.023	221.1
SR ~ elevation + average valley depth	-0.21±0.05	<0.001***	0.03±0.10	0.768	2.87±0.09	<0.001***	0.631	534.3
SR ~ elevation + average sample depth	-0.21±0.05	<0.001***	0.02±0.10	0.848	2.87±0.09	<0.001***	0.628	534.3
SR ~ elevation + plot depth	-0.25±0.06	<0.001***	0.09±0.05	0.061	2.90±0.11	<0.001***	0.704	447.6
SR ~ elevation + maximum depth	-0.20±0.05	<0.001***	0.08±0.09	0.812	2.88±0.09	<0.001***	0.636	533.7

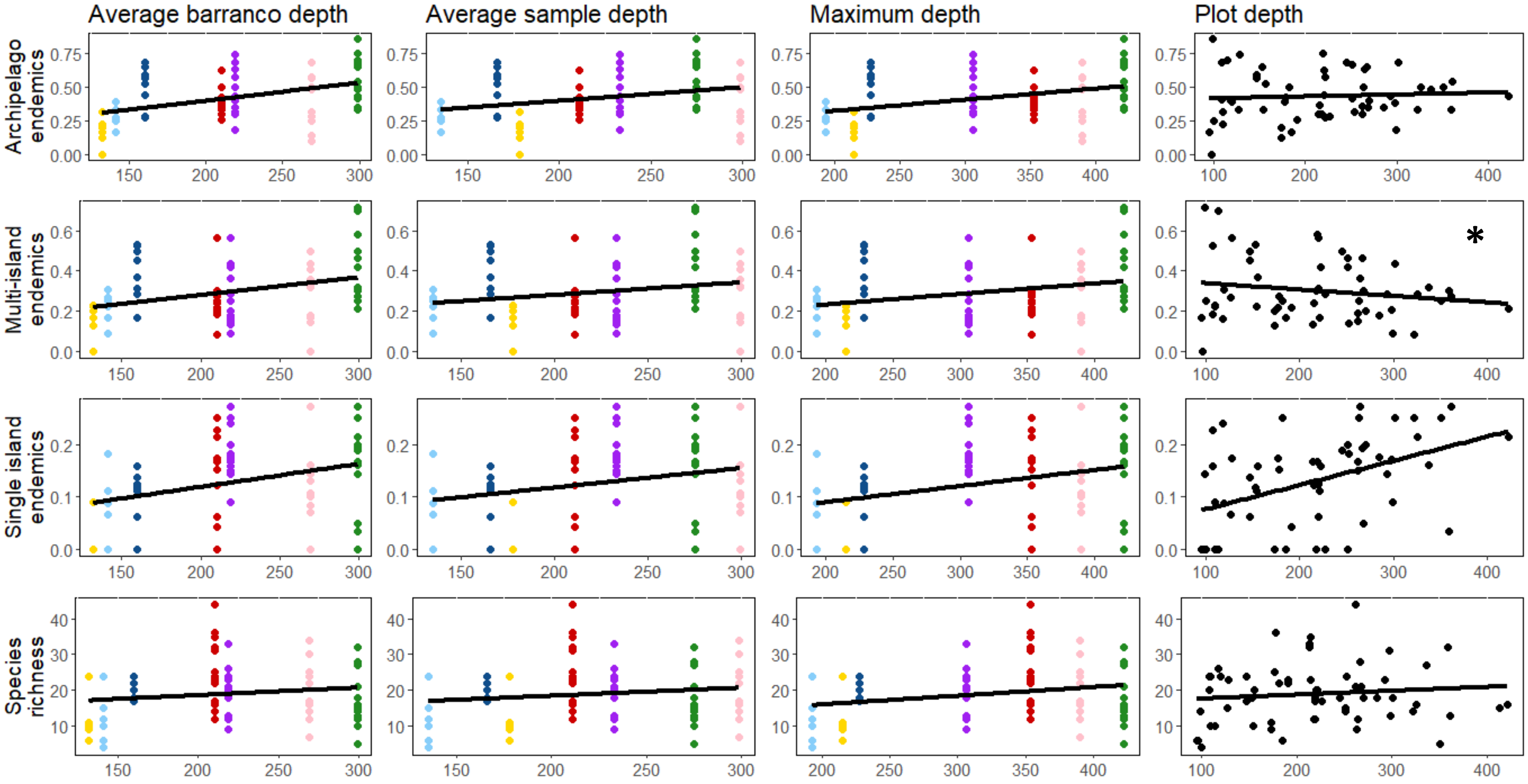

Figure 4-4 The observed relationships between percent endemism (AE, MIE, SIE) and all four depth metrics. The bottom row shows the relationship between species richness (SR) and depth in metres. Relationships are not significant with the exception of MIE and plot depth (*P*= 0.055), denoted with *****. Points are coloured by barranco, which correspond to the colours in **Figure 4-3**.

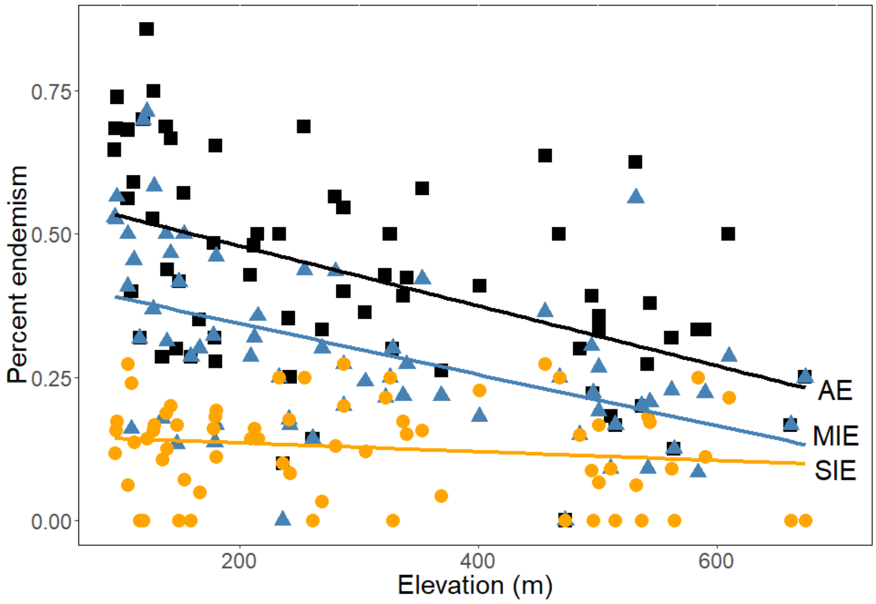

Figure 4-5 The observed relationships between percent endemism (AE, MIE, SIE) and elevation. Both AE and MIE show significant relationships with elevation (*P*<0.001), except when plot depth is included in the model. SIE shows no relationship with elevation. See **Table 4-4** for model outputs.

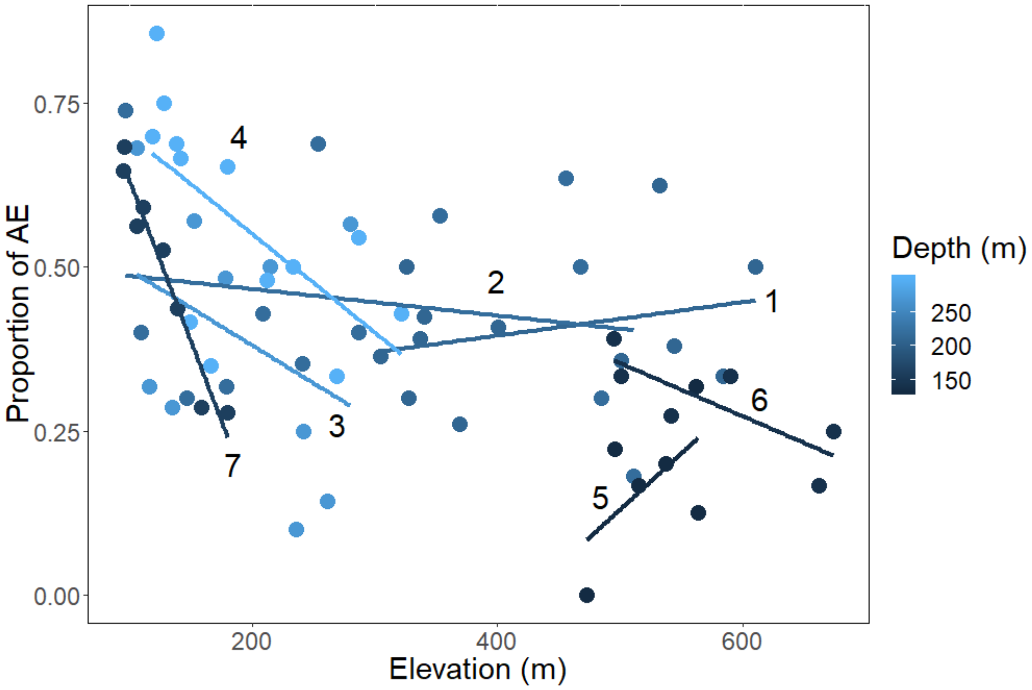

Figure 4-6 The relationship between pAE and elevation for each barranco. General linear models showed that pAE decreased significantly for barrancos 4 (slope=-0.007±0.003, *P*=0.012, R^2=0.44), 6 (slope=-0.004±0.002, *P*=0.045, R^2=0.69) and 7 (slope=-0.021±0.002, *P*<0.001, R^2=0.92). The relationship was not significant for the remaining barrancos. The

colour scale reflects the change in average depth sampled between the barrancos, with lighter colours indicating deeper barrancos and darker colours indicating shallower barrancos. Although each barranco is situated on a different part of the elevational gradient, the general trend shows a decrease in pAE with elevation. Numbers indicate the barranco ID.

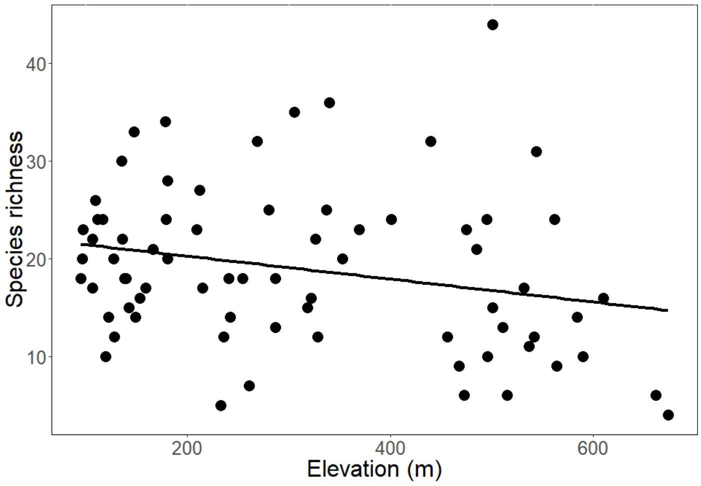

Figure 4-7 The relationship between species richness and elevation is a decreasing one (P<0.001). See **Table 4-4** for R^2 values.

4.6 Discussion

On a global scale, archipelago endemics have been shown to increase with elevation (Steinbauer et al. 2016) but looking more closely at small-scale topographic variation may reveal more intricate patterns of endemism. We documented a decrease in the percent endemism with increasing elevation, a result that opposed our first prediction, derived from previous studies. We also did not find an effect of barranco depth on percent endemism.

Using four different measures of barranco depth, at the plot level and the barranco level, we were unable to detect an effect of depth on percent endemism or species richness both within and between barrancos. It may be that such small-scale topography provides insufficient isolation, or the isolation has not persisted long enough, for speciation to occur within the barrancos, which could explain why there is just one barranco endemic. The relationship between barranco depth and elevation is strongly intertwined: barranco depth increases with elevation initially, as the barrancos carve into the mountain sides, and then begins to decrease until the barrancos eventually disappear, merging and levelling out towards the sides of the caldera. Thus, the relationship between depth and elevation should be a unimodal one. Within our sample area, we capture the initial increase in depth with elevation and, although non-significant, we begin to see a decrease in depth in our most highly elevated barranco (barranco 6; **Figure 4-3**). Detecting a relationship between percent endemism and depth is difficult as the variable is collinear with elevation. Although non-significant, depth shows weak positive relationships with endemism (**Figure 4-4**). Future work could aim to tease apart these variables.

We find an increase in percent endemism (pAE and pMIE) with decreasing elevation. Higher habitat heterogeneity, through increased topographic complexity, may explain why we find this pattern, as the barrancos become more pronounced at lower elevations. The steep topography creates areas of light and shade, hot and cold, and dry and moist habitat, as well as extreme habitats like the steep, eroded barranco walls. High habitat heterogeneity and steep environmental gradients increase the number of niches, resulting in adaptation to diverse environmental conditions, increasing the probability of speciation (Golestani et al. 2012, Stein et al. 2014, Huang et al. 2017). Furthermore, areas with high habitat heterogeneity are more likely to provide refuge for species during past climatic change, allowing species to persist (Fjeldså et al. 1999, Kallimanis et al. 2010, Harrison and Noss 2017). The northern part of La Palma is the oldest part of the island and may be a potential refuge for endemics that evolved under past environmental conditions.

Furthermore, due to cold air pooling, the temperatures at barranco bottoms are cooler than normally expected at low elevations (Geiger et al. 2003, Dobrowski 2011), thus, high-elevation species are perhaps able to survive at lower elevations in barrancos. This may result in asymmetric dispersal down the barrancos but not up. Indeed, we did find that laurel forest species were present at lower elevations in the barrancos. Furthermore, barranco habitat may be important for dispersal between islands. The dispersal of high-elevation endemics is hindered by elevation-driven isolation, whereby species become more isolated at higher elevations due to the increasing remoteness from equivalent habitats (Steinbauer et al. 2016). The suitable habitat provided in these barrancos at low elevations may act as stepping-stones for endemics dispersing from high elevation zones on other islands, thereby lessening elevation-driven isolation in these environments. An alternative reason why we find more AEs at lower elevations in the barrancos might be due to the prevalence of this unique habitat. The barranco bed habitat is common in the Canary Islands, but relatively rare beyond the archipelago. This may allow speciation to build up and persist through time.

In our sample area, we found that exotic species make up only 4% of species. Previous work on La Palma found the proportion of exotics (non-natives) to peak at an elevation of 500m, after which there is a strong decrease with increasing elevation (Steinbauer et al. 2017). As we sampled up to an elevation of 674m, the majority of our study area is located near the peak range for exotic species, indicating that exotics are largely excluded from the barrancos. As well as exotic plants, barrancos may also restrict the access of exotic herbivores to certain areas, particularly the steep barranco sides, which may act as refugia from exotic herbivores that preferentially feed on endemic plant species (Cubas *et al.* 2019).

The pattern we observed between endemism and elevation may not be representative of the entire elevation gradient as our plots only reach 674m a.s.l., whereas the highest elevations on La Palma are in excess of 2000m. Using elevational belts, Steinbauer *et al.* (2016, 2017) found an overall increase in the percentage of AEs with elevation on La Palma, but in a non-linear manner, with a slight dip in endemism at approximately 500m, consistent with our result. With regard to species richness, we find the same pattern: species richness decreases with elevation. This is not unexpected and may be due to the decrease in area with elevation. This follows similar patterns reported for many taxa, of either a monotonic decrease or a humped-shaped relationship (Rahbek 1995).

Although we found no significant effect of barranco depth on percent endemism, we argue that the role barrancos play in the diversity and evolutionary dynamics of endemics species warrants further investigation within the Canary Islands and elsewhere, not least because of the relatively restricted elevation gradient we studied here and the co-linearity with elevation. Future work may also consider the different geological ages of barrancos, although in this study system age variation is unlikely due to their close proximity to each other. Barrancos appear to be rich in endemic species, not only on La Palma but also other islands in the Canaries, where the highest number of endemics occur on steep slopes (Otto et al. 2016). The primary habitats for most El Hierro endemics are the rocky, steep sites, made up of old bedrock (Von Gaisberg and Stierstorfer 2005). Considering the fact that the accessible area of the barrancos is very limited due to the extremely steep slopes and the rugged scarps forming waterfalls in times of run-off, the recorded number of species and endemics in these isolated barrancos is remarkable. Whether or not the depth of the barrancos plays a role in endemism, the presence of barrancos themselves may be important in offering a unique habitat for endemics and may explain why we see fluctuations in elevation–endemism gradients.

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4.8 Contributions by the Authors

All authors developed the central ideas. V.C, N.K and C.L collected data in the field. V.C, R.F, A.C.A and M.J.S analysed the data and prepared the manuscript. All authors provided comments on the final manuscript.

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4.11 Supporting Information

S1. Model outputs from linear mixed effects models. Barranco was included as a random factor (intercept) in all models. pAE = percentage of archipelago endemics, pMIE = percentage of multi-island endemics, pSIE = percentage of single-island endemics, SR = species richness.

