Functional traits of vascular plants on islands across spatial scales

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"To understand how anything very complex works, or even to know that there is something complex at work, man needs to see little tiny bits of it at a time. And this is why islands have been so important to our understanding of life"

Douglas Adams, Last Chance to See

Abstract

Islands have unique and disharmonic floras, resulting from the filtering effects of dispersal and climate and, in some cases, their high evolutionary diversification rates. Due to their small size and distinct boundaries, islands are excellent model systems for ecological and evolutionary research, and contribute essential input to ecological theories such as the species-area relationship, immigration and extinction, and community assembly. The equilibrium theory of island biogeography (ETIB) is a seminal theory in ecology, but it is limited because it does not consider, explicitly, the dynamic nature of islands and the differences in ecological strategies among species. Islands are indeed dynamic entities, and such dynamics operate at various spatial and temporal scales, which have been shown to influence island biodiversity patterns. Species' ecological strategies likely strongly influence species immigration and extinction probabilities in islands, affecting species assembly and evolutionary trajectory. Thus, I focused my doctoral dissertation on providing a mechanistic understanding of insular biodiversity patterns and their drivers by integrating island dynamics, species ecological strategies (through functional traits), across different spatial scales - global, regional, and local. Specifically, I investigated insular floras' taxonomic and functional diversity patterns and how they related to island dynamics. To do that, I used two types of islands with distinct dynamics: oceanic and barrier islands.

On a global scale, I assessed oceanic islands' functional trait composition of endemic and non-endemic species and the linkage between taxonomic and functional diversity with island ontogeny. I mobilized trait data of over 2500 plant species from seven iconic archipelagos (Canary Islands, Cook Islands, Galapagos, Hawaii, Juan Fernandez, Madeira, and New Zealand) (chapter I). I found that insular endemic species were more functionally dispersed than non-endemic species and kept adding novel traits to the trait space as islands aged. I also found that while island age is a good predictor of islands species, it was less effective in predicting functional diversity.

At a regional and local scale, I used barrier islands as a model system (the Frisian Islands) to investigate the patterns and drivers of multifaceted diversity (i.e., taxonomic, functional, and phylogenetic diversity) in highly dynamic landscapes. I used species distribution data from literature, combined with trait information from databases and published studies to determine if historical and current island features (i.e., geomorphological dynamics, historical area, modern area, and habitat heterogeneity)

shaped multifaceted diversity (chapter II). I found that although larger islands accumulated more unique functional and phylogenetic species, smaller islands that had high habitat heterogeneity had lower functional diversity. This trade-off between area and heterogeneity may be attributed to high interspecific competition, favoring stronger competitors with specific traits. At a local scale, I combined data on species distribution and cover, from the monitoring program maintained by the Wadden Sea National Park authorities, with data of plant functional traits from databases and published studies, to explore changes in taxonomic and functional diversity as a result of disturbance and biotic forces along habitat maturity gradients (chapter III). The results of this chapter showed that functional and taxonomic diversity trends along habitat maturity were highly habitat-dependent, but species showed a consistent higher investment in resource acquisition and competition traits (plant height and leaf dry matter content) as habitats got more mature.

I found that across spatial scales, islands' floras seemed to be functionally similar. This similarity could come primarily from the dispersal filtering islands are subjected to, and in the case of barrier islands, this trait homogenization might be exacerbated by the high disturbance frequency happening in those types of islands, where only species with similar ecological strategies would be able to colonize and persist. Furthermore, I show that our understanding of insular floras, as well as its relationship with islands dynamics, can be strengthened by integrating a functional perspective, either via functional differences between endemic and non-endemic species at global scale or via decoupling responses between multifaceted diversity at regional and local scales.