Model	**Slope**				**Intercept**	***P***	R^2	**AIC**
	Elevation	***P***	**Depth**	***P***				
pAE ~ elevation + average valley depth	-0.07±0.03	0.010*	0.04±0.04	0.210	0.41±0.03	<0.001***	0.373	-37.598
pAE ~ elevation + average sample depth	-0.08±0.03	0.005**	0.01±0.04	0.719	0.41±0.03	<0.001***	0.363	-36.345
pAE ~ elevation + plot depth	-0.04±0.03	0.247	-0.05±0.03	0.048	0.40±0.06	<0.001***	0.563	-32.640
pAE ~ elevation + maximum depth	-0.07±0.03	0.005**	0.04±0.03	0.268	0.41±0.03	<0.001***	0.366	-37.258
pMIE ~ elevation + average valley depth	-0.07±0.02	0.002**	0.01±0.03	0.659	0.29±0.02	<0.001***	0.305	-53.898
pMIE ~ elevation + average sample depth	-0.08±0.02	<0.001***	-0.01±0.03	0.707	0.29±0.02	<0.001***	0.297	-53.903
pMIE ~ elevation + plot depth	-0.04±0.03	0.128	-0.07±0.02	0.002**	0.29±0.04	<0.001***	0.523	-49.875
pMIE ~ elevation + maximum depth	-0.07±0.02	<0.001***	0.01±0.03	0.743	0.29±0.02	<0.001***	0.304	-53.754
pSIE ~ elevation + average valley depth	0.00±0.01	0.824	0.03±0.02	0.117	0.12±0.02	<0.001***	0.361	-127.60
pSIE ~ elevation + average sample depth	-0.00±0.01	0.930	0.03±0.02	0.282	0.12±0.02	<0.001***	0.368	-127.57
pSIE ~ elevation + plot depth	-0.02±0.01	0.239	0.03±0.01	0.014*	0.1320.02	<0.001***	0.345	-106.48
pSIE ~ elevation + maximum depth	-0.00±0.01	0.916	0.03±0.02	0.139	0.12±0.02	<0.001***	0.360	-127.35
SR ~ elevation + average valley depth	-3.63±1.39	0.009**	0.06±2.26	0.979	18.35±2.02	<0.001***	0.426	494.05
SR ~ elevation + average sample depth	-3.66±1.38	0.008**	-0.07±2.33	0.976	18.34±2.01	<0.001***	0.426	494.00
SR ~ elevation + plot depth	-3.92±1.46	0.007**	1.17±1.24	0.344	18.70±2.31	<0.001***	0.479	417.77
SR ~ elevation + maximum depth	-3.40±1.35	0.011*	1.04±2.17	0.633	18.45±1.96	<0.001***	0.425	493.86

S2. Table showing the percentage of models that were significant (*P*<0.05) for elevation and depth after randomly sampling 6 plots from each valley 100 times.

Model	**Elevation (%)**	**Depth (%)**
pAE ~ elevation + average valley depth	84	7
pAE ~ elevation + average sample depth	95	0
pAE ~ elevation + plot depth	86	6
pAE ~ elevation + maximum depth	94	4
pMIE ~ elevation + average valley depth	81	0
pMIE ~ elevation + average sample depth	81	0
pMIE ~ elevation + plot depth	81	0
pMIE ~ elevation + maximum depth	89	0
ppSIE ~ elevation + average valley depth	0	4
pSIE ~ elevation + average sample depth	0	0
pSIE ~ elevation + plot depth	7	21
pSIE ~ elevation + maximum depth	0	4
SR ~ elevation + average valley depth	90	0
SR ~ elevation + average sample depth	94	0
SR ~ elevation + plot depth	97	24
SR ~ elevation + maximum depth	92	4

Chapter 5 Scientific floras can be reliable sources for some trait data in a system with poor coverage in global trait databases

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5.1 Statement of contribution of joint authorship

I planned the project, collected La Palma field data and TRY data, analysed the data, wrote and compiled the manuscript and prepared the figures and tables. Dagmar Hanz collected La Palma field data. Paola Barajas-Barbosa collected Tenerife field data. Richard Field, Adam Algar and Manuel Steinbauer supervised and assisted with compiling the manuscript. Trait data from Floras was collected from students at University of Bayreuth and University of Göttingen. All authors aided in project conception and provided feedback on the manuscript.

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5.2 Abstract

Aim: Trait-based approaches are increasingly important in ecology and biogeography, but progress is often hampered by the availability of high-quality quantitative trait data collected in the field. Alternative sources of trait information include scientific floras and taxonomic monographs. Here we test the reliability and usefulness of trait data acquired from scientific floras against trait values measured in the field, and those in TRY, the most comprehensive global plant trait database.

Location: Tenerife and La Palma, Canary Islands, Spain.

Methods: We measured leaf area and specific leaf area (SLA) in the field for 451 native vascular plant species and compared them with equivalent trait data digitised from the most recent and comprehensive guide of the Canarian flora, and data sourced from TRY. We regressed the field-measured traits against their equivalents estimated from the literature and used the regression models from one island to predict the trait values on the other island.

Results: For leaf area, linear models showed good agreement between values from the scientific flora and those measured in the field (r^2=0.86). These models were spatially transferable across islands. In contrast, for specific leaf area we found a weak relationship between field-measured values and the best estimates from the scientific flora (r^2 = 0.11). Insufficient data were available in the TRY database for our study area to calculate trait correlations with other data sources.

Conclusions: Scientific floras can act as useful data sources for quantitative plant trait data for some traits but not others, whilst the TRY database contains many traits, but is incomplete in species coverage for our study region, and oceanic islands in general.

Key words: Canary Islands, leaf area, prediction, Scientific Flora, specific leaf area, trait data, TRY

5.3 Introduction

Functional trait-based approaches in ecological research have, in recent years, enhanced our understanding of biodiversity and how traits relate to ecosystem functioning. Functional traits are morphological, physiological or phenological features of organisms, measurable at the individual level, that impact individual performance and fitness (Violle et al., 2007). While the classification of species into functional groups has a long tradition (Raunkiaer, 1934; Weiher et al., 1999), the definition of a 'trait' has shifted from a simple grouping towards a more quantitative categorisation, allowing more predictive science within ecology (McGill et al., 2006). Trait-based approaches are now abundantly used to answer research questions across a variety of topics including community ecology (Mouillot et al., 2013; Satdichanh et al., 2015), species diversity gradients (Costa et al., 2018; Lamanna et al., 2014; Si et al., 2017; Whittaker et al., 2014), responses to environmental change (Bjorkman et al., 2018; Liu et al., 2018; Winchell et al., 2020), and niche dynamics (Costa, Gerschlauer, et al., 2018; Reif et al., 2016).

Functional traits have been particularly important in understanding the role of plant diversity in ecosystem functioning, and efforts have been made to identify trait–trait correlations and trade-offs to develop an economic spectrum for plant traits (Chave et al., 2009; Díaz et al., 2016; Kong et al., 2019; Reich, 2014; Shen et al., 2019; Wright et al., 2004). This, in turn, has aided the quantification of trait–environment relationships to understand how abiotic factors influence functional characteristics (Bruelheide et al., 2018; Ordoñez et al., 2009). Recognising the importance of plant functional traits in ecology has increased the demand for plant trait data (Kattge et al., 2020). However, acquiring such data is a challenge. The fundamental source of trait data is through the direct measurements of plant individuals, either in the field or under experimental conditions. A major disadvantage of these direct methods of data collection is their intensiveness—they require a significant amount of time, equipment and money. Even if resources are abundant, accessibility to field sites can be difficult and field work can be disrupted. This can lead to biased data collection, whereby field sites that are easier to access, such as those at low elevations or near roads, are preferentially chosen. As a result, the data may be limited in geographic or taxonomic coverage. Furthermore, measuring traits in the field can be destructive—collecting leaf and stem samples can be detrimental to an individual's survival. This is important to consider when studying rare or endangered species, for which non-destructive methods should be preferred (if acquiring a collection permit is even possible).

An alternative source for trait information is to rely on data that have been sampled in the past and made available via global databases (Kattge et al., 2020; Kleyer et al., 2008). This has benefited trait-based research by making plant trait data accessible to more researchers and it has allowed recent studies to examine plant trait variation across larger geographic and phylogenetic scales (e.g. Díaz et al. 2016; Bjorkman et al. 2018; Bruelheide et al. 2018). For plants, the TRY database is the largest collection of plant functional traits and holds an impressive amount of trait records for almost 280,000 species (Kattge et al., 2020). Despite efforts to update and improve trait databases, they are still incomplete (Jetz et al., 2016; Schrodt et al., 2015) and large taxonomic and geographic gaps remain. These knowledge gaps are non-randomly distributed, such that some species and regions are underrepresented (Cornwell et al., 2019; Jetz et al., 2016; Schrodt et al., 2015). There are also biases towards certain traits and trait values. Easily measured traits are more likely to be reported than those that are difficult, or require more resources, to measure. In addition, bias towards higher or lower trait values has been found for frequently measured traits in the TRY database (Sandel et al., 2015), and certain trait values may go unreported (but see Scheffer et al. 2015).

Outside of these databases, a wealth of information about plant form and function exists in the literature that is yet to be digitised. Information on plant species has been assembled and published in thousands of scientific floras (Floras hereafter) and taxonomic monographs for centuries. In fact, attempts to assemble botanical knowledge were made in ancient times and date as far back as AD 77 (see Pliny & Healey 2004). Floras catalogue all known plant species in a given geographic region and represent some of the oldest collections of plant information in the botanical literature. They contain detailed taxonomic descriptions, keys, illustrations and sometimes distribution maps, geographical and ecological information that can be used for locating and identifying species (Frodin, 2001). Such detailed descriptions of plant morphology often systematically provide values for some traits. They may even include basic information on intraspecific variation, such as when maximum and minimum values are reported for a given trait, or when different values are reported for different regions.

Trait values extracted from Floras have the potential to be used for ecological purposes (Hawkes, 2007; W. D. Kissling et al., 2010; W. Daniel Kissling et al., 2008; Whittaker et al., 2000), and there is a growing effort to mobilize and integrate them into global biodiversity databases (Weigelt et al., 2020). Data from Floras and checklists provide highly representative and complete data from large regions, which is beneficial to macroecological research, but this data type is currently underutilized compared to fine-scale, high resolution data, such as site-specific trait measurements (König et al., 2019). Comparing data quality with systematically collected field data is necessary to understand how data from Floras can be successfully applied in trait-based research. Thus, the aim of our study is to compare trait data obtained via three different methods of collection: 1) Floras, where trait information is extracted from species descriptions and identification keys, 2) field work, where established quantitative plant traits are measured directly in the field, specific to the geographic location of interest and 3) the TRY database, where a species list of the focal region is used to download data for the focal traits.

We use the islands of Tenerife and La Palma in the Canary Islands (Spain) as the study system, for which an up-to-date, comprehensive and modern Flora is available (Muer et al., 2016). Oceanic islands are an appropriate study system for trait-based research (Ottaviani et al., 2020) due to their spectacular radiations and disproportionately high numbers of endemic species (Kier et al., 2009; Stuessy et al., 2006). Island systems have the potential to answer fundamental questions in functional ecology (Patiño et al., 2017) but the use of trait-based research on islands remains underexploited (Ottaviani et al., 2020) and readily available trait data for island species are rare. Leaves are at the core of plant functional ecology due to their role in carbon acquisition and transpiration, which influences biochemical cycling and ecosystem functioning (Press, 1999). Thus we specifically focus on two commonly used traits: leaf area and specific leaf area (SLA), for which precise measurements are not usually recorded in Floras. We estimate leaf area and SLA using simpler trait measurements recorded in Floras and evaluate how well these estimates reflect leaf area and SLA measured directly from specimens collected in the field. We expected that leaf area estimated using leaf length and leaf width would be strongly positively correlated with field-measured leaf area, and that SLA estimated using leaf thickness would be positively correlated with field-measured SLA. We also tested the ability of traits from Floras to predict field traits using independent data by using trait data from one island to predict trait values on another.

5.4 Methods

5.4.1 Field data

We studied traits of native vascular plant species of the islands of Tenerife and La Palma, Canary Islands, Spain. The latest plant checklist of the Canary Islands classifies species into to six categories: definitely native (either endemic or not), probably native, possibly native, probably introduced, introduced non-invasive and introduced invasive (Arechavaleta et al., 2009). We focused on species within the definitely native category only. Leaf traits were measured using standardised protocols for measurement of plant functional traits (Pérez-Harguindeguy et al., 2013): leaf area is the one-sided area of a fresh adult leaf, and SLA is the leaf area divided by its dry mass. We aimed to measure these traits for five adult individuals per species but, due to logistical constraints and the rarity of certain species, this was not always possible. If sampling more than one individual per species, we took samples from different locations across the islands where possible, to account for environmental variation in trait values. Species were sampled where botanical experts or the Flora indicated they were located. We collected between 10 and 100 adult leaves per individual, depending on the species: for most species we collected 10–20 leaves but for species with small leaves we collected up to 100 to accurately measure their mass. Where possible, we sampled leaves that were not in the shade. Leaves were cut from the stem and the petiole was removed. Up to 10 leaves were scanned per individual using an A4 scanner and leaf area calculated for each leaf using WinFOLIA software (version: 2016b Pro; Regent Instruments Canada Inc., 2016) for Tenerife specimens and ImageJ software (version 1.52a, Schneider et al. 2012) for La Palma specimens. We used the mean value for leaf area per species. The two software packages produced near-identical average values for leaf area per species (paired-*t*(44) = 1.32, *p* = 0.19; Pearson's *r* = 0.99). The leaf samples were weighed, then oven-dried and weighed again to calculate both fresh mass and dry mass per leaf. For compound leaves, we kept the entire leaf intact for scanning. Specific leaf area (SLA) was calculated by dividing the leaf area by its oven-dried mass (Pérez-Harguindeguy et al., 2013). We calculated leaf dry matter content (LDMC) of a single leaf by dividing the oven-dry mass by its fresh mass.

5.4.2 Flora data

We sourced plant trait data from the most recent and comprehensive guide to the Canarian flora (Muer *et al.* 2016). The information in the Flora is based on expert knowledge and contains species from all islands in the archipelago. These data were supplemented using other Floras to increase data coverage (Bramwell & Bramwell, 1974; Hohenester & Welß, 1993; Schönfelder & Schönfelder, 2018). In some instances, we recorded data for subspecies when the trait values were known to differ between subspecies found on different islands. This ensured the field and Flora data matched as precisely as possible, according to our aim throughout: that the data we obtained would be those typically used in trait-based research using the data source in question. We extracted the following leaf traits: leaf length, leaf width and leaf thickness (information on SLA was not provided). Maximum and minimum values were often reported for these traits but we calculated and used the mean values. We used leaf length and leaf width to estimate leaf area using the following formula:

$$estimated\ LA = \frac{LL \times LW \times \pi}{2}$$

where LA = leaf area, LL = leaf length, LW = leaf width. This equation assumes elliptical shaped leaves. SLA is normally calculated by dividing leaf area by its dry mass. Dry mass will depend on the volume and density of the leaf. In the absence of information on dry mass or leaf density, we cannot estimate SLA directly. However, it still may be possible to obtain a proxy for SLA in the absence of dry mass data if variation in volume has a greater influence. Given that leaf volume, LV = LA x Lth, where Lth is leaf thickness, then:

$$SLA = \frac{LA}{LV \times LD}$$

where LD is leaf density (dry mass per unit volume; (Poorter et al., 2009)). Thus, assuming invariant LD across species, SLA will vary as a function of Lth:

$$estimated\ SLA \sim \frac{1}{Lth}$$

Following this reasoning, we test whether SLA, measured in the field, can be estimated from the Lth values in the Flora. As a test-of-concept, we also test whether SLA varies with 1/Lth using only our field data. Lastly, leaf thickness has also been shown to correlate reasonably well with SLA x LDMC (Vile et al., 2005). We tested this by regressing leaf thickness from the Flora with SLA x LDMC as calculated from field data.

5.4.3 TRY data

Species names in TRY, our species list and the Flora were resolved using the Taxonomic Name Resolution Service (Boyle et al., 2013). We used the resolved species list to download the following traits from the freely available data: leaf length, leaf width, leaf thickness, leaf area and specific leaf area. To ensure consistency with field data, TRY data were filtered to include only measurements from living adult individuals in their natural environments.

5.4.4 Statistical Analyses

Simple linear regressions were carried out with field data as the dependent variable and Flora data as the independent variable. We removed *Kunkeliella retamoides* from the analysis—this species has tiny ephemeral leaves that are reduced to scales, making it difficult to define the functional equivalent of the leaf, which led to different definitions across data sources, and thus non-comparable values between field and Flora datasets. We regressed field-measured leaf area against Flora-estimated leaf area and field-measured SLA against Flora-estimated SLA. We also regressed field-measured leaf area and SLA against leaf length and leaf width obtained from the Flora to determine how well each measurement predicted leaf area and SLA by itself. Furthermore, to scrutinise our method of estimating SLA using Flora data, we regressed field-measured SLA with field-measured 1/Lth. We compared these models with a second set of models that included leaf type (simple vs. compound) and leaf shape (broad-leaved vs. needle-like) as interaction variables in order to determine if the regression slope differed between these groups (see supporting information). We also compared leaf thickness from field data and Flora data. All variables were $\log_e$ transformed to improve the residuals of the regressions. In addition, we compared trait values obtained from the Flora with those from TRY using Pearson's *r*.

Firstly, we looked at the relationships across all the data (La Palma + Tenerife). Secondly, we modelled La Palma data only and tested the predictions of this model against data from Tenerife (with field-measured leaf area from Tenerife as the dependant variable and predicted values from La Palma regressions as the independent variable). We also did the reverse, regressing observed values from La Palma against values predicted from Tenerife. We then compared the slope and intercept parameters of the observed vs. predicted values against the 1:1 line (i.e. slope=1, intercept=0) using a one-sample t-test to determine the spatial transferability of the models. All analyses were carried out in R (version 3.6.1, R Core Team 2017).

5.5 Results

5.5.1 Data coverage

We measured traits for 451 definitely native species in the field (**Table 5-1**); 398 of these were measured on Tenerife and the remaining 53 on La Palma. From the Floras, we compiled a list of 554 definitely native species (including all 451 species sampled in the field) from La Palma and Tenerife that had values for at least one of our selected traits (most species came from Muer et al. (2016)). We found data for only 24 out of these 554 species in TRY, of which just five were endemic to the Canary Islands (**Table 5-1**). When considering individual traits, eight definitely native species had measurements for leaf area in TRY and 16 had measurements for SLA. Due to this low coverage of the TRY data, we were unable to conduct meaningful comparisons with the field and Flora data. Leaf thickness was scarcely reported in the Flora (only

4% of native species; **Table 5-1**) and only for species with clearly succulent leaves (to within 0.1 mm precision). Thus, our sample size for the regression of field-measured SLA with estimated SLA is very small (*n* = 18) and is not representative of all leaf types.

To maintain consistency among data sources, we focus primarily on definitely native species occurring on La Palma and Tenerife, as these were the species measured for the field data. However, for informative purposes, in **Table 5-2** we also report Flora and TRY data for all species, including exotics, occurring across the entire Canary Island archipelago. We considered probably introduced, introduced non-invasive and introduced invasive as exotic species.

Table 5-1 Trait coverage for native species occurring on La Palma and/or Tenerife from each data source. Columns show the numbers (and percentages) of species that have a value for each trait in each data source, respectively; totals are the numbers of species with at least one measured trait. The percentage is in reference to the number of La Palma/Tenerife species recorded in the Flora.

	Flora	**Field work**	**TRY**
Leaf length	267 (48%)	-	8 (1.4%)
Leaf width	215 (39%)	-	8 (1.4%)
Leaf thickness	22 (4%)	401 (72%)	22 (4.0%)
Leaf area	192 (35%)	392 (71%)	8 (1.4%)
Specific leaf area	22 (4%)	384 (69%)	16 (2.9%)
Total no. of species	**554 (100%)**	**451 (81%)**	**24 (4%)**

Table 5-2 Trait coverage for all Canary Island species in the Flora and in the TRY database. Columns show the total number (and percentage) of species that have a value for at least one measured trait. Numbers are shown for all species (which includes exotics) and for definitely native species. The percentages relate to the number of species recorded in the Flora of the relevant category (all or definitely native).

Trait	**Flora**		**TRY**	
	All species	Definitely native	All species	Definitely native
Leaf length	1060 (47%)	403 (47%)	43 (2%)	9 (1%)
Leaf width	974 (44%)	335 (39%)	111 (5%)	9 (1%)
Leaf thickness	42 (2%)	37 (4%)	256 (11%)	23 (3%)
Leaf area	882 (39%)	306 (35%)	141 (6%)	8 (1%)
Specific leaf area	42 (2%)	37 (4%)	220 (10%)	17 (2%)
Total no. of species	**2237 (100%)**	**865 (100%)**	**270 (12%)**	**24 (3%)**

5.5.2 Linear regressions

The relationship between field-measured leaf area and Flora-estimated leaf area was strong for the overall dataset (r^2 = 0.86, p<0.001, df =146; **Figure 5-1**), and when considering Tenerife (r^2 = 0.82, p<0.001, df = 116) and La Palma (r^2 = 0.96, p<0.001, df = 23) separately. This relationship did not differ between leaf groups (supporting information 5.11). Relationships between leaf area and leaf length or leaf width were also significant (leaf length: r^2 = 0.64; p<0.001; df = 192, leaf width: r^2 = 0.69; p<0.001; df = 162; **Figure 5-1**).

Field-measured SLA was not significantly correlated with estimated SLA for the overall dataset (r^2 = 0.11, p = 0.17, df = 16; **Figure 5-1**), neither was it when looking at Tenerife only (r^2 = 0.20, p = 0.08, df = 14). We did not analyse for La Palma only because not enough species from La Palma had trait values for leaf thickness and SLA. No significant relationship was found between SLA and either leaf length or leaf width for Tenerife or La Palma (**Figure 5-1**). When testing this using only field data, we found the r^2 values to be extremely low (df = 382, r^2 = 0.07, p<0.001; supporting information 5.11.S1). The addition of leaf type and shape as interactions terms did not improve the regression model (r^2 = 0.08; supporting information 5.11). In addition, there was no relationship between leaf thickness and SLA x LDMC (r^2 = 0.01, p = 0.71, df = 16; supporting information 5.11.S4). Leaf thickness measured from the field showed a reasonably strong and significant relationship with leaf thickness from the Flora (df = 18, r^2 = 0.49, p<0.001). Due to the low sample size no further analysis was conducted using SLA.

Correlations between Flora data and TRY data using all species (including exotics) showed a significant correlation for leaf area (Pearson's r = 0.89, p<0.001, df = 65) and leaf width (Pearson's r = 0.63, p<0.001, df = 67), but not for leaf length (Pearson's r = -0.18, p = 0.31, df = 31). This was due to an incorrect leaf length value (or incorrect units) for *Phoenix canariensis* in the TRY data (0.55 cm). When this species was removed, leaf length values correlated well (Pearson's r = 0.64, p<0.001, df = 30). We could not make any further comparisons of traits among data sources because, although the numbers in **Table 5-1** and **Table 5-2** look promising, often trait values are not available for the same set of species.

Table 5-3 Univariate linear regressions with field-measured traits as the response variables (LA$_{\text{field}}$ = field-measured leaf area, SLA$_{\text{field}}$ = field-measured specific leaf area, Lth$_{\text{field}}$ = field-measured leaf thickness) and Flora-measured traits as the explanatory variables (LA$_{\text{flora}}$ = Flora-estimated leaf area, LL$_{\text{flora}}$ = leaf length from Flora, LW$_{\text{flora}}$ = leaf width from Flora, SLA$_{\text{flora}}$ = Flora-estimated specific leaf area, Lth$_{\text{flora}}$ = leaf thickness from Flora). SLA$_{\text{field-est}}$ = SLA estimated using 1/Lth from field data. All data were log$_e$ transformed (except Lth$_{\text{field}}$ and Lth$_{\text{flora}}$). SE = standard error.

	All Data					**Tenerife**					**La Palma**				
	df	Slope±SE	Intercept±SE	r^2	p	df	Slope±SE	Intercept±SE	r^2	p	df	Slope±SE	Intercept±SE	r^2	p
LA$_{\text{field}}$ ~ LA$_{\text{flora}}$	146	0.93±0.03	-0.52±0.11	0.86	<0.001	116	0.91±0.04	-0.47±0.13	0.82	<0.001	23	0.99±0.04	-0.71±0.16	0.96	<0.001
LA$_{\text{field}}$ ~ LL$_{\text{flora}}$	192	1.48±0.08	-0.71±0.16	0.64	<0.001	155	1.40±0.09	-0.61±0.18	0.59	<0.001	27	1.83±0.12	-1.61±0.25	0.90	<0.001
LA$_{\text{field}}$ ~ LW$_{\text{flora}}$	162	1.34±0.07	1.58±0.09	0.69	<0.001	132	1.26±0.08	1.63±0.10	0.66	<0.001	23	1.90±0.15	1.09±0.19	0.87	<0.001
SLA$_{\text{field}}$ ~ SLA$_{\text{flora}}$	16	0.32±0.29	4.58±0.21	0.20	0.06	14	0.26±0.14	4.66±0.19	0.20	0.08	-	-	-	-	-
SLA$_{\text{field}}$ ~ SLA$_{\text{field-est}}$	382	0.25±0.05	4.56±0.07	0.07	<0.001	312	0.28±0.04	4.62±0.05	0.14	<0.001	50	0.41±0.23	4.10±0.32	0.06	0.09
SLA$_{\text{field}}$ ~ LL$_{\text{flora}}$	189	-0.11±0.09	4.55±0.17	0.01	0.20	153	-0.09±0.05	5.01±0.09	0.02	0.08	27	0.23±0.18	1.63±0.38	0.06	0.20
SLA$_{\text{field}}$ ~ LW$_{\text{flora}}$	161	-0.02±0.08	4.44±0.10	0.00	0.84	131	0.02±0.05	4.90±0.06	0.00	0.64	23	0.39±0.18	1.82±0.24	0.16	0.05
Lth$_{\text{field}}$ ~ Lth$_{\text{flora}}$	18	0.48±0.11	1.07±0.48	0.49	<0.001	15	0.49±0.14	1.12±0.53	0.46	0.003	-	-	-	-	-

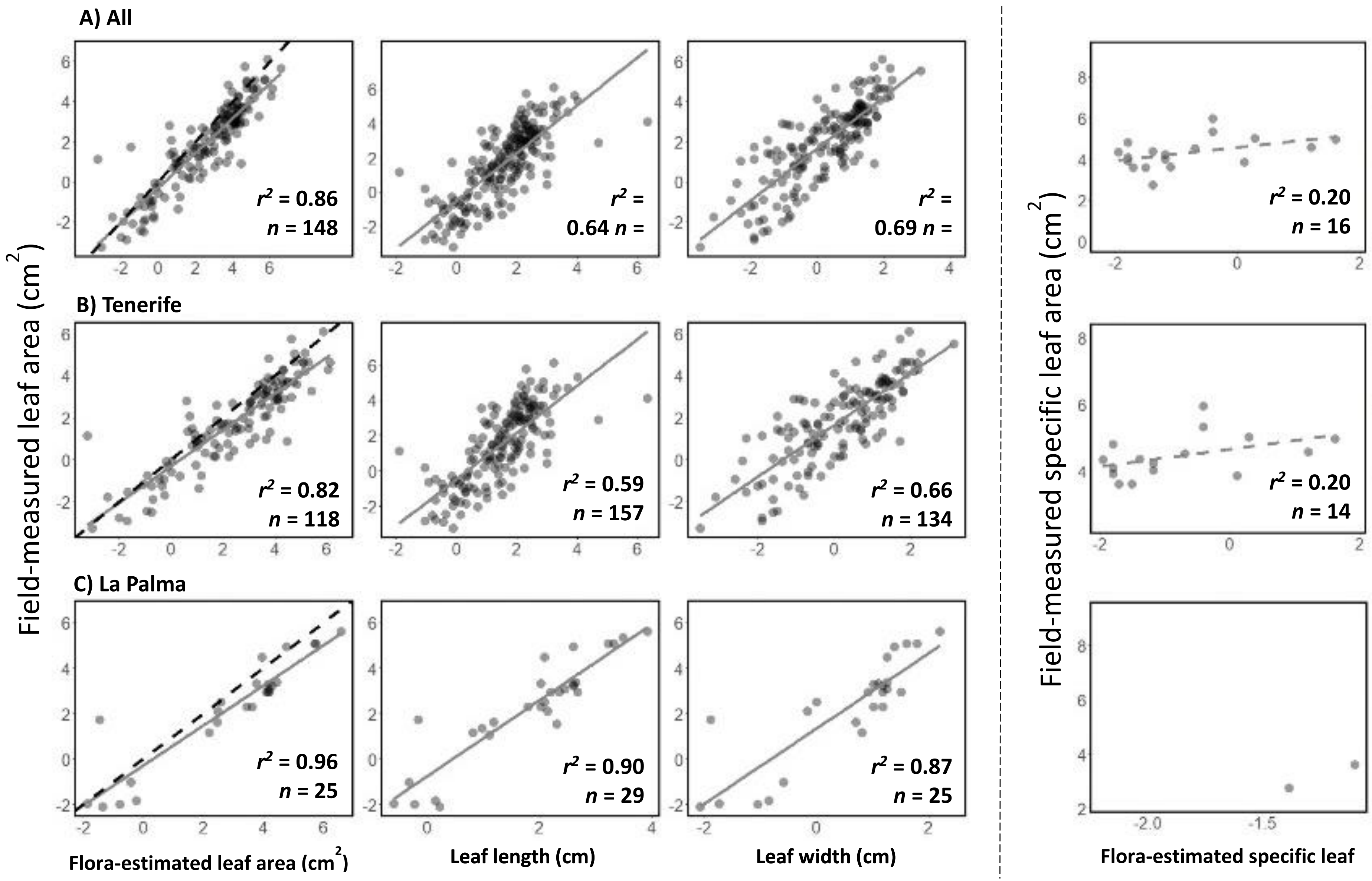

A) All
B) Tenerife
C) La Palma
Field-measured leaf area (cm²)
Field-measured specific leaf area (cm²)
r² = 0.86
n = 148
r² =
0.64 n =
r² =
0.69 n =
r² = 0.20
n = 16
r² = 0.82
n = 118
r² = 0.59
n = 157
r² = 0.66
n = 134
r² = 0.20
n = 14
r² = 0.96
n = 25
r² = 0.90
n = 29
r² = 0.87
n = 25
-2
0
2
4
6
8
-2.0
-1.5
Flora-estimated leaf area (cm²)
Leaf length (cm)
Leaf width (cm)
Flora-estimated specific leaf

Figure 5-1 Scatter plots showing the relationship between field-measured leaf area (on the Y-axis) and Flora traits (on the X-axis) for A) all data, B) Tenerife only and C) La Palma only. The grey lines are the linear regression models (grey dashed lines indicate a non-significant relationship). The black dashed lines are the 1:1 lines (not shown on the leaf length and leaf width graphs because the axes are on different scales). The left hand panel shows relationships between field-measured SLA and Flora-estimated SLA. All axes are $\log_e$ transformed. See **Table 5-3** for regression equations.

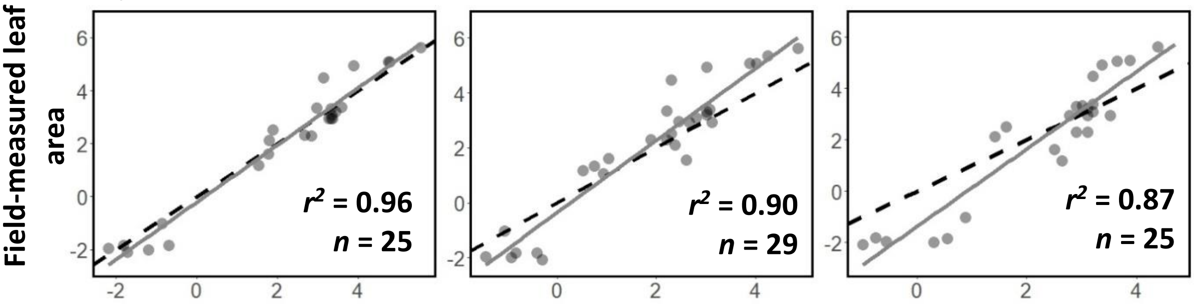
5.5.3 Cross-island predictions

We used the linear regression models to predict leaf area outside the geographical range of input data (i.e. the other island), using Flora data. We then correlated these predicted values with the observed values. All La Palma models successfully predicted leaf area on Tenerife; there was a strong positive relationship between the observed values on Tenerife and the predicted values from La Palma models based on Flora data ($r^2 = 0.79$). This was also true the other way around, i.e. observed values from La Palma vs. predicted values from Tenerife models ($r^2 = 0.85$). Again, leaf width had a higher predictive power than leaf length (**Table 5-4**). For leaf area predictions on both La Palma and Tenerife, the slope and intercept were very close to, and not significantly different from, 1 and 0 respectively (i.e. the 1:1 line: **Table 5-4**; **Figure 5-2**). For leaf length, the slope differed significantly from 1 but the intercept did not differ from 0 for both islands. For leaf width, the slope and intercept differed significantly from 1 and 0 for both islands.

Table 5-4 Observed vs. predicted regressions for field-measured leaf area (LA), where Flora-estimated leaf area, leaf length and leaf width were used as explanatory variables. Predicted LA values from La Palma models were regressed against observed values from Tenerife (top) and vice versa (bottom). SE = standard error. All regressions were significant at P <0.001. ‘Slope P’ and ‘Intercept P’ are P-values from one-sample t-tests comparing slopes with 1 and intercepts with 0. All data were $\log_e$ transformed.

		df	**Slope±SE**	**Slope *p***	**Intercept±SE**	**Intercept *p***	***r^2***
Tenerife observed LA vs. Predicted La Palma LA	Flora-estimated leaf area	116	0.95±0.04	0.06	-0.19±0.10	0.07	0.82
	Leaf length	155	0.76±0.05	<0.001	0.27±0.14	0.05	0.59
	Leaf width	132	0.66±0.04	<0.001	0.91±0.12	<0.001	0.66
La Palma observed LA vs. Predicted Tenerife LA	Flora-estimated leaf area	23	1.08±0.05	0.11	-0.21±0.15	0.17	0.96
	Leaf length	27	1.31±0.08	<0.001	-0.35±0.21	0.10	0.90
	Leaf width	23	1.51±0.12	<0.001	-1.37±0.33	<0.001	0.87

A) Predictions from Tenerife data



B) Predictions from La Palma data

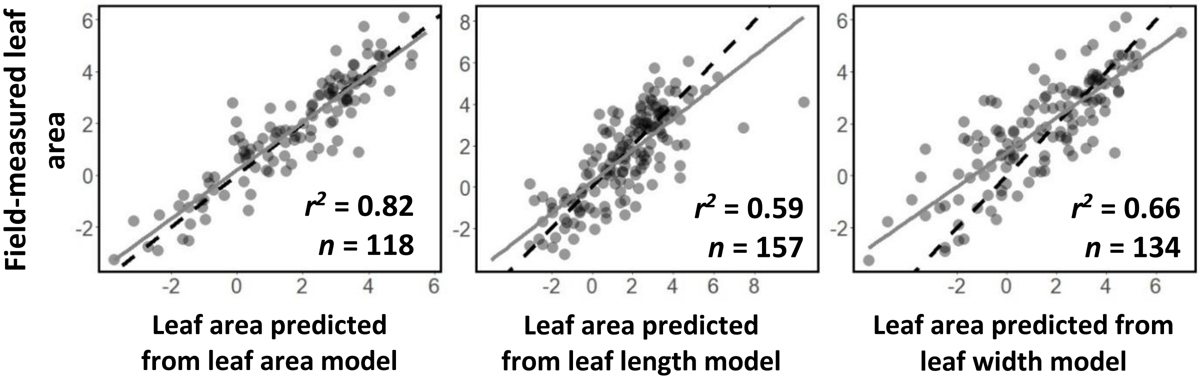


Figure 5-2 Scatter plots showing the observed vs predicted leaf area. Predictions (X-axes) are based on leaf area, leaf length and leaf width models. A) The observed La Palma data ($\log_e$ transformed) were regressed against predictions from Tenerife data, B) The observed Tenerife data ($\log_e$ transformed) were regressed against predictions based on La Palma data. Grey lines are the linear regression models; black dashed lines are the 1:1 lines. See **Table 5-4** for regression equations.