Zusammenfassung

Inseln beherbergen einzigartige und disharmonische Floren, die auf die Filterwirkung der Ausbreitung und des Klimas sowie in einigen Fällen auf ihre hohen evolutionären Diversifizierungsraten zurückzuführen sind. Aufgrund ihrer geringen Größe und ihrer ausgeprägten Grenzen sind Inseln hervorragende Modellsysteme für die ökologische und evolutionäre Forschung und leisteten bereits einen wesentlichen Beitrag zu ökologischen Theorien wie der Beziehung zwischen Artenvielfalt und Fläche, Einwanderung und Aussterben sowie dem Aufbau von Gemeinschaften. The equilibrium theory of island biogeography (ETIB) ist eine bahnbrechende Theorie in der Ökologie, aber sie ist begrenzt, weil sie die dynamische Natur von Inseln und die Unterschiede in den ökologischen Strategien zwischen Arten nicht explizit berücksichtigt. Inseln sind in der Tat dynamische Gebilde, und diese Dynamik findet auf verschiedenen räumlichen und zeitlichen Ebenen statt, die nachweislich die Muster der biologischen Vielfalt auf Inseln beeinflussen. Die ökologischen Strategien der Arten haben wahrscheinlich einen starken Einfluss auf die Wahrscheinlichkeit der Einwanderung und des Aussterbens von Arten auf Inseln, was sich auf die Artenzusammensetzung und den Verlauf der Evolution auswirkt. Daher konzentrierte ich mich in meiner Doktorarbeit darauf, ein mechanistisches Verständnis der insularen Biodiversitätsmuster und ihrer Triebkräfte zu erlangen, indem ich die Inseldynamik und die ökologischen Strategien der Arten (durch funktionale Merkmale) über verschiedene räumliche Skalen - global, regional und lokal - integrierte. Konkret untersuchte ich die taxonomischen und funktionalen Diversitätsmuster von Inselfloren und deren Zusammenhang mit der Inseldynamik. Dazu verwendete ich zwei Arten von Inseln mit unterschiedlicher Dynamik: ozeanische Inseln und Barriereinseln.

Auf globaler Ebene untersuchte ich die Zusammensetzung der funktionellen Merkmale endemischer und nicht-endemischer Arten auf ozeanischen Inseln sowie die Verbindung zwischen taxonomischer und funktioneller Vielfalt und der Ontogenese der Inseln. Zu diesem Zweck habe ich funktionelle Merkmale von über 2500 Pflanzenarten auf sieben ikonischen ozeanischen Archipelen (Kanarische Inseln, Cookinseln, Galapagos, Hawaii, Juan Fernandez, Madeira und Neuseeland) ausgewertet (Kapitel I). Ich fand heraus, dass insulare endemische Arten funktionell weiterverbreitet waren als nicht endemische Arten und dass mit zunehmendem geologischen Alter der Inseln immer neue Merkmale hinzukamen. Außerdem stellte ich fest, dass das Alter einer Insel zwar ein guter Prädiktor für die Artenvielfalt auf der Insel ist, dass es aber bei der Vorhersage der funktionellen Vielfalt weniger effektiv ist.

Auf regionaler und lokaler Ebene verwendete ich Barriereinseln als Modellsystem (die Friesischen Inseln), um die Muster und Triebkräfte der vielfältigen Vielfalt (d. h. der taxonomischen, funktionalen und phylogenetischen Vielfalt) in hochdynamischen Landschaften zu untersuchen. Auf regionaler Ebene verwendete ich Daten zur Artenverteilung aus der Literatur in Kombination mit Merkmalsinformationen aus Datenbanken und veröffentlichten Studien, um festzustellen, ob historische und aktuelle Inselmerkmale (d. h. geomorphologische Dynamik, historische Fläche, moderne Fläche und Habitatheterogenität) die Vielfalt beeinflussen (Kapitel II). Ich fand heraus, dass größere Inseln zwar mehr funktional und phylogenetische einzigartige Arten anhäuften, dass aber kleinere Inseln, die eine hohe Habitatheterogenität aufwiesen, eine geringere funktionale Vielfalt aufwiesen. Dieser Diskrepanz zwischen Fläche und Heterogenität kann auf starke interspezifische Konkurrenz zurückgeführt werden, der stärkere Konkurrenten mit spezifischen Merkmalen begünstigt. Auf lokaler Ebene habe ich Daten zur Artenverteilung und -bedeckung aus dem Betreuung und Überwachungsprogramm der Wattenmeer-Nationalparkbehörden mit Daten zu funktionellen Merkmalen von Pflanzen aus Datenbanken und veröffentlichten Studien kombiniert, um Veränderungen der taxonomischen und funktionellen Vielfalt als Folge von Störungen und biotischen Kräften entlang von Lebensraum-Reifegradienten zu untersuchen (Kapitel III). Die Ergebnisse dieses Kapitels zeigten, dass die Entwicklung der funktionellen und taxonomischen Vielfalt entlang des Reifegrades der Lebensräume stark vom Lebensraum abhängt, dass aber die Arten mit zunehmendem Reifegrad der Lebensräume durchgängig höhere Investitionen in Ressourcenerwerb und Konkurrenzmerkmale (Pflanzenhöhe und Blatttrockenmassegehalt) aufweisen.