5.6 Discussion

We have demonstrated that a combination of easily obtained leaf parameters—leaf length and leaf width—can be used to estimate leaf area as a non-destructive alternative to field sampling. Furthermore, we were able to successfully predict independent field-measured data on leaf area across islands in the Canaries, indicating that the reliability of Floras as sources of trait data may be transferable to new regions.

Our estimates of leaf area correlated strongly with field-measured leaf area on both La Palma and Tenerife despite assuming an elliptical shape. Other studies using leaf length and width to estimate leaf area have found similar results (Kraft et al., 2008; Pandey & Singh, 2011; Shi et al., 2019). Accounting for the differences in leaf type (simple vs. compound) and leaf shape (broadleaf vs. needle-like) did not improve our models. In fact, we find that the species that diverge furthest from the 1:1 line are a mix of species with simple or compound leaves. Thus, the variation in leaf type and leaf shape does not necessarily correspond to variations of leaf area (leaf shape probably relates more closely to leaf perimeter). Therefore, the additional variance in leaf area due to leaf shape that is not accounted for in the model (e.g. from compound or severely lobed leaves) does not have a sufficient effect on leaf area to render a parsimonious model uninformative.

To evaluate the performance of the leaf area model, we used it to make predictions on a different island. The success of the predictions could be driven by the climatic overlap between islands as leaf area is linked to climate and microclimate (Byars et al., 2007; Guerin et al., 2012; Peppe et al., 2011; Sumida et al., 2018). Also, the phylogenetic relatedness within the Canary Island flora means that many species occurring on different islands belong to the same genera and are morphologically similar, such as *Argyranthemum*, which might contribute to the strong predictive ability. Nonetheless, despite considerable overlap, the climates of Tenerife and La Palma are different in some areas—La Palma receives the highest levels of precipitation in the archipelago due the north-easterly trade winds, and is cooler and wetter than Tenerife in some places, whereas Tenerife, being taller, reaches lower temperatures than La Palma at its summits. Also, although many of the closely related species are morphologically similar, some genera have radiated into species that are morphologically quite different (Jorgensen & Olesen, 2001). Therefore, despite both environmental and trait differentiation, the model predicts well across islands. Whether or not this can be translated beyond the Canary Island archipelago is a subject for further study. Intraspecific trait differences could be present in native species occurring on both the islands and the continent and could potentially have an island–continental gradient.

Despite our expectation, and considering that SLA is a function of leaf thickness (Pérez-Harguindeguy et al., 2013; Witkowski & Lamont, 1991), we only found a weak and non-significant relationship between field-measured SLA and Flora-estimated SLA. Accounting for differences between leaf groups only slightly improved these estimations. Perhaps a more complex model is required—assuming a constant volume to mass ratio for leaves is simplistic, because plants invest more or less in structural elements based on their ecological strategies (Westoby et al., 2002). Therefore, accounting for different leaf strategies might reveal different relationships. However, Vendramini et al. (2002) found a clear association between SLA and leaf thickness, but when accounting for leaf strategies (succulent, sclerophyllous and tender-leaf) this relationship disappeared. SLA is also a function of LDMC (Vile et al., 2005), thus, future research could see how the relationship differs across different LDMC values. Our attempt to estimate SLA using leaf thickness from available Flora data was unsuccessful. Leaf thickness seems to be scarcely reported in Floras, perhaps due the difficulty of making precise measurements, resulting in little variation. Furthermore, it is possible that leaf thickness from Floras are obtained from dried herbarium specimens, which would not be comparable to measurements from fresh leaves. This might account for the unexplained variation in the relationship between field-measured leaf thickness and Flora leaf thickness. We therefore encourage researchers to continue reporting true values for SLA.

We have identified significant gaps in the TRY database for the Canary Islands—only 3% of the definitely native species in the Canary Islands had any trait data, of which only 5 species were endemic to the archipelago (representing only 1% of the endemic species). Trait data may be scarce for islands in general, due to the high proportion of endemic species. If island data are disproportionally underrepresented in the TRY database, this could hinder trait-based research in insular systems (Ottaviani et al., 2020). The lack of data available for Canary Island endemics in TRY makes data available in the Flora all the more valuable—many Canary Island endemics are extremely rare and some are critically endangered (e.g. *Lotus eremiticus*). As well as lacking species, the TRY database often also lacks simple morphological traits in favour of more complex ones that are assumed to be more informative about plant functions. For example, researchers may provide data for SLA, but not upload the measurements used to calculate this (leaf area and leaf dry mass), which are useful in their own right. Floras provide highly representative data that are currently underexploited in ecology and, although the trait data they contain are limited in precision, these data have been shown to represent a more complete and unbiased view of spatial variation in functional traits (König et al., 2019). Thus, Floras provide complementary information to the data that are available in TRY.

In addition to the limitations of field data and TRY data, there are also clear limitations to using data from Floras. Firstly, the lack of standardised taxonomy across geographic regions is present, and probably reinforced, in Floras. However, applications are available to aid in resolving species lists once they have been digitised, for example the Taxonomic Name Resolution Service (Boyle et al., 2013). Secondly, Floras lack standardised vocabulary and definitions for the traits they describe, though recent efforts to harmonise the terminology around plant characteristics might alleviate this (Garnier et al., 2017; Hoehndorf et al., 2016). Finally, it is not always clear whether the data from Floras were collected in a standardised way, due to a lack of transparency. The limitations referred to here have been addressed by recent efforts to collate trait and distribution data from Floras and checklists, where trait values are standardised by language, terminology and unit of measurement (Global Inventory of Floras and Traits (GIFT)—Weigelt et al. 2020). This provides a standardised way of digitising and presenting the data in Floras and checklists worldwide.

A promising avenue for future research would be to evaluate digitalised herbarium specimens as a source of trait data. There are some clear advantages to using herbarium specimens to gather trait data, namely that the measurements are precise and the geographical/temporal origin of the specimens are known. However, there may be bias from using this type of data, whereby the most appealing specimens are collected. This may not accurately represent a species mean for a given trait.

5.6.1 Concluding remarks

We have demonstrated that Floras can provide some valuable data for the Canary Islands, whereas the TRY database currently cannot, a situation that we expect will affect other insular systems with high numbers of endemic species. This points towards a need for more field work to fill in gaps and reduce bias. However, due to the high cost and typically destructive nature of field sampling, it may not be feasible to sample rare and endangered species if we are to protect them. Thus, Floras remain an important resource in the emerging field of functional island biogeography, for which a lot of new data are required.

5.7 Acknowledgements

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5.8 Author contributions

All authors conceived the initial idea. VC, DH and MPBB collected the data. VC, ACA and RF analysed the data. VC, ACA and RF led the writing. All authors commented on, and edited, the final manuscript.

5.9 Data Availability

Data will be available on FigShare by August 2021 (https://figshare.com/s/f216133811b345c322e7). Until then, data are available on request.

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5.11 Supporting information

S1. Linear regressions with SLA (mm^2mg^{-1}) as the response variable and 1/leaf thickness (mm) as the explanatory variable using field data only. Both variables are $\log_e$ transformed. SE = standard error, df = degrees of freedom.

	df	Slope±SE	Intercept±SE	r^2	*p*
Intercept	382	0.26±0.05	4.56±0.07	0.07	<0.001
Tenerife	312	0.28±0.04	4.62±0.05	0.14	<0.001
La Palma	50	0.41±0.23	4.10±0.32	0.06	0.09

S2. Linear regressions with field-measured leaf area (cm^2) as the response variable and Flora-estimated leaf area (cm^2) as the explanatory variable. Both variables are $\log_e$ transformed. Leaf type (simple/compound) and leaf shape (broadleaf/needle-like) are included as interaction terms. $r^2 = 0.87$, $n = 104$.

	Estimate	SE	T values	*p*
Intercept	-0.74	1.23	-0.60	0.55
Leaf area	0.87	0.33	2.61	0.01
Leaf type Simple	0.15	1.25	0.12	0.91
Leaf shape Needle	0.11	0.28	0.39	0.70
Leaf area: Leaf type Simple	-0.15	0.29	-0.51	0.61
Leaf area: Leaf shape Needle	0.20	0.12	1.67	0.10

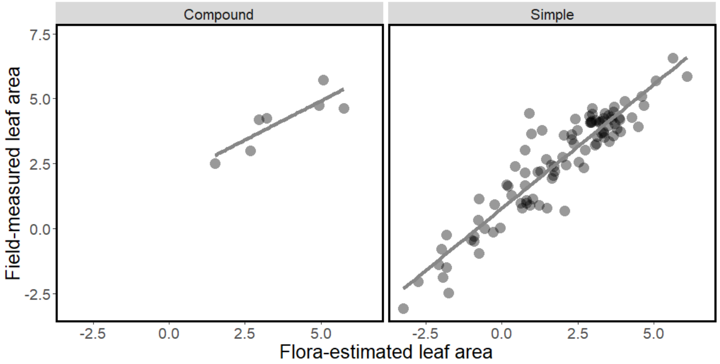
S3. Linear regressions with SLA (mm^2mg^{-1}) as the response variable and 1/leaf thickness (mm) as the explanatory variable using field data only. Both variables are $\log_e$ transformed. Leaf type (simple/compound) and leaf shape (broadleaf/needle-like) are included as interaction terms. SE = standard error. $r^2 = 0.08$, $n = 237$.

	Estimate	**SE**	**T values**	***p***
Intercept	4.95	0.55	8.93	0.00
SLA(1/Lth)	-0.10	0.36	-0.28	0.78
Leaf type Simple	-0.54	0.51	-1.06	0.29
Leaf shape Needle	0.02	0.26	0.07	0.95
SLA(1/Lth): Leaf type Simple	0.26	0.30	0.86	0.39
SLA(1/Lth): Leaf shape Needle	0.18	0.22	0.84	0.40

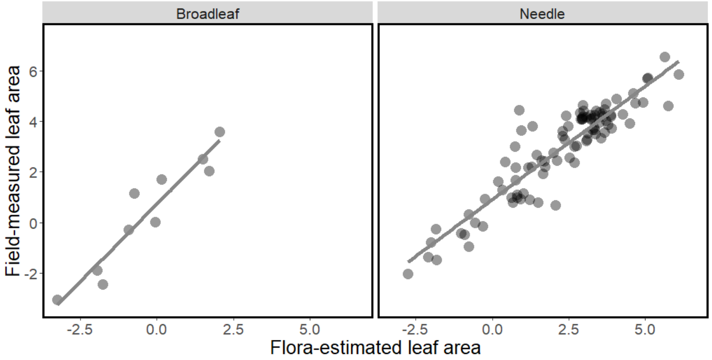
S4. Linear regressions with SLA (mm^2mg^{-1}) x LDMC ($mg\ g^{-1}$) from field data as the response variable and leaf thickness (mm) from Flora data. Both variables are $\log_e$ transformed. Regressions were carried out for all data and Tenerife separately. We did not have enough samples from La Palma to do a regression. SE = standard error, df = degrees of freedom.

	df	**Slope±SE**	**Intercept±SE**	***r*²**	***p***
All data	16	-0.22±0.59	5.11±0.78	0.01	0.71
Tenerife	14	0.11±0.14	5.68±0.18	0.04	0.43
La Palma	-	-	-	-	-

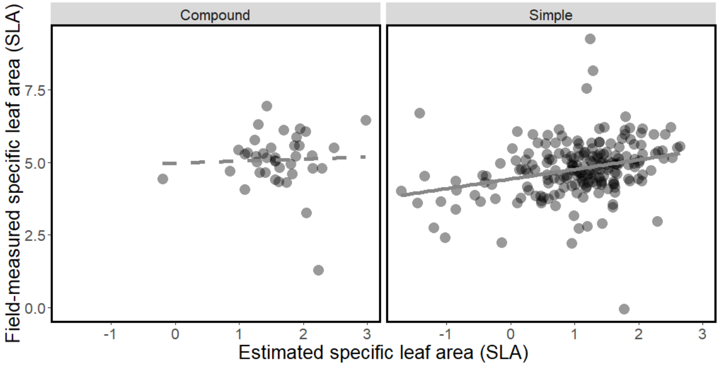
S5. Scatter plots showing field-measured leaf area on the Y-axis and Flora-estimated leaf area on the X-axis for compound leaves and simple leaves. Solid lines indicate a significant relationship.



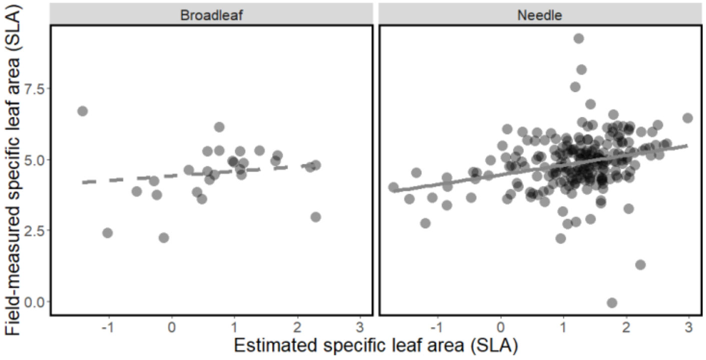
S6. Scatter plots showing field-measured leaf area on the Y-axis and Flora-estimated leaf area on the X-axis for broad leaves and needle-like leaves. Solid lines indicate a significant relationship.



S7. Scatter plots showing field-measured SLA on the Y-axis and SLA estimated using 1/Lth from field data on the X-axis for compound leaves and simple leaves. Solid lines indicate a significant relationship.



S8. Scatter plots showing field-measured SLA on the Y-axis and SLA estimated using 1/Lth from field data on the X-axis for broad leaves and needle-like leaves. Solid lines indicate a significant relationship.



Chapter 6 Links to rare climates do not translate into distinct traits for island endemics

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6.1 Statement of contribution of joint authorship

I planned the project, gathered the data, analysed the data, wrote and compiled the manuscript and prepared the figures and tables. Dagmar Hanz collected some of the herbaria trait data. Trait data from Floras was collected from students at University of Bayreuth and University of Göttingen. Richard Field, Adam Algar and Franziska Schrodt supervised and assisted with compiling the manuscript. Manuel Steinbauer supervised and provided climate data. The remaining authors provided feedback on the project and commented on the manuscript.

The authors comprise two working groups. The first group comprises island researchers looking to incorporate functional traits into island biogeography: Richard, Field, Dagmar Hanz, Martha Paola Barajas-Barbosa, Carl Beierkuhnlein, Jose María Fernández Palacios, Severin Irl, Holger Kreft and Patrick Weigelt. The second is the FREE working group, whose research examines the ‘causes and consequences of functional rarity from local to global scales’: Adam Algar, Pierre Denelle, Pierre Gauzere, Matthias Grenié, Nathan Kraft, Brian Maitner, François Munoz, Wilfried Thuille and Cyrille Violle.

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6.2 Abstract

Current models in island biogeography treat species as though they are functionally equivalent, focussing primarily on species richness. The functional composition of island biotas in relation to island biogeographic variables remains largely unknown. Using plant trait data (plant height, leaf area, flower length) for 896 species in the Canary Islands, we quantified functional trait distinctiveness for endemic and non-endemic species and linked this to the mean climatic rarity of each species' range. We did this for each island in the archipelago, relating functional trait distinctiveness and climatic rarity to island age. Endemics show a link to climatically rare habitats that is consistent with island geological change through time; however functional trait distinctiveness did not differ between endemics and non-endemics and remained constant with island age. Thus, there is no link between trait distinctiveness and occupancy of rare climates, at least for the traits measured here.

6.3 Introduction

Islands have been highly influential to theoretical developments in ecology and evolution (Darwin & Wallace, 1858; MacArthur & Wilson, 1967; Carlquist, 1974; Whittaker *et al.*, 2008). The isolated nature of islands coupled with high levels of *in situ* speciation means islands harbour high proportions of endemic species and contribute substantially to global biodiversity (Kier *et al.*, 2009). Current models in island biogeography use island area, age and isolation to predict changes in species richness (MacArthur & Wilson, 1967; Whittaker *et al.*, 2008). However, focusing on species richness treats species as though they are functionally equivalent (Schrader *et al.*, 2021). Indeed, many researchers have pointed out the importance of incorporating functional trait-based approaches into island biogeography (Borregaard *et al.*, 2016; Santos *et al.*, 2016; Patiño *et al.*, 2017; Ottaviani *et al.*, 2020; Schrader *et al.*, 2021), yet studies in functional island biogeography remain limited due to the lack of comprehensive trait data for endemic species (but see

Weigelt *et al.*, 2020). Thus, the reasons why and how functional traits vary within and across islands remain unknown.