Meine Ergebnisse zeigen, dass die Inselfloren über räumliche Skalen hinweg funktional ähnlich zu sein scheinen. Diese Ähnlichkeit könnte in erster Linie auf Filtereffekte auf Grund von Ausbreitungshindernissen zurückzuführen sein, denen Inseln ausgesetzt sind. Im Falle von Barriereinseln könnte die beobachtete Merkmalshomogenisierung durch die hohe Störungshäufigkeit auf solchen Inseln noch verstärkt werden, wo nur Arten mit ähnlichen ökologischen Strategien in der Lage wären, sich anzusiedeln und zu überleben. Darüber hinaus zeige ich, dass unser Verständnis von Inselfloren sowie ihrer Dynamiken durch die Integration einer funktionalen Perspektive gestärkt werden kann, entweder durch funktionale Unterschiede zwischen endemischen und nicht-endemischen Arten auf globaler Ebene oder durch die Entkopplung von Reaktionen zwischen Vielfalt auf regionaler und lokaler Ebene.

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Thesis introduction

On the ecological importance of islands

Island biotas are commonly species-poor, i.e., islands have fewer species per unit of area than their mainland source pool (Rosenzweig, 1995; Williamson, 1981) and are also thought to be disharmonic, i.e., different compositions than their mainland source pool (Carlquist, 1966). The disharmony of islands is hypothesized to be a consequence of dispersal and climatic filtering, as island colonization only selects from the dispersive subset of the species source pool, and islands' climates tend to be different from the climate of the closer continents (Whittaker et al., 2007; Williamson, 1981). Disharmony can also be promoted by high diversification rates, and islands are known to be a fertile ground for evolutionary diversification (Carlquist, 1966; Losos et al., 2010). For example, Hawaiian lobeliads are made of 126 species across six genera, which all originated from one colonization event (Givnish et al., 2009). Additionally, at times of radical environmental changes on continents, islands can also serve as refugia for biodiversity (Condamine et al., 2017; Weigelt & Kreft, 2013), as is the case of laurel forest in the Macaronesia islands, which is the only remnants of an ancient forest that was once wildly distributed across central and southern Europe (Axelrod, 1975). Continental laurel forest was eradicated by drastic climatic events triggered by geological changes in the Mediterranean (Blondel, 1999).

Because of this unique biota, islands have attracted the attention of researchers for centuries (Caujapé-Castells et al., 2010; Kier et al., 2009; Weigelt, Jetz, & Kreft, 2013) and have often served as study model systems (Warren et al., 2015). Islands' small size, distinct boundaries, and youth, along with their potential for replication within archipelagos (Losos et al., 2009), make them excellent model systems. Island research has provided essential input to prominent evolutionary and ecological concepts. Darwin's five-week stay in the Galapagos islands was of great influence on his work, serving as the most important source of evidence for Darwin's thinking on evolution (Losos et al., 2009). Other examples of islands' research contribution are the species–area relationship (Rosenzweig, 1995; Triantis et al., 2012) immigration and extinction (MacArthur et al., 1967), and community assembly (Diamond et al., 1975). Thus, islands advance our understanding of the mechanisms underpinning island biodiversity assembly is a key interest in ecology. However, many studies in island biogeography focus on oceanic islands, and little attention is paid to islands with different origins and dynamics, which can also provide fresh insights into island biogeography (Ali 2017).