In a set of species, some traits are more distinct than others. Functional trait distinctiveness (herein functional distinctiveness) is a relatively recent index that measures how distinct species traits are in relation to a given set of species (e.g. a community, an island biota, a regional species pool, Violle *et al.*, 2017). Assessing patterns of trait distinctiveness of endemic and non-endemic species on islands may shed light on the ecological, evolutionary and biogeographic processes that influence the composition of island biotas. However, the trait distinctiveness of endemic species relative to non-endemic native species, and the mechanisms that drive species distinctiveness within islands, are not straightforward to elucidate.

Due to strong dispersal and environmental filters, island biotas are often a non-random subset of the continental source pool with certain phylogenetic groups being under- or over-represented (Carlquist, 1974; König *et al.*, 2021). Evolutionary processes on islands therefore occur from an already biased set of species. Endemic species evolving through in situ speciation are commonly associated with adaptive radiations (Carlquist, 1974; Schluter, 2000; Stuessy *et al.*, 2006), where trait divergence is high but genetic differentiation is low. Thus, a number of distinct characteristics, often referred to as island syndromes (Burns, 2019), are typical for island species—a well-known example being the evolution of secondary woodiness in plants (Lens *et al.*, 2013). Given the unique circumstances under which island biotas are shaped and the distinctive qualities of island endemic species, we might expect to see distinct combinations of functional traits (Keppel *et al.*, 2018; Ottaviani *et al.*, 2020; Veron *et al.*, 2021). On the other hand, speciation on islands may not always be driven by strong adaptation resulting in diversification. Species can evolve slowly through drift and this may not necessarily reflect adaptive change. Therefore, we might expect the traits of endemics to change very little following in situ evolution. Comparing trait composition of endemic species with non-endemic species (which maintain gene flow) could provide insight into the processes influencing trait evolution on islands.

Islands vary in their climatic heterogeneity, often as a function of age. This is because elevational range and topography increase and decrease over the geological lifespan of an island due to volcanic activity and erosional processes, which in turn influences the climate by creating strong climatic gradients. Climate heterogeneity plays a key role in determining species' composition and evolutionary outcomes on islands (Irl *et al.*, 2015; Carvajal-Endara *et al.*, 2017; Taylor *et al.*, 2019). Thus, the links between species traits and climate likely influence species distinctiveness (Raphael & Molina, 2013). Species radiating into empty niches may become specialised to spatially scarce habitats (Gaston, 1994). Recent evidence from the Canary Islands shows that evolutionary successful lineages (including many endemics) are abundant in marginal habitats (Fernández-Palacios *et al.*, 2021) and many island endemics are associated with rare environments at high elevations (Steinbauer *et al.*, 2016b). If species traits have adapted to these once-empty niches, then trait distinctiveness should be linked to climate rarity. On the other hand, if species utilise generalist strategies to occupy a broad array of environmental conditions, the relationship between trait distinctiveness and climatic rarity may be weak. We also cannot discount the role of stochastic processes: allopatric divergence and genetic drift could create scenarios where species traits are not explicitly linked to their environment via adaptive processes. Thus, the question that remains unanswered is: by occupying rare climates, do endemic species evolve distinct traits?

Ecological and evolutionary outcomes on oceanic islands are influenced by island area, isolation and heterogeneity (Simpson, 1953; MacArthur & Wilson, 1967; Schluter, 2000). These island features are not static, but change through time (see **Figure 6-1a**). The General Dynamic Model (GDM; Whittaker et al. 2008) proposes how changes in these parameters influence immigration, speciation and extinction over the course of an island's geological development (from emergence to subsidence). Furthermore, the GDM postulates that species diversity is related to topographic heterogeneity, predicting a unimodal relationship through time. Here, we use the GDM's framework to make predictions for the functional rarity dynamics of endemic species on oceanic islands, specifically the relationships between functional distinctiveness, climate rarity and endemism. We test two competing hypotheses: H1) the endemic specialisation hypothesis and H2) the endemic expansion hypothesis and compare these with a null hypothesis (H0) (**Figure 6-1**), which we outline below. For each hypothesis, we predict how the functional distinctiveness and climatic rarity of endemics and non-endemics change through island ontogeny.

The **endemic specialisation hypothesis:** species colonising islands become established in the coastal, lowland habitats, followed by niche differentiation and speciation associated with inland expansion, with the resulting endemic species characterised by increased specialisation as they speciate into climatically rare, montane habitats (Ricklefs & Cox, 1972, 1978; Ricklefs & Bermingham, 1999). This may lead to the evolution of many distinct species that support new functions (Borregaard *et al.*, 2016). As islands age, high-elevation environments are lost to erosion and submergence, leading to the extinction of endemic species. Thus, we expect trait distinctiveness of endemics to follow a hump-shaped relationship (**Figure 6-1**, H1). For non-endemic native species, we expect the opposite relationship for functional distinctiveness, in part because rarity is relative, but also because the distinctiveness of endemics may enhance the colonising success of immigrating species by reducing competition (Darwin, 1859; Strauss *et al.*, 2006; Park *et al.*, 2020). Many non-endemics are subject to continued gene flow, increasing the genetic variation, and potentially phenotypic variation of the non-endemic pool. In this case, we expect non-endemics to be less distinct and less specialised as they are widespread, occupying both rare and common climates. Functional distinctiveness of endemics and non-endemics collapse as islands reach old age.

The **endemic expansion hypothesis** begins similarly to the previous hypothesis: endemic species initially speciate through inland expansion into rarer habitats (hence the small hump in **Figure 6-1**, H2). However, this is followed by expansion across habitat zones – based on the idea that populations of established endemics can undergo multiple expansions (Ricklefs & Bermingham, 1999), and that they are not doomed to continued range-restriction and specialisation. Therefore, this hypothesis predicts that endemics occupy rare climates in the youngest islands, but quickly spread to occupy both rare and common habitats. Under this scenario, immigrating non-endemic species become less competitive and so the colonising space for incoming non-endemics becomes progressively smaller. Thus, in contrast to the previous hypothesis, non-endemics are more distinct relative to the endemics. These hypotheses show strong similarities to the taxon cycle (Wilson, 1961). Currently, there is currently little evidence linking plants to this concept.

Both the endemic specialisation and the endemic expansion hypotheses predict that trait distinctiveness tracks climatic rarity, in that species with distinct traits occur in climatically rare habitats, while species with common traits occur in climatically common habitats. In contrast, our null hypothesis predicts no relationship between climatic rarity and functional distinctiveness (**Figure 6-1**, H0). This suggests endemic species evolve through geographic isolation alone, with little trait change, as they spread inland and to higher elevations (Steinbauer *et al.*, 2016b). Lower species richness on islands compared to the mainland (Whittaker & Fernández-Palacios, 2007; Kreft *et al.*, 2008) could result in weak inter-specific competition (Schluter, 1988), reducing the selective pressure to occupy and adapt to rare climates and resulting in little trait change (or a very long lag behind the shift into rare climates).

We tested these hypotheses for endemic and non-endemic native (NEN) plants on the Canary Islands. Because part of our aim was to compare between different islands, we divided the endemic group into single-island endemics (SIEs) and multi-island endemics (MIEs). For each group, we used plant functional trait data and climatic variables to estimate functional distinctiveness and climatic rarity, respectively, and tested whether differences between the endemic groups differ within and between islands of different ages, as predicted by our hypotheses.

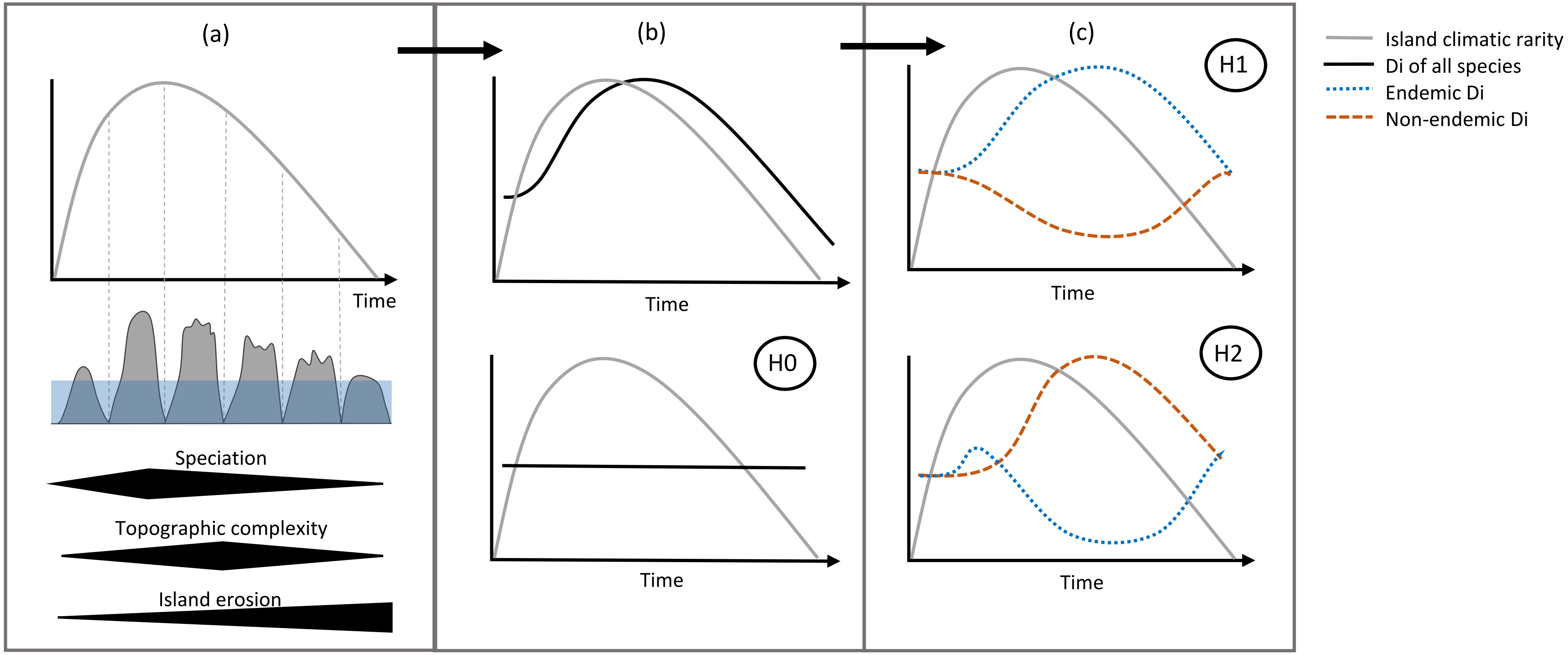

Figure 6-1 Different scenarios of how functional trait distinctiveness (D_i) changes with respect to climatic through island ontogeny: a workflow of our hypotheses. Panel (a) shows how we expect climatic rarity to change as islands age. Beneath the graph is a schematic diagram: the shaded humps represent islands at different stages in their geological evolution, the black bars represent the variation in speciation, topographic complexity and island erosion through time (Whittaker *et al.*, 2008, 2017; Borregaard *et al.*, 2016). This island ontogeny is what is considered on the x-axis of all plots. Panel (b) shows two

alternative scenarios for D_i: the top graph shows D_i tracking climatic rarity, the bottom graph shows no change in D_i with island ontogeny (H0). In the instance that D_i does track climatic rarity, panel (c) shows how this may play out differently for endemic and non-endemic species. H1) The endemic specialisation hypothesis. H2) The endemic swamping hypothesis. Note that D_i is relative.

6.4 Methods

6.4.1 Study area

The Canary Islands (Spain) are an active volcanic archipelago consisting of seven major islands (**Figure 6-2**). The climate is of subtropical Mediterranean-type, which varies quite drastically within islands, particularly in the young and middle-aged islands due to the north-eastern trade winds and topographic variation generating a precipitation gradient from the north east to the south west slopes (del Arco Aguilar *et al.*, 2010). In contrast, the eastern islands of Fuerteventura and Lanzarote are much lower in elevation and relatively uniform in climate. The strong climatic gradients and high environmental heterogeneity (Barajas-Barbosa *et al.*, 2020), particularly on the younger islands, have generated considerable ecosystem diversity, which manifests as habitat zones in the form of elevational belts from the coast to the mountaintops (Fernández-Palacios & de Nicolás, 1995; del Arco Aguilar *et al.*, 2010). Approximately one third of the Canarian plant species are endemic to the archipelago, one third native non-endemic, and one third exotic (Arechavaleta *et al.*, 2009). Several of the plant lineages are thought to have undergone adaptive radiations, including *Argyranthemum*, *Aeonium*, *Echium*, *Sonchus*, *Tolpis*, *Cistus* and *Micromeria* (Schenk, 2021).

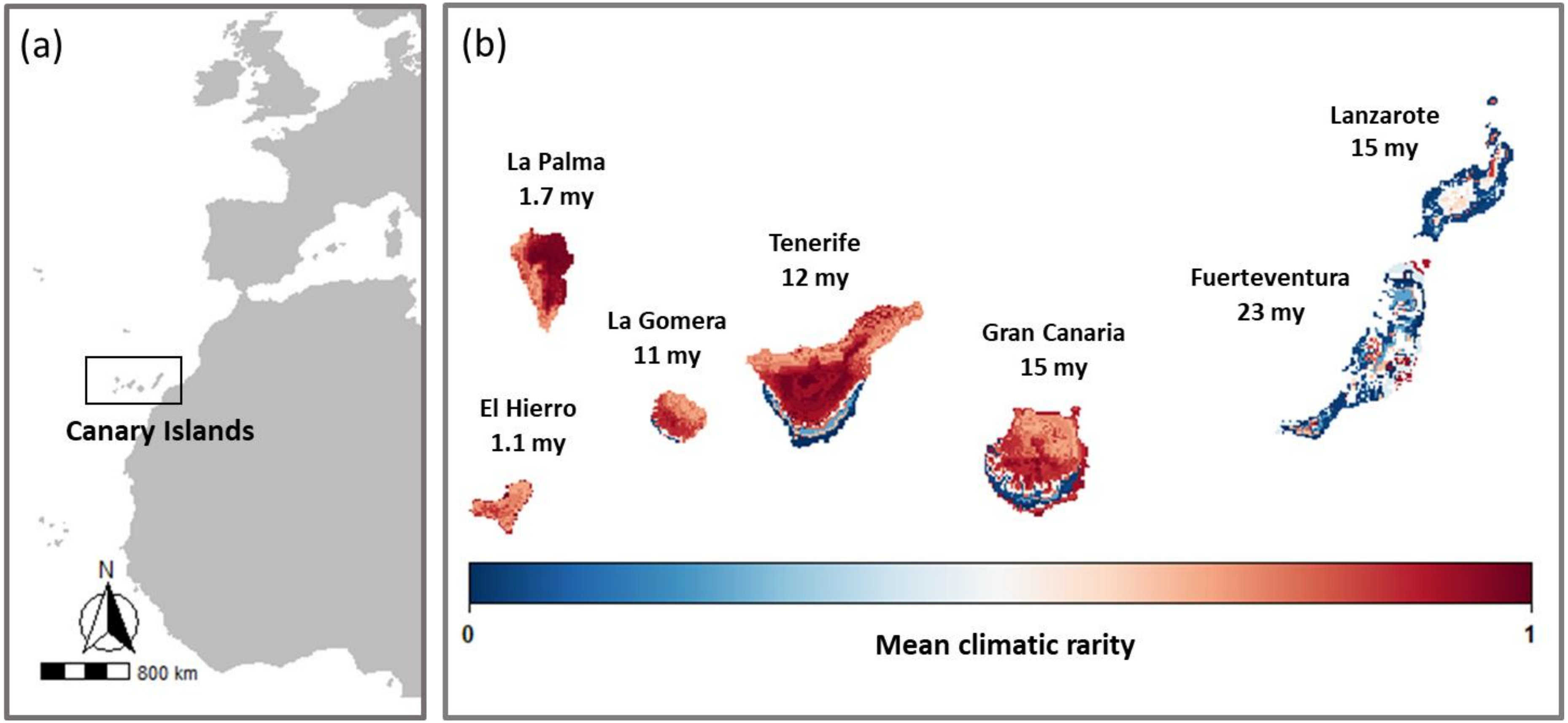

Figure 6-2 (a) Map of the location of the Canary Islands. (b) Map of the Canary Islands. Colour gradient indicates the climatic rarity index for 500x500m grid cells (before it is aggregated by species). Climatic rarity is scaled between 0 and 1 with values closer to 1 indicating a rare climate. This is calculated at the archipelago level, thus the values for each grid cell indicate the rarity of that cell relative to all other cells in the archipelago. Islands are labelled with their approximate ages (van den Bogaard, 2013), my = million years. Areas of white space appear where grid cells have missing data.

6.4.2 Trait data

We used three plant traits: maximum plant height, maximum leaf area and maximum flower length. Plant height is a commonly used measure of plant size. It determines a plant's ability to compete for light sources and has important consequences for seed dispersal (Westoby *et al.*, 2002; Muller-Landau *et al.*, 2008). Leaf area is a measure of leaf size. Leaves play a large role in carbon acquisition and transpiration, as well as being important for the interception of light and CO_2 (Press, 1999). Flower length is a proxy for flower size. Flower petals are important for energy balance and transpiration. All three traits show relationships with environmental variables, including temperature and precipitation (Moles *et al.*, 2009; Paušič *et al.*, 2019; Dong *et al.*, 2020). We used maximum trait values as they reflect the species fitness response to environmental gradients and generally have better data coverage.

Data were sourced from the literature (Bramwell & Bramwell, 1974; Hohenester & Welß, 1993; Eggli, 2002; Muer *et al.*, 2016; Schönfelder & Schönfelder, 2018), online herbarium specimens from GBIF (www.gbif.org) and JSTOR (www.plants.jstor.org), and species descriptions (see Hanz et al. 2022, in prep). We used maximum leaf length and leaf width values to calculate maximum leaf area using the following formula:

$$LA = \frac{LL \times LW \times \pi}{2}$$

where LA = leaf area, LL = leaf length, LW = leaf width. Leaf length and leaf width can accurately estimate leaf area (Kraft *et al.*, 2008; Pandey & Singh, 2011; Shi *et al.*, 2019; Cutts *et al.*, 2021).

The current plant checklist for the Canary Islands places species into six categories: definitely native (including endemics), probably native, possibly native, probably introduced, introduced non-invasive and introduced invasive (Arechavaleta *et al.*, 2009). We only include species that are in the first three of these categories (i.e. excluding introduced species). We used principal components analysis to visualise where endemics and non-endemics sit in Canary Island trait space.

Plant trait data are scarce for the Canary Islands, with many species missing from online and literature sources (Beierkuhnlein *et al.*, 2021; Cutts *et al.*, 2021), which is why we are limited to the aforementioned traits. However, trait choice can strongly influence results (Zhu *et al.*, 2017; Mouillot *et al.*, 2021) because the position of a species in trait space relative to other species might change depending on the traits chosen. To understand the impact of our choice of traits, we also examine an expanded set of traits for Tenerife species (sufficient data on additional traits were not available for other islands). In addition to the three traits mentioned above, we have field measurements for the following traits for Tenerife species: specific leaf area (SLA), stem specific density (SSD) and leaf dry matter content (LDMC). See supporting information S1 for trait measurement protocols.

6.4.3 Species occurrence data

In order to estimate the mean climatic conditions within each species' range, we used species occurrence data from Atlantis 3.1 (www.biodiversidadcanarias.es/biota), a governmental, open-access database with occurrence data of Canary Islands species. The data are presence only, at a resolution of 500x500m, and are not exhaustive, but are particularly good for endemic species, for which there has been long-term sampling. For more information see Steinbauer *et al.* (2016) supporting information S6, which provides a review of the data quality. We used the taxonomy from the most recent checklist for Canary Island plants—FloCan (Beierkuhnlein *et al.*, 2021).

6.4.4 Rarity indices

We calculated functional distinctiveness (D_i) and climatic rarity at the archipelago scale (i.e. rarity of any one grid cell relative to all the grid cells in the archipelago) and for each individual island (i.e. rarity of any one grid cell relative to all the grid cells in the focal island).

a) Functional distinctiveness

D_i measures the mean functional distance to all other species in the community (Violle *et al.*, 2017). We calculated D_i using a Euclidean distance matrix of the three (maximum plant height, maximum leaf area, maximum flower length, see results section). We used the following equation:

$$D_i = \frac{\sum_{\substack{j=1, \\ i \neq j}}^{N} d_{ij}}{N-1}$$

Where N is the number of species, d_{ij} is the distance in trait space between species i and j (Grenié *et al.*, 2017; Violle *et al.*, 2017). All three traits were log-transformed. There were five instances where a species had a zero value for leaf area because they do not possess leaves (e.g. *Euphorbia canariensis*). This creates an issue when transforming the data. We did not want to remove these species as they represent rare trait values, so we replaced the zeros with an arbitrary value that is less than the minimum value for all the other species. As the minimum value for leaf area was 2.36mm, we replaced the zeros with a value of 0.5mm. D_i was scaled between 0 and 1 using the following formula: (x–min(x)) ÷ (max(x) – min(x)).

b) Climatic rarity

We computed climatic rarity following Irl *et al.* (2015). Mean annual precipitation and mean annual temperature were interpolated, at a resolution of 500x500m to match the occurrence data, using data obtained from meteorological stations on the Canary Islands, provided by Agencia Estatal de Meteorología (see Irl *et al.*, 2015). Precipitation was log-transformed because ecologically meaningful variation among smaller values is underemphasised when using the raw data, which are strongly right-skewed. Climatic rarity was calculated as follows. Firstly, temperature and precipitation variables were divided into equal sized bins. We trialled using 10, 20 and 30 bins. We report the results using 20 bins as this produced slightly higher R^2 values, thus explaining more of the variance (but see supporting information S2 for results from 10 or 30 bins). Next, each grid cell was assigned a temperature and precipitation bin. The combination of these bins was used as a climatic rarity index. The climatic rarity index is the number of cells that each climate occurs in; for example, if a grid cell shared its particular temperature-precipitation combination with 10 other grid cells, the climatic rarity value for those cells would be 10. The climate rarity index was reverse-coded (by subtracting the maximum value and adding one) and scaled between zero and one so that high values represented very rare climates for ease of comparison with D_i. To obtain a climatic rarity value for each species, we took the mean climatic rarity value of all the grid cells where the focal species was present. Thus, this index was centred on the species, not the geographic location. The index was calculated for the entire archipelago (archipelago-level climatic rarity) and separately for each island (island-level climatic rarity). Comparisons between endemism groups use archipelago-level climatic rarity, whereas comparisons between islands use island-level climatic rarity.

6.4.5 Statistical analysis

To compare D_i and climatic rarity between endemism groups and between islands, we conducted phylogenetically corrected ANOVAs using the 'caper' and 'phytools' packages in R (Revell, 2012; Orme *et al.*, 2018; R Core Team, 2021). The phyANOVA() function is simulation-based and conducts posthoc comparisons of means between groups. We set the number of simulations to 10,000 and used Bonferroni correction for pairwise comparisons. Phylogenetic information for the Canary Island species was obtained by pruning a mega seed plant phylogeny (Smith & Brown 2018). The resulting tree contained polytomies at the species level with 25% of the nodes unresolved. Unresolved trees can underestimate phylogenetic diversity (Swenson, 2009), so we randomly resolved the phylogeny prior to analysis. Many of the species in our data occurred on multiple islands, which created multiple observations for the same species. This led to computational difficulties when preparing the data for the phylogenetic ANOVA, as the comparative.data() function in the caper package cannot handle duplicate species. To troubleshoot this, we added the duplicates to the phylogeny as sister species, with branch lengths of 0.001 (Grenié *et al.*, 2017). To visualise the relationship of D_i and climatic rarity with island age, we plotted a line graphs using ranked ages (**Figure 6-6**).

6.5 Results

Overall, we collected trait, climate and phylogenetic data for 896 native species (271 SIE, 205 MIE, 420 NEN; **Table 6-1**), representing approximately 87% of the SIEs, 90% of MIEs and 50% of non-endemic natives from the Canary Islands. Fuerteventura and Lanzarote naturally have very few SIEs, so their sample sizes are small.

Correlations between traits were significant but weak: plant height–leaf area r = 0.35, $p < 0.001$; plant height–flower length r = 0.11, $p < 0.001$; leaf area–flower length r = 0.26, $p < 0.001$. Principal components analysis revealed that the species groups strongly overlap in Canary Island trait space, with the endemic species nested within the non-endemic natives, which occupied the core and the periphery (**Figure 6-3**).

D_i and climatic rarity did not correlate overall (r = -0.008, p = 0.79), nor did they correlate within each endemism group (SIE r = 0.02, p = 0.68; MIE r = -0.15, p = 0.82; NEN r = 0.03, p = 0.56) or within each island (El Hierro r = 0.06, p = 0.27; La Palma r = 0.09, p = 0.05; La Gomera r = 0.06, p = 0.22; Tenerife r = 0.04, p = 0.32; Gran Canaria r = 0.04, p = 0.33; Lanzarote r = -0.005, p = 0.93; Fuerteventura r = 0.06, p = 0.30).

Table 6-1 Number of species with complete data, which includes all three traits (max plant height, max leaf area, max flower length), climatic rarity and phylogenetic data. Our sample size as a percentage of the total number of species present is indicated in brackets. SIE = single island endemic, MIE = multi-island endemic, NEN = non-endemic native. Note that (except for SIEs) many of the species occur on multiple islands, so that adding the island figures surpasses the archipelagic total.

	SIE	**MIE**	**NEN**
Total	271 (87%)	205 (90%)	420 (50%)
El Hierro	12	98	245
La Palma	34	137	281
La Gomera	30	127	273
Tenerife	104	177	386
Gran Canaria	71	125	350
Fuerteventura	8	56	268
Lanzarota	12	46	240

6.5.1 Functional distinctiveness

A phylogenetic ANOVA revealed no significant difference in D_i between the endemism groups (F = 14.16, p = 0.25, R^2 = 0.03; **Figure 6-4**). However, pairwise comparisons showed a significant difference between SIEs and MIEs, with MIEs being more distinct (p = 0.007). For between-islands comparisons of D_i (**Figure 6-5**), a phylogenetic ANOVA indicated no significant difference for SIEs (F = 1.93, p = 0.05, R^2 = 0.04) or MIEs (F = 0.41, p = 0.51, R^2 = 0.003), and a significant effect for NENs (F = 4.52, p = 0.004, R^2 = 0.01). Pairwise comparisons revealed some differences for NENs, with D_i decreasing in Lanzarote and Fuerteventura, but no pairwise differences were found between islands for SIEs or MIEs (**Figure 6-5**). In all cases, the proportion of variance in functional distinctiveness explained by endemism class or island was small.

6.5.2 Climatic rarity

Climatic rarity varied across the archipelago (**Figure 6-2b**). There was a noticeable difference between the five high-elevation islands in the west, which possess more rare climates, and the two older islands (Fuerteventura and Lanzarote) in the east, which contain very few areas of rare climate. Within islands, rare climates tend to be found at areas of high elevation or high topographic complexity (**Figure 6-2b**). Climate space is shown in **Figure 6-3**, where it appears endemic species are occupying a wider range of climates, including cold and dry climates, compared to non-endemics.

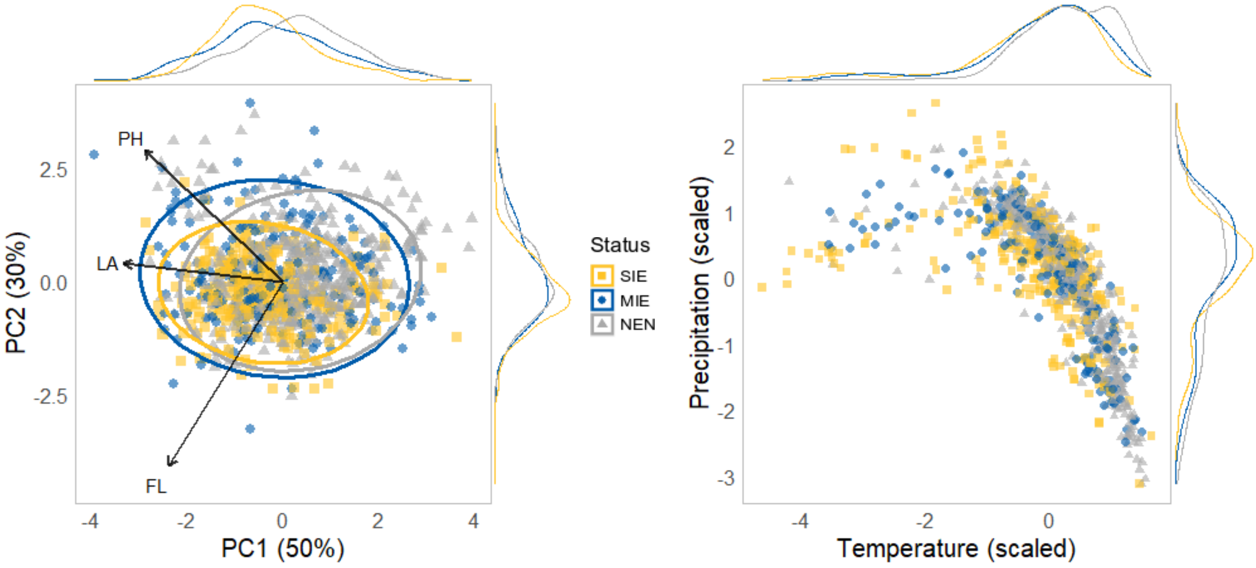

Figure 6-3 Left: Functional trait space represented using principal components analysis for the Canary Islands based on three traits: maximum plant height (PH), maximum leaf area (LA) and maximum flower length (FL), Ellipses show 95% confidence. Right: Position of species in climate space (mean annual temperature and precipitation). Precipitation is log-transformed. At the top and left of each graph, marginal density distribution plots are shown for each endemism group. SIE = single island endemic, MIE = multi-island endemic, NEN = non-endemic native.

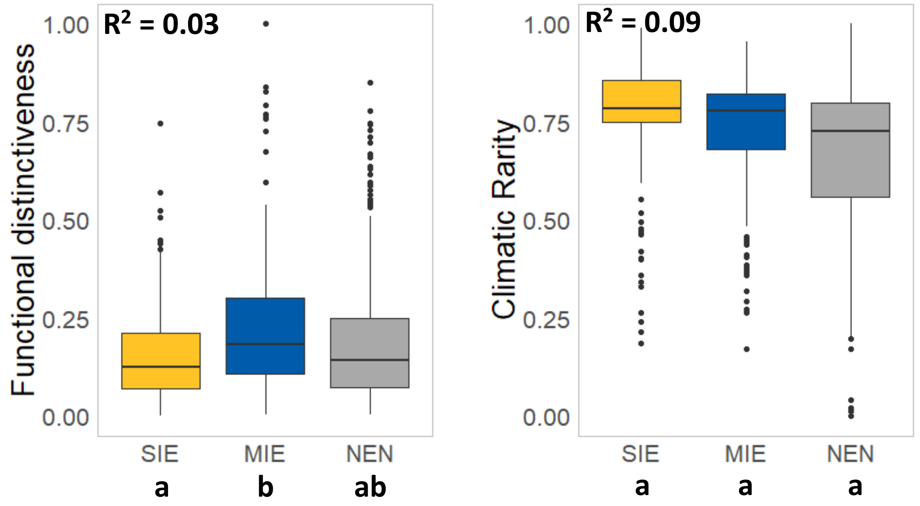

Figure 6-4 Functional distinctiveness and climatic rarity (at the archipelago-level) for each endemism group across the entire Canary archipelago. Differing letters indicate pairwise significant differences between groups ($p<0.05$). SIE = single island endemic, MIE = multi-island endemic, NEN = non-endemic native.

Endemism increases with climatic rarity: endemics were found in rarer climates compared to non-endemics, with SIEs occupying the rarest climates ($F=42.04$, $p=0.02$, $R^2 = 0.09$). However, pairwise comparisons showed no significant differences between pairs of groups (SIE–MIE: $p=0.27$; SIE–NEN: $p=0.06$; MIE–NEN: $p=0.13$; **Figure 6-4**). Comparing between islands revealed a strong pattern for SIEs ($F=145.67$, $p<0.001$, $R^2 = 0.75$): they are found in very rare climates in the young and middle-aged islands (El Hierro, La Palma and La Gomera), for which there were no pairwise differences, but are found in progressively less rare climates as the islands increase in age. MIEs show a similar, but much less pronounced pattern across islands ($F=56.98$, $p<0.001$, $R^2 = 0.32$), and the pattern for NENs is similar but weak ($F=28.72$, $p<0.001$, $R^2 = 0.09$). See **Figure 6-5** for pairwise difference across islands and supporting information 6.11.S3 and 6.11.S4 for ANOVA tables and pairwise P values.

6.5.3 Assessing the impact of trait choice using Tenerife data

We used data from the island of Tenerife to investigate the impact of our choice of traits by calculating D_i (at the Tenerife scale) using an expanded set of traits. The two measures of D_i (3-trait and 6-trait) showed a strong positive correlation (*r* = 0.77, p <0.001) and in both cases, functional distinctiveness showed a similar pattern in relation to endemicity. Again, principal components analysis revealed a nested pattern, but this pattern was much clearer when using the expanded set of traits. These results are shown in supporting information 6.11.S5.