Barrier islands are a good example of an understudied system, that has already contributed to the field in the past (Palmgren 1915-1917 on the Åland archipelago and MacArthur Wilson 1967 on the Florida Keys). Approximately 15% of the world's coastlines are home to barrier islands, which can be found on nearly every continent (Davis, 1994a). Barrier islands usually have elongated shaped and are commonly part of a series of islands, forming a chain (Hoyt, 1967). They are composed of unconsolidated sediment, and processes of constant erosion and sediment deposit cause the islands to move over time (Fitzgerald et al., 1984). Those islands have a highly dynamic nature and play an important ecological role by providing unique habitats for many species of migratory birds, marine mammals, and fish. They also serve as shoreline shields, protecting the mainland from storms and waves (Hoyt, 1967). Barrier island habitats, such as salt marshes, provide essential ecosystem services, like nutrient cycling, and were shown to have high carbon sequestration capacity (Burden et al., 2019; Ouyang et al., 2013).

Equilibrium and dynamic theories of island biogeography

The equilibrium theory of island biogeography from MacArthur and Wilson (1967) is perhaps the most notorious outcome of island research and remains strongly influential to this day. MacArthur and Wilson's work derives from a combination of the long-known notion that species numbers increase with increasing area their own observations that island isolation seem to explain variations in pacific birds' data (MacArthur et al., 1963), and the idea that species compositions vary across ecological timescales (van Docters Leeuwe, 1936). Although MacArthur and Wilson's proposed equilibrium model is a seminal theory in the field of ecology, it is not without its limitations. Research made since its publication has demonstrated some of the ETIB limitations. For instance, the addition of climate variables as well as the disturbance history of islands greatly explain variations of insular biodiversity (Barajas-Barbosa et al., 2020; Fahrig et al., 1993; Kreft et al., 2008; Weigelt et al., 2016).

One major limitation of the ETIB is that it does not consider the fact that islands are highly dynamic systems, and their dynamism takes place across a range of spatial and temporal scales, ranging from daily tidal dynamics (Fitzgerald et al., 1984), to geological and climatic changes that happen over the span of thousands to millions of years (Weigelt et al., 2016). Recent models of biogeography incorporate such dynamism and highlight their importance for key ecological processes (e.g. immigration, speciation, and extinction), meaning that dynamism also influences island biodiversity patterns

(Heaney, 2000; Whittaker et al., 2008). For instance, on barrier islands, storm events and tides are essential for the maintenance of indigenous biodiversity in local habitats such as saltmarshes and dunes, as storms and tides cause periodic erosions that break naturally formed monocultures, giving opportunity for pioneer species to establish and naturally rejuvenate the habitats (Groot et al., 2017). On the longer time scales, e.g. millions of years, changes in sea level and climate during the Late Quaternary (the last 2.6 million years) are tightly linked to the current proportions of island endemics, likely because of the significant changes to island size and connectivity caused by these oscillations (Weigelt et al., 2016).

To account for the dynamism of islands, specifically oceanic islands that have a limited lifespan due to subsidence and erosion (Neall et al., 2008), Whittaker et al. (2008) proposed the general dynamic model of oceanic island biogeography (GDM). The GDM postulates that islands' geological dynamics affect the assembly of island biota and lead species richness to a hump-shaped relationship with age, with low species richness in the early and late stages and high species richness in the middle stages. The GDM also suggests that early stage islands have more resources than species, which can lead to adaptive radiation to fill these resource space. Although the GDM addresses some of the limitations of the EITB, it still treats species as being ecologically equivalent. Both models assume that all species have the same chance of establishing themselves or going extinct. The assumption that species are ecologically equivalent is not entirely accurate, as the suitability of a species for a particular environment, its ability to disperse and compete, all depend on its ecological strategy. These strategies can be quantified through the measurement of a species' functional traits.