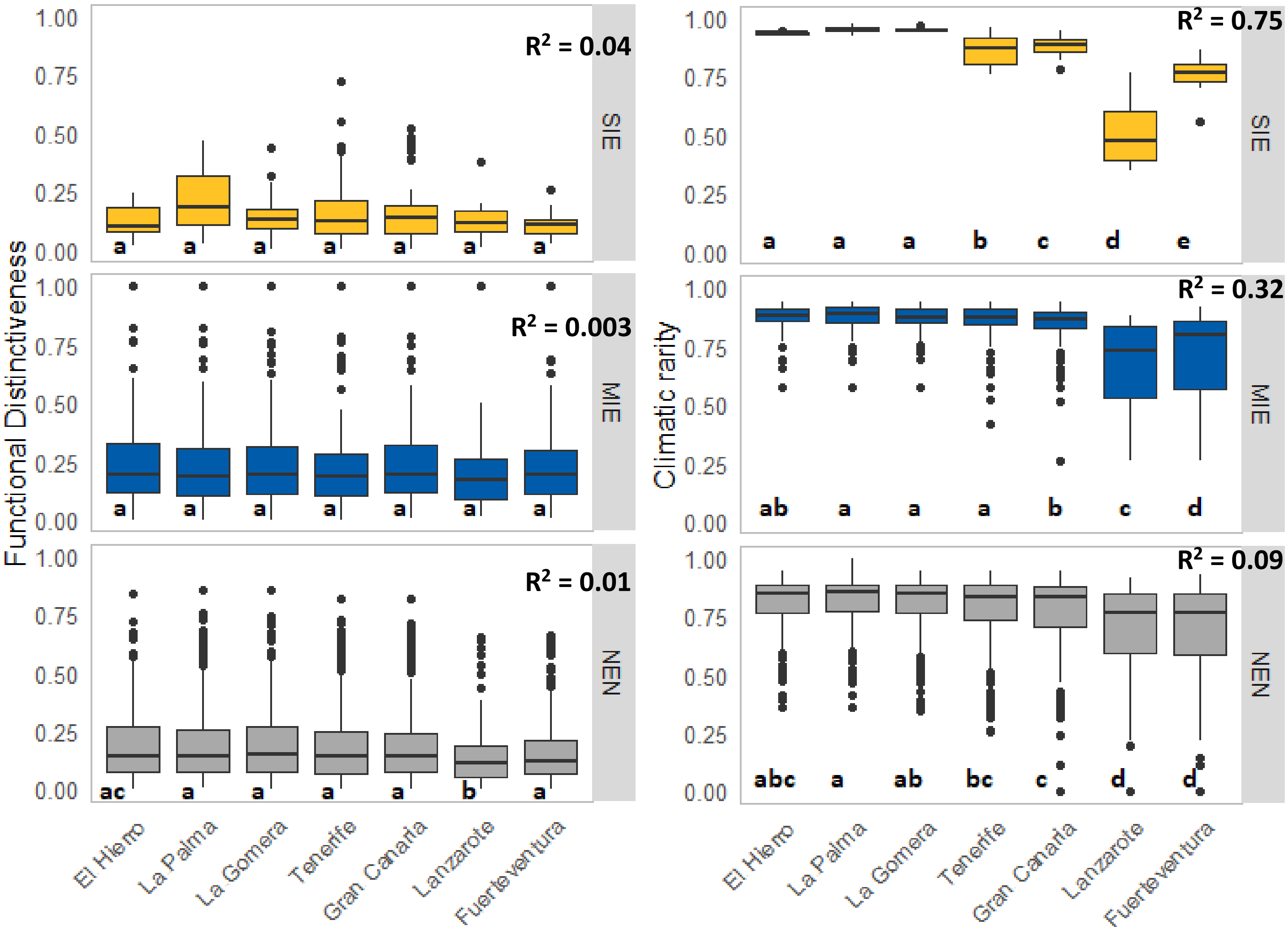

Figure 6-5 Functional distinctiveness and climatic rarity (at the island level) for each island. Differing letters indicate pairwise significant differences between groups (p<0.05). SIE = single island endemic, MIE = multi-island endemic, NEN = non-endemic native.

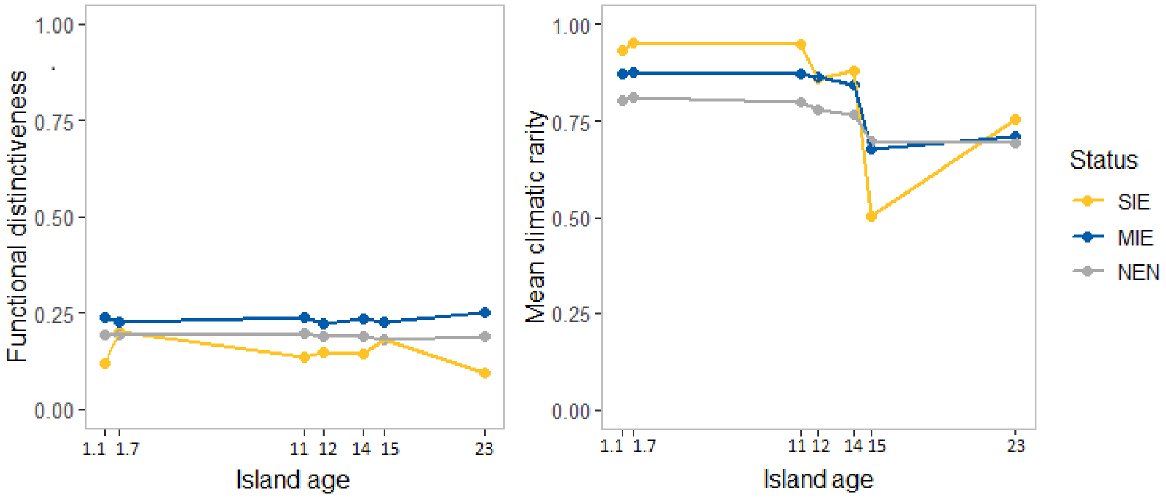

Figure 6-6 Line graphs representing functional distinctiveness and climatic rarity (at the island level) with increasing island age (million years old). Island ages are obtained from van den Bogaard (2013). Points correspond to mean values for each island. SIE = single island endemic, MIE = multi-island endemic, NEN = non-endemic native.

6.6 Discussion

The General Dynamic Model posits that the geological evolution of an island influences the evolution of species, thus linking species diversity to island age (Whittaker *et al.*, 2008). In this study, we investigated how this translates to species traits, specifically examining functional distinctiveness of endemic and non-endemic species, and how they relate to the rarity of the climate where species occur. We tested two hypotheses (against a null) to explain the relationship between functional distinctiveness, climatic rarity and endemism: 1) the endemic specialisation hypothesis and 2) the endemic expansion hypothesis.

All species showed a decline in the occupancy of rare climates with increasing island age, but no concordant pattern is seen for functional distinctiveness, which remains constant through time and does not differ between endemism groups. The lack of relationship between functional distinctiveness and climatic rarity rejects the endemic specialisation and the endemic expansion hypotheses, which both expect functional distinctiveness to relate to climatic rarity and for there to be marked differences in functional distinctiveness between endemic and non-endemic species. Therefore, our results most closely align with the null hypothesis, which predicts no relationship between climatic rarity and functional distinctiveness and no trend of functional distinctiveness with island age.

One of the main premises of the GDM is that topographic heterogeneity will be maximised on middle-aged islands, coinciding with the availability of empty niche space (Whittaker *et al.*, 2008). More recent work has shown environmental heterogeneity and species richness to peak early during island ontogeny (Steinbauer *et al.*, 2013; Barajas-Barbosa *et al.*, 2020). Here, we found that endemics, particularly single-island endemics, are already occupying rare climates in the younger islands, with the decline beginning at middle-age (La Gomera-Tenerife), suggesting a very early peak in the diversity of available niche space and coinciding with changes in elevation (Borregaard *et al.*, 2016). In older islands, there are fewer opportunities to occupy rare climates, as topographic heterogeneity decreases as a result of erosion and subsidence. Non-endemics occupied rare climates similarly through time, with a small decline in climatic rarity in the oldest islands. Thus, endemic species appear to be more closely linked to the rarity of the climate than non-endemics.

Evolution on islands is typified by high rates of trait diversification following ecological opportunity (Carlquist, 1974; Jorgensen & Olesen, 2001; Givnish *et al.*, 2009; Losos & Ricklefs, 2009) and island endemics are often used as examples of adaptive radiations (Schluter, 2000; Schenk, 2021). Despite occupying rarer climates, we found that endemics are no more distinct in their traits than non-endemic natives. We would expect species with distinct traits to occupy the peripheries of trait space but our results show considerable overlap of the species groups, with single-island endemics being slightly more clustered in the centre. This may be indicative of specialisation and niche packing, particularly considering that, as a group, endemics occupy a wide range of climate space overall (**Figure 6-3**). Therefore, it is possible that endemics are experiencing selection without it driving them into novel areas of trait space. In fact, diversifying lineages may decrease trait distinctiveness by producing more similar species.

Allopatric speciation is maximised in middle-aged islands when topography and climate are highly dissected (Whittaker *et al.*, 2008). Non-adaptive processes commonly drive evolution on islands but have often received less attention (Simoes *et al.*, 2015) and the imprint of this in functional trait space is less easy to predict or interpret. Within-island allopatry and relaxed competition on islands may lessen selective pressure, allowing genetic drift to become a more prominent evolutionary process (Stuessy *et al.*, 2006). Therefore, non-adaptive speciation might explain the lack of distinct traits for single-island endemics. It could be that there is a lag between climate shifts and trait divergence, particularly for species that have colonised more recently. Alternatively, environmental filtering may select species that already have relevant adaptations (Donoghue, 2008).

Trait choice can greatly influence the outcome of hypothesis tests (Zhu *et al.*, 2017; Mouillot *et al.*, 2021). Trait data are scarce for island endemics (Cutts *et al.*, 2021), and thus our choice of traits was limited. However, the traits we used – plant height, leaf area and flower length – have been linked to environmental conditions in terms of temperature and precipitation (Byars *et al.*, 2007; Guerin *et al.*, 2012; Givnish *et al.*, 2014; Tao *et al.*, 2016; Paušič *et al.*, 2019). Nevertheless, we used data for a broader suite of traits, available only for Tenerife, to determine whether expanding our trait set would fundamentally alter patterns of functional distinctiveness. The use of more traits did not affect the results in such a way that one would draw different conclusions—functional distinctiveness followed the same pattern with respect to endemism. Still, it is possible that even the Tenerife example did not capture the 'right' traits; the objection that the 'right' traits were not measured is, of course, an unfalsifiable hypothesis, and thus it is impossible to eliminate. However, a potential candidate set of traits for future investigation would be those linked to dispersal. Insularity has an effect on the composition of dispersal traits in islands (Gillespie *et al.*, 2012), and limited dispersal has been linked to lower speciation area thresholds, which could produce endemics, on islands (Kisel & Barraclough, 2010). Similarly, species that are able to disperse well enough to colonise areas with rare climates, such as montane habitats, but unable to maintain gene flow with populations in rarer climates, such as mountain-tops, may be more likely to specialise on these climates, creating a link between distinctiveness of dispersal traits and climatic rarity.

Endemic species on islands have fuelled the curiosity of generations of biologists because of their spectacular radiations and unique characteristics. However, trait evolution on islands remains a rather elusive subject. Some species demonstrate ecological shifts (e.g. Kim et al., 1996), but whether these shifts are followed by trait divergence is less well understood and rigorous tests are lacking. We find that rare climate occupancy for island endemics is dynamic with increasing island age, yet we find no signal in the distinctiveness of their traits. The hypotheses we lay out here are simplistic and do not capture all the possible influences and stochastic processes that shape functional trait composition. Nevertheless, we see this as a practical step towards integrating functional traits into island theory and towards understanding the functional signature of island species.

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6.8 Author contributions

VC, RF, ACA, FS and MJS developed the initial idea and hypotheses. MPBB collected Tenerife field data. VC and DH digitised herbarium specimens. VC, RF, ACA, FS analysed the data. All authors provided feedback throughout the process, commented on, and edited, the final manuscript.

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6.12 Supporting Information

S1. Tenerife trait measurements

For Tenerife species, we measured the following traits in the field: leaf dry matter content (LDMC), specific leaf area (SLA), stem specific density (SSD). These were to be used in combination with maximum plant height, maximum leaf area and maximum flower length to assess the impact of our trait choice (see S6). We followed standardised protocols based on the handbook by Pérez-Harguindeguy et al. (2013). We aimed to measure these traits for five adult individuals per species, taking samples from different locations where possible to account for variation in climate. Leaf and stem samples were collected from adult plants. We collected 10-100 adult leaves per individual, depending on the species—for species with small leaves we collected up to 100 to obtain accurate mass measurements. Leaves were cut from the stem and the petiole was removed. Stem samples were taken from secondary stems where possible to minimise disturbance and cut to approximately 10cm.

LDMC is the oven-dry mass of a leaf divided by its fresh mass. We weighed the fresh leaves for each individual, then the leaves were dried in an incubator at 80°C for at least 24 hours. Dried leaves weighed again.

SLA is the leaf area divided by its oven-dry mass. To calculate leaf area, up to 10 leaves per individual were scanned using an A4 scanner and leaf area calculated for each leaf using WinFOLIA software (version: 2016b Pro; Regent Instruments Inc., Québec, Canada, 2016).

SSD is the dry mass per unit of fresh stem volume. The exact volume of the stem was determined by measuring its exact length and diameter, which was measured at three points along the stem. To determine the dry mass, stems were dried in an incubator at 80°C for at least 24 hours and then weighed.

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S2. Trialling different levels of precision for computing climatic rarity.

Climatic rarity was computed using binned data for temperature and precipitation. The size of the bins was determined by splitting the range of each variable up equally. For the results in the text, the range was divided by 20, and that result was used as a bin size. The workflow below shows how we got to this value for temperature and precipitation (precipitation is transformed prior).

Temperature: $\frac{\text{Max temp – min temp}}{20} = \frac{20.807 - 3.459}{20} = 0.867°\text{C}$

Precipitation: $\frac{\text{Max log(precip) – min log(precip)}}{20} = \frac{3.104 - 1.884}{20} = 0.061\text{mm}$

As this number is somewhat arbitrary, we also trialled using fewer divisions and more divisions, i.e. 10 and 30, which resulted in larger and smaller bin widths, respectively. R^2 values were slightly lower in both instances, thus we stuck with the middle bin width size in the main text. One of the models became non-significant when using a lager bin width—comparing climatic rarity between endemism groups (p-value is highlighted in grey). See the results below.

Climatic rarity between endemism groups with larger bin widths

(max-min)/10 Temp bin = 1.735°C; precipitation bin = 0.122mm

	df	Sum sq	Mean sq	F	P	R^2
Endemism	2	1.249	0.625	25.523	0.098	0.05
Residual	893	21.858	0.024			

Climatic rarity between islands with larger bin widths

(max-min)/10 Temp bin = 1.735°C ; precipitation bin = 0.122mm

	df	Sum sq	Mean sq	F	P	R^2
Island SIE		4.058	0.676	93.218	**0.000**	0.66
Residual		2.083	0.007			
Island MIE		3.388	0.565	54.929	**0.000**	0.3
Residual		7.986	0.010			
Island NEN		3.116	0.519	35.521	**0.000**	0.09
Residual		31.651	0.016			

Climatic rarity between endemism groups with smaller bin widths

(max-min)/30 Temp bin = 0.578°C ; precipitation bin = 0.041mm

	df	**Sum sq**	**Mean sq**	**F**	**P**	**R^2**
Endemism	2	1.808	0.904	42.264	**0.020**	0.086
Residual	893	19.098	0.021			

Climatic rarity between endemism groups with smaller bin widths

(max-min)/30 Temp bin = 0.578°C ; precipitation bin = 0.041mm

	df	**Sum sq**	**Mean sq**	**F**	**P**	**R^2**
Island SIE		3.008	0.501	121.696	**0.000**	0.72
Residual		1.182	0.004			
Island MIE		3.186	0.531	56.260	**0.000**	0.3
Residual		7.333	0.009			
Island NEN		3.848	0.641	29.916	**0.000**	0.9
Residual		41.182	0.021			

S3. ANOVA tables between endemism groups

We used phylogenetically corrected ANOVA's to compare functional distinctiveness and climatic rarity between endemism groups. Here, we repot the ANOVA tables and posthoc pairwise comparisons.

ANOVA tables

Functional distinctiveness

	df	**Sum sq**	**Mean sq**	**F**	**P**	**R^2**
X	2	0.646	0.323	14.161	0.253	0.031
Residual	893	20.368	0.023			

Climatic rarity

	df	**Sum sq**	**Mean sq**	**F**	**P**	**R^2**
X	2	2.208	1.104	42.039	**0.022**	0.086
Residual	893	23.452	0.026			

Pairwise P-values

Functional distinctiveness

	SIE	**MIE**	**NEN**
SIE	1.000	**0.007**	1.000
MIE	**0.007**	1.000	0.959
NEN	1.000	0.959	1.000

Pairwise P-values

Climatic rarity

	SIE	**MIE**	**NEN**
SIE	1.000	0.286	0.061
MIE	0.286	1.000	0.130
NEN	0.061	0.130	1.000

S4. ANOVA tables and pairwise comparisons between islands

We used phylogenetically corrected ANOVA’s to compare functional distinctiveness and climatic rarity between islands. Here, we repot the ANOVA tables and the pairwise comparisons between islands. We conducted separate ANOVAS for single island endemics (SIE), multi-island endemics (MIE) and non-endemic natives (NEN). The pairwise comparisons use the bonferroni correction.