A trait-based approach

Functional traits are individual morphological, physiological, and ecological features that affect individual performance and fitness (Garnier et al., 2016). The origins of trait-based ecology can be traced back to the 19th century, when Alexander von Humboldt developed vegetation classifications based on growth forms, recognizing the importance of plants' different forms and functions (Garnier et al., 2016). Although researchers have already used trait-based ecology a century ago, in the last decade research using trait-based approaches has considerably increased, and was successfully used to answer long-standing ecological questions and to inform for nature conservation strategies (de Bello, 2021). The success of trait-based or functional ecology is partially due to the ability to overcome some limitations of taxonomic-based ecology by providing a more accurate understanding of the mechanisms underpinning biodiversity patterns (Fukami et al., 2005). For example, trying to predict changes in community compositions using only species' taxonomic identity might not be effective, as taxonomic classifications do not provide information on species adaptations and interactions with the environment, or other species. However, forecasting changes in certain traits by using predictable environment-trait relationships might yield more accurate results, since species' responses to environmental variables and biotic interactions are determined by their functional traits (Adler et al., 2014; de Bello, 2021; Díaz et al., 2007; Díaz et al., 2016; Fukami et al., 2005).

Trait-based approaches are also increasingly used in applied research to address environmental challenges, aiding in the development of better carbon sequestration strategies and more efficient agricultural systems (Deyn et al., 2008; Wood et al., 2015). In those systems, trait variations can be directly linked with environmental alterations and changes in management, improving agricultural practices towards more sustainable and resilient systems (Isaac et al., 2018; Martin et al., 2015).

On islands, the trait composition of colonizing species is expected to strongly influence immigration and extinction probabilities (Vargas et al., 2014) thus influencing island species assembly and evolutionary trajectory. Understanding the mechanism behind island assembly and evolution is a key step towards more efficient conversation practices, as islands are especially vulnerable to biological invasions and anthropogenic pressures (Fernández-Palacios et al., 2021; Myers et al., 2000; van Kleunen et al., 2015). For example, in the Hawaiian rainforest, the use of a trait-based approach to select species used in restoration efforts was successful in increasing natural seedling recruitment of native plants, while simultaneously reducing the proliferation of invasive species at restoration sites (Ostertag et al., 2015).

Recently, the trait-based approach to investigating the island assembly process are gaining more attention (Barajas-Barbosa et al., 2022; Hanz et al., 2022; Schrader, Westoby, et al., 2021), but there is still much to be understood regarding patterns and drivers of insular functional diversity (Ottaviani et al., 2020; Schrader, Wright, et al., 2021). Identifying biases in the trait composition of islands species help us understand well-known biogeographical patterns, such as island disharmony (Carlquist, 1974), insular woodiness (Lens et al., 2013), and adaptative radiations (García-Verdugo et al., 2014; Givnish et al., 2009), which so far have been studied mostly from a taxonomic perspective, (but see König et al., 2021; Taylor et al., 2019). Finally, a trait-based approach can explain beyond *how many* species are found on the island, it can help us understand *what kind* of species are there (Schrader et al., 2023).

The scale problem

Mechanisms influencing biodiversity occur at different spatial scales, from the interactions between individuals within a single population to the large-scale variables that drive global biodiversity. Consequently, the results of a study can change significantly depending on the scale being observed (Levin, 1992). For instance, in a study on drivers of plant diversity in grasslands Dembicz et al., 2021 found that the importance of different variables changed with size of the area being studied. Variables like soil pH and terrain elevation became more important when studying larger areas, while heat-load index and slope inclination were more important when studying smaller areas. In another study investigating the impact of logging on butterfly diversity, Hamer et al. (2000) found that the effects of logging on butterfly diversity were minor at small scales, but became more pronounced at larger scales, showing larger negative effects.

There is a well-accepted assumption that when analyzed in fine spatial scales, plant communities tend to be more functionally different as coexisting species would compete for the same resources (de Bello et al., 2009; Kraft et al., 2010; Weiher et al., 1995). Conversely, on broader spatial scales there is a tendency for species with similar traits to coexist under similar environmental conditions (Freschet et al., 2010; Weiher et al., 1995). However, when reviewing empirical studies about functional diversity scaling Leibold et al. (2018) found most studies (14 out of 19) did not confirm this assumption and were not consistent in their findings. While there is robust evidence of the scale dependency of functional diversity, how functional diversity patterns change with scale remains unclear (Matthews et al., 2020).

Even with a large number of published studies that investigate drivers of diversity, our overall understanding of diversity patterns and drivers remains limited, as most studies focus on one diversity facet (i.e. taxonomic diversity) at a single spatial scale (Chase et al., 2018). By combining information from different spatial scales across different diversity facets, researchers can gain a deeper understanding of the mechanisms underlying the observed patterns.

Thesis outline

Understanding island species strategies and their relation to environmental variables, across different spatial scales, can broaden our knowledge of spatial patterns of insular biodiversity, and the mechanisms underpinning island biodiversity assembly. In this thesis, I use oceanic and barrier islands to investigate the assembly of island floras from a trait-based perspective. Particularly, I focus on understanding the role of island characteristics as drivers of functional diversity and trait composition of island floras across different spatial scales. Consequently, this thesis is divided into three chapters, one of which corresponds to a specific spatial scale, starting with a global approach in chapter one, followed by chapter two at the regional scale, and lastly, chapter three looking at a local scale (Figure 0.1).

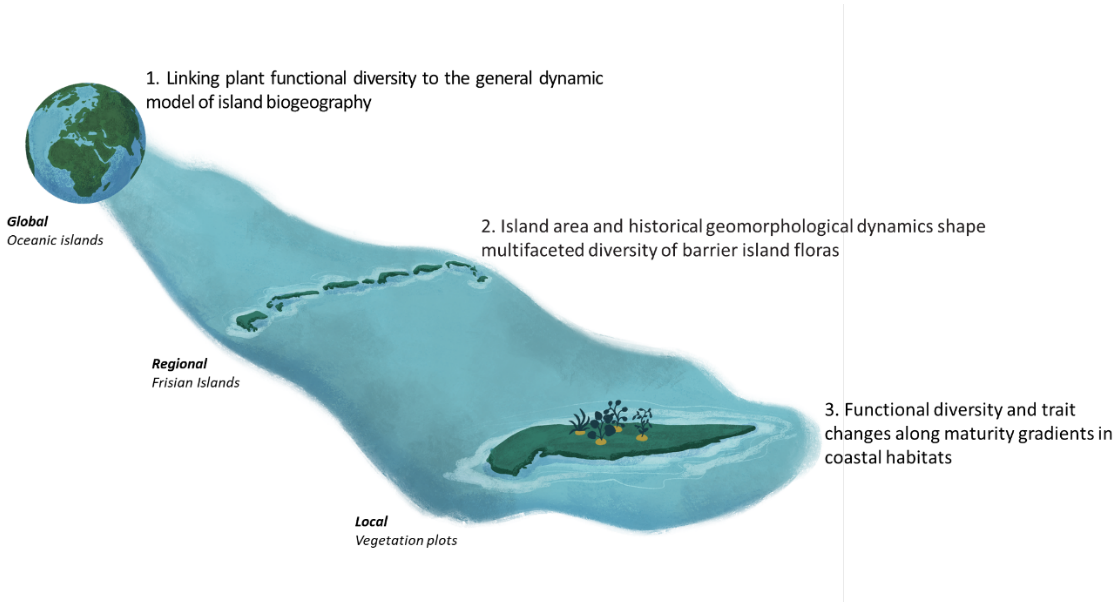

Figure 0.1 Illustration of the three spatial scales addressed in each chapter and their titles

In chapter one, I take a trait-based approach to the General Dynamic Model. Despite functional traits potential to answer important questions in island biogeography, such as the mechanisms underlying island flora assembly and speciation, quantitative studies at large spatial scales are scarce. To address this gap, I use data from seven iconic oceanic archipelagos, (Canary Islands, Cook Islands, Galapagos, Hawaii, Juan Fernandez, Madeira, and New Zealand) to investigate the trait space and functional composition of oceanic island floras and the linkages between functional diversity and oceanic island ontogeny in the framework of the GDM.