ANOVA tables

Functional distinctiveness SIE

	df	**Sum sq**	**Mean sq**	**F**	**P**	**R^2**
X		0.149	0.025	1.924	0.050	0.04
Residual		3.594	0.013			

Functional distinctiveness MIE

	df	**Sum sq**	**Mean sq**	**F**	**P**	**R^2**
X		0.081	0.014	0.404	0.505	0.003
Residual		25.846	0.033			

Functional distinctiveness NEN

	df	**Sum sq**	**Mean sq**	**F**	**P**	**R^2**
X		0.669	0.112	4.524	**0.004**	0.01
Residual		46.981	0.025			

Pairwise P-values

Functional distinctiveness SIE

	EH	**LP**	**LG**	**T**	**GC**	**F**	**L**
EH	1.000	0.183	1.000	1.000	1.000	1.000	1.000
LP	0.183	1.000	0.498	0.137	0.233	0.485	0.445
LG	1.000	0.498	1.000	1.000	1.000	1.000	1.000
T	1.000	0.137	1.000	1.000	1.000	1.000	1.000
GC	1.000	0.233	1.000	1.000	1.000	1.000	1.000
F	1.000	0.485	1.000	1.000	1.000	1.000	1.000
L	1.000	0.445	1.000	1.000	1.000	1.000	1.000

Functional distinctiveness MIE

	EH	**LP**	**LG**	**T**	**GC**	**F**	**L**
EH	1.000	1.000	1.000	1.000	1.000	1.000	1.000
LP	1.000	1.000	1.000	1.000	1.000	1.000	1.000
LG	1.000	1.000	1.000	0.897	1.000	1.000	1.000
T	1.000	1.000	0.897	1.000	1.000	1.000	1.000
GC	1.000	1.000	1.000	1.000	1.000	1.000	1.000
F	1.000	1.000	1.000	1.000	1.000	1.000	0.174
L	1.000	1.000	1.000	1.000	1.000	0.174	1.000

Functional distinctiveness NEN

	EH	**LP**	**LG**	**T**	**GC**	**F**	**L**
EH	1.000	1.000	1.000	1.000	1.000	1.000	**0.015**
LP	1.000	1.000	1.000	1.000	1.000	**0.017**	**0.002**
LG	1.000	1.000	1.000	1.000	1.000	**0.002**	**0.002**
T	1.000	1.000	1.000	1.000	1.000	**0.015**	**0.002**
GC	1.000	1.000	1.000	1.000	1.000	**0.006**	**0.002**
F	1.000	**0.017**	**0.002**	**0.015**	**0.006**	1.000	**0.002**
L	**0.015**	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	1.000

ANOVA tables

Climatic rarity SIE

	df	Sum sq	Mean sq	F	P	R^2
X		2.351	0.392	145.667	**0.000**	0.75
Residual		0.772	0.003			

Climatic rarity MIE

	df	Sum sq	Mean sq	F	P	R^2
X		2.926	0.488	56.978	**0.000**	0.32
Residual		6.651	0.009			

Climatic rarity NEN

	df	Sum sq	Mean sq	F	P	R^2
X		3.612	0.602	28.723	**0.000**	0.09
Residual		40.263	0.021			

Pairwise P-values

Climatic rarity SIE

	EH	LP	LG	T	GC	F	L
EH	1.000	1.000	1.000	**0.002**	**0.006**	**0.002**	**0.002**
LP	1.000	1.000	1.000	**0.002**	**0.002**	**0.002**	**0.002**
LG	1.000	1.000	1.000	**0.002**	**0.002**	**0.002**	**0.002**
T	**0.002**	**0.002**	**0.002**	1.000	**0.029**	**0.002**	**0.002**
GC	**0.006**	**0.002**	**0.002**	**0.029**	1.000	**0.002**	**0.002**
F	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	1.000	**0.002**
L	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	1.000

Climatic rarity MIE

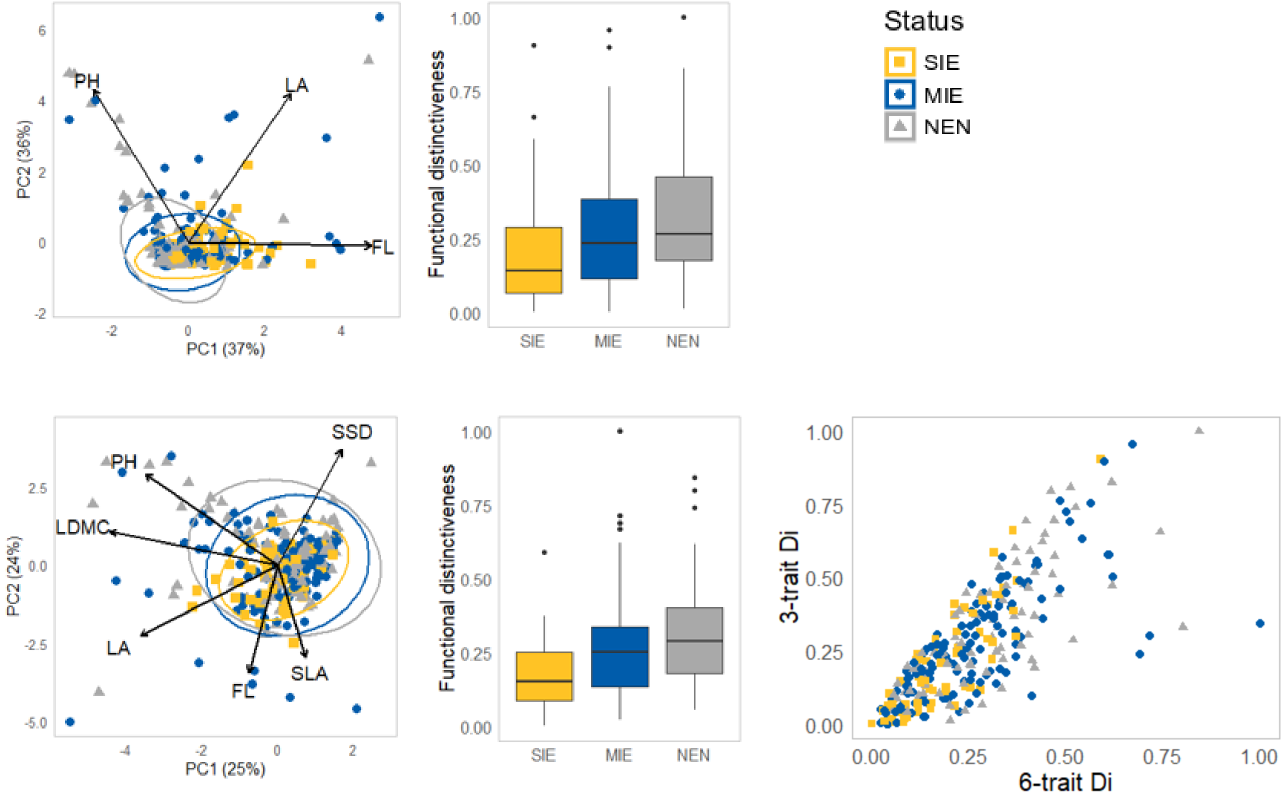
	EH	LP	LG	T	GC	F	L
EH	1.000	1.000	1.000	1.000	0.185	**0.002**	**0.002**
LP	1.000	1.000	1.000	0.972	**0.002**	**0.002**	**0.002**
LG	1.000	1.000	1.000	1.000	**0.002**	**0.002**	**0.002**
T	1.000	0.972	1.000	1.000	**0.015**	**0.002**	**0.002**
GC	0.185	**0.002**	**0.002**	**0.015**	1.000	**0.002**	**0.002**
F	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	1.000	**0.004**
L	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	**0.004**	1.000

Climatic rarity NEN

	EH	LP	LG	T	GC	F	L
EH	1.000	1.000	1.000	1.000	0.838	**0.002**	**0.002**
LP	1.000	1.000	1.000	**0.002**	**0.002**	**0.002**	**0.002**
LG	1.000	1.000	1.000	0.055	**0.002**	**0.002**	**0.002**
T	1.000	**0.002**	0.055	1.000	1.000	**0.002**	**0.002**
GC	0.838	**0.002**	**0.002**	1.000	1.000	**0.002**	**0.002**
F	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	1.000	1.000
L	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	1.000	1.000

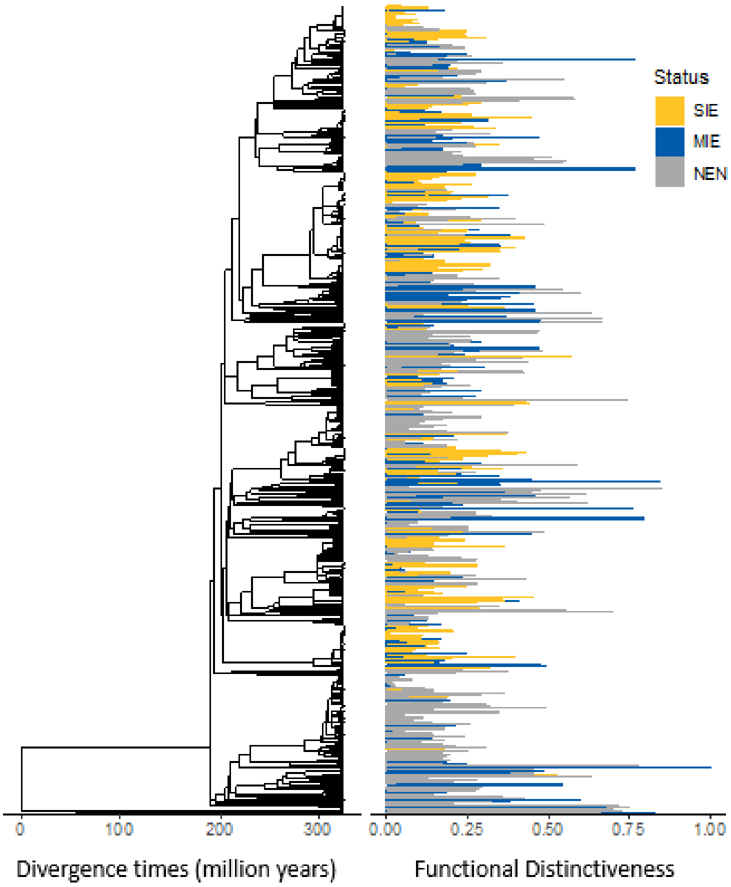
S5. Assessing the impact of trait choice using Tenerife data

Functional trait space and functional distinctiveness for species groups on Tenerife: single-island endemics (SIE), multi-island endemics (MIE) and native non-endemics (NEN). Principal components analysis is used to represent trait space. Ellipses show the 95% confidence. We calculated functional distinctiveness using a Euclidean distance matrix. The top two figures show trait space and functional distinctiveness calculated using three traits: maximum plant height (PH), maximum leaf area (LA) and maximum flower length (FL). Data for these traits are available for all other islands in the Canaries. The bottom two graphs show trait space and functional distinctiveness calculated using three additional traits that are only available for Tenerife: specific leaf area (SLA), leaf dry matter content (LDMC), stem specific density (SSD). All traits were transformed to achieve normality. PH, LA, FL and SLA were log10-transformed. SSD and LDMC were square root-transformed. The bottom right graph shows a scatter plot for both measures of functional distinctiveness (Di).



S6. Phylogenetic tree of all species included in the study.

The phylogeny was obtained from Smith & Brown (2018). The bars in right panel show functional distinctiveness for each species, coloured by endemism status: single-island endemics (SIE), multi-island endemics (MIE) and native non-endemics (NEN). Higher values (longer bars) mean species are more distinct.



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Chapter 7 General discussion

Standing on the island of La Palma, it appears obvious that endemic species have an affinity for extreme habitats; the wind-battered coast, the steep barranco cliff faces barren of soil and the frosty mountain tops. The position of a species in trait space, on the other hand, is much harder to 'see'. The broad aim of this thesis was to understand how topography and climate influence patterns of endemism on oceanic islands, particularly in relation to the functional composition of endemic and non-endemic floras. Endemism varies with island area, age and isolation (Kreft *et al.*, 2008; Triantis *et al.*, 2008; Steinbauer *et al.*, 2016), but little is known about how this is reflected in functional trait space. Overall, I find that endemism patterns in the Canary Islands vary with respect to their abiotic environment (elevation, climate, island age), but not with respect to the distinctiveness of their traits (plant height, leaf area, flower length).

With the knowledge that islands experience multi-scale isolation, in Chapter 4, I zoomed into a relatively understudied type of isolation—the deep barrancos of La Palma. Barranco depth, as a measure of isolation, did not influence the proportion of endemic species. Existing evidence points towards higher proportions of endemism at higher elevations (Steinbauer *et al.*, 2016). However, I found that endemics occurred in higher proportions at lower elevations within the barrancos. This could reflect generally higher levels of habitat heterogeneity and topographic variation in the barranco area—the barrancos are deeper at lower elevations. **Figure 6-2b** depicts the rarity of the climate across the archipelago—the climate in the north and north-west of La Palma is noticeably very rare; incidentally, this is the location of the steep-sided barrancos. Perhaps, rather than each barranco providing sufficient isolation to increase endemism, it is the whole barranco area that provides the topographic heterogeneity that allows endemism to flourish. Indeed, Carlquist (1974) hypothesised that barrancos increase ecological opportunity in the lowlands.

A focus on functional traits can provide deeper understanding into ecological and evolutionary processes than can species richness (McGill *et al.*, 2006). With the increasing use of trait-based approaches in island research, the state of the current trait data with respect to islands needs to be assessed. I have done this for my study area, the Canary Islands, finding that only 3% of the native flora occur in the TRY database (Chapter 5). By comparing traits measured from the field with traits digitised from floras, I have begun to tease apart which traits can be obtained from existing resources from those that require direct measurements in the field. Leaf area estimations using literature sources proved to be highly congruent with those measured in the field, thus, I felt confident to use this trait in Chapter 6. Collecting trait data from the field can be quite a monumental task for community-level research, especially on islands. Island endemics are often found in rare environments and hard-to-reach places—the barranco cliff faces being just one example. Assessment of existing trait data will help streamline the process of gathering further trait data, whilst also minimising the environmental impact of sampling rare or endangered species.

The finding that trait data from scientific floras accurately represent traits measured in the field for island species opened new lines of enquiry previously unavailable due to limited trait data. In Chapter 6, I specifically focussed on functional distinctiveness, a measure of species rarity (Violle *et al.*, 2017), extending the General Dynamic Model of oceanic island biogeography (Whittaker *et al.*, 2008) to consider functional traits. I investigated the relationship between species rarity (in the form of distinct traits) and occupancy in rare climates and how this relationship changed as islands increased in age. Functional distinctiveness of species and their occupancy in rare climates showed different patterns with respect to island age: functional distinctiveness remained constant, whereas occupancy in rare climates declined. Endemics did not expand into novel areas of trait space and their functional position with respect to non-endemics remained constant across islands.

With respect to the abiotic environment, endemic species and non-endemic species showed similar general trends, but the trend for endemics was much stronger. Examining endemics in more detail, SIEs and MIEs showed differing patterns: SIEs showed no relationship with elevation (**Figure 4-5**), yet they showed the strongest relationship between climate rarity and island age (**Figure 6-6**). Conversely, the proportion of MIEs decreased with elevation but showed a weaker relationship with island age and climate rarity. The elevation relationships found in Chapter 4 are in opposition to trends found in previous research (Steinbauer *et al.*, 2013, 2016) and could be specific to the barrancos of La Palma, especially considering I did not sample the entire elevation gradient. Nevertheless, an even distribution of SIEs along the elevational gradient is consistent with SIEs occupying the largest area of climate space (**Figure 6-3**).

Endemics and non-endemics showed little difference with respect to functional traits as they occupied similar positions of trait space. Indeed, it was recently found that intraspecific trait variation in the Canary Islands was similar between endemic and non-endemic species (Hanz et al., 2022). However, small differences were detected between SIEs and MIEs—MIEs were slightly more distinct in their traits. The sample size for SIEs (271) was higher than MIEs (205), yet SIEs were more clustered in trait space (**Figure 6-3**). Thus, SIEs show more similarity in their traits than MIEs and this cannot be explained as an artefact of species richness. The fact that SIEs have arisen more recently than MIEs could explain the clustering in trait space as they have had less time for divergence. Alternatively, it could be that there is little trait adaptation following speciation, not what one would expect if adaptive radiations are dominant. These differences were not statistically strong and may not reflect general patterns, however, this finding is intriguing given that SIEs are more evenly spread in terms of elevation and climate.

There is a clear link between endemism and the abiotic environment, but the link between endemism and functional trait composition is ambiguous. The distribution of endemics throughout the abiotic environment may not be accompanied by adaptation or measureable phenotypic change. Of course, the fact that endemics are not more distinct in their traits may simply mean that the traits measured here do not reflect ecological adaptation. It is possible that outcomes of island biogeographic processes are (currently) more easily identified using environmental gradients than functional traits.

7.1 Recommendations for future research

Future research in functional island biogeography should examine different aspects of functional trait space in relation to endemism, either by using different traits (when the data become available) or by focusing on alternative facets of functional diversity. Dispersal traits are of particular interest for island species—dispersal ability is important for colonising species, but loss of dispersal ability over time is considered an island syndrome. This thesis focused only on leaf and stem traits but these do not reflect the full extent of trait differences across species (for example, below ground traits are not considered). Future researchers should strive to develop an all-encompassing set of traits that capture functions of growth, reproduction and survival.

The route to endemism can vary, introducing scepticism to the idea that island endemics have distinct characteristics compared to non-endemics. Future research using functional traits on islands could instead be guided by a species' evolutionary history, for example by comparing neo-endemics and palaeo-endemics; or by comparing species that have speciated through cladogenesis (lineage-branching) with those that have experience anagenetic change (e.g. Fernández-Palacios *et al.*, 2021).

Most importantly, it is crucial that researchers are aware of what island trait space might look like under different scenarios: different processes can lead to the same outcome, and different outcomes may be the result of the same process. The island literature is bursting with ideas and theories about evolution, but how they link to present day species phenotypes and distribution is still up for debate.

7.2 Concluding remarks

Island endemics are valued for their novelty, which is why they have been extensively studied, but they are often grouped together and generalised by their supposed commonalities. Thus, the extent to which endemic species converge on an ‘endemic syndrome’ is uncertain (Gorman et al., 2014). This thesis found an endemic signature in relation to the abiotic environment, in that they occur widely but with an affinity for rare or extreme habitats, but not in relation to functional traits. The distinctive nature of island evolution admired by Carlquist may give rise to endemic species that are ironically, not-distinct!

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