In chapter two, I aim to help fill the knowledge gap on the relationship between island dynamics and characteristics and different facets of vascular plant diversity. The well-studied influence of these factors on taxonomic diversity contrasts with the limited understanding of their influence on functional and phylogenetic diversity. Using barrier islands, a highly dynamic and understudied island type, I investigate how island geomorphology, modern and historic area, and habitat heterogeneity, shape functional, phylogenetic, and taxonomic diversity of vascular plants.

In chapter three, I aim to deepen our understanding of community assembly mechanisms and maintenance biodiversity in dynamic ecosystems. The context-dependency of habitat maturation makes it hard for ecologists to formulate a general theory, going beyond species' taxonomic identity and considering functional traits might help unveil the mechanisms underpinning this process. I assess the changes in functional and taxonomic diversity as well as trait mean values, across different stages of habitat maturity in three habitats with similar geomorphological dynamics (dune, dune slacks, and salt marshes).

1 Linking plant functional diversity to the general dynamic model of island biogeography

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Abstract

Trait-based approach may be pivotal to answer central questions in island biogeography, such as the mechanism underpinning island flora assembly and speciation, but quantitative studies at large spatial extents are scarce. Furthermore, contemporary biogeographical models of island biodiversity such as the Equilibrium Theory of Island Biogeography and the General Dynamic Model (GDM) treat species as ecologically equivalent and do not consider variation in functional traits across species. Here, we address these gaps by investigating the trait space and functional composition of oceanic islands' floras as well as investigating linkages between functional diversity and oceanic islands' ontogeny in the framework of the GDM. To this end, we used data from seven iconic oceanic archipelagos (Canary Islands, Cook Islands, Galapagos, Hawaii, Juan Fernandez, Madeira, and New Zealand). We found that endemic species were wider spread in the trait space than non-endemic species but were mainly shrubs, which could be the product of evolutionary convergence towards woody growth forms. We also found that functional evenness follows a hump-shaped trend of richness over island age of species richness, pointing out high levels of functional redundancy on islands. In addition, functional dispersion of endemic species monotonously increased with island age, while it decreases for non-endemic natives. This result suggests that endemic species add novel traits to the islands' trait space and that there is no saturation of the trait space - even when islands are already in the late stages of their lifecycle. Moreover, we found little evidence that GDM-derived predictions can be applied to functional diversity. Our research contributes to the growing collection of literature on the global functional island biogeography field, further enhancing our understanding of the functional assembly mechanism of islands' floras.

1.1 Introduction

The isolated nature and peculiar ontogeny of oceanic islands have led to the evolution of unique biotas, and many endemic species (Carlquist, 1974; Kier et al., 2009). Thus, island biotas have been attracting the interest of researchers for a long time (Darwin, 1859; Losos & Ricklefs, 2009; MacArthur & Wilson, 1963; Whittaker et al., 2017). One of the most prominent outcomes of island research, the equilibrium theory of island biogeography (ETIB) by MacArthur and Wilson (1967), aims at understanding the effects of the island features area and isolation on the rates of colonization and extinction and consequently the number of species on an island. However, the main representation of ETIB, processes such as speciation, highly relevant on remote islands (Losos et al., 2009), are not included, and islands are considered static entities, and ontogenetic dynamics are not accounted for. Moreover, species strategy differences, likely influencing colonization and extinction rates are not explicitly included (Patiño et al., 2017; Vargas et al., 2014). This limits our understanding of processes underlying the range or dispersion of species strategies (i.e., functional diversity) and the role of island environments and dynamics shaping functional diversity patterns on oceanic islands (Ottaviani et al., 2020; Schrader, Wright, et al., 2021). Although a trait-based approach has the potential to answer central questions in island biography, knowledge about the functional aspect of oceanic islands has so far been mostly anecdotal, with few quantitative exceptions. Oceanic islands are dynamic systems, that arise from the bottom of the ocean and have limited life spans (Neall et al., 2008). Once formed, islands are constantly subjected to subsidence and erosion that shape their area and topography, creating and erasing habitats as islands age, until their complete submergence (Carracedo et al., 2011; Price et al., 2002). Aiming at incorporating these ontogenetic dynamics into island biogeography theory (Whittaker et al., 2008), proposed the general dynamic model of oceanic island biogeography (GDM). The GDM proposes that this ontogenetic dynamism would produce common trends in island species richness, with species richness showing a hump-shaped relationship with island age (Diversity = $\text{Area}_{\log}$ + Time − Time^2). GDM predicts low species richness at early stages, as islands are smaller and with fewer resources available. As islands age, they grow and become more complex in their topography, which will increase species richness. Species richness will continue to rise until islands reach their maturity and maximum carrying capacity. From then on, islands start to erode and loss of area and habitats will drive species richness down until islands' complete submergence. At early stages, islands would have high rates of colonization and also speciation, as the availability of unexploited resources would stimulate the arise of adaptative radiations. When islands reach their maximum carrying capacity, extinction rates start to increase and are further augmented by islands' loss of area and diminishing topographic complexity (Borregaard et al., 2017; Whittaker et al., 2008). The GDM makes clear-cut predictions about species richness but is agnostic about other facets of diversity.

Functional diversity measures the variation in species traits that affect individual performance and fitness (Garnier et al., 2016) and can help explain evolutionary trajectories, assembly processes, and patterns of biodiversity (Díaz et al., 2016; Lens et al., 2013; Losos, 2009; Tilman, 2013). In islands, dispersal and environmental filtering can lead islands' floras to have an over- or under-representation of certain traits (Carvajal-Endara et al., 2017; König et al., 2021; Taylor et al., 2019; Weigelt et al., 2015), or sometimes a complete lack of certain taxonomic or functional groups (Gillespie, 2007). A striking example of overrepresentation is the high proportion of woody island species (Patiño et al., 2017). This pattern could be the result of secondary woodiness, where herbs evolve woodiness (shrubs and trees) by a gradual increase in xylem growth, thus producing remarkable shifts in growth form (Antonelli, 2009). This shift might bring ecological advantages, such as better light interception and competitive advantages due to higher stature (Darwin, 1859), stronger drought tolerance (Lens et al., 2013), and an increased pollination probability due to an extended lifespan (Wallace, 1878). In addition, it may translate into variation in plant ecological strategies (i.e., functional diversity), not only across but also within plant growth forms (i.e., shrubs, trees, and herbs).

Despite efforts to reveal general trends of functional diversity in relation to island ontogeny across archipelagos (e.g., in snails at the regional level, Kraemer et al., 2022), our knowledge of general trends of functional assembly of island flora, and to what extent these are shaped by island ontogeny, remain uncertain (Borregaard et al., 2017). Following the life cycle of oceanic islands, one can assume that functional diversity follows species richness and presents a hump-shaped curve, as a result of either chance (i.e., higher species richness increasing the trait space) or ecological opportunities (Borregaard et al., 2017). The assumption that this hump shape results from ecological opportunities, is that ecological opportunities would be limited at the early stages, with high rates of colonization, and late stages, with high extinction rates, while peaking in the intermediate phases. Yet, divergence outcomes in the shape between functional diversity and island ontogeny may emerge due to strong dispersal filtering, and competition at later stages (Carlquist, 1974; Kraft, Adler, et al., 2015; Mayfield et al., 2010). Specifically, competition amongst species could generate two diverging outcomes at later stages: i) exclusion of functionally redundant species, inhibiting a decline in functional diversity; or ii) species convergence to an optimal assortment of trait combinations causing a decline in functional diversity (Grant & Grant, 2006; Mayfield & Levine, 2010; Whittaker & Fernández-Palacios, 2007).

Species that share the same biogeographical status, such as native non-endemic, endemic, or introduced species, might present different patterns of species richness and functional diversity (Irl et al., 2020; Rosindell et al., 2021; Whittaker et al., 2014). As showcased for the functional assembly of the Canary Islands (Barajas-Barbosa et al., 2022; Hanz et al., 2022), species with different biogeographical distributions contribute differently to the functional diversity of an island, and were distinctively distributed across different environmental gradients. Specifically, on Tenerife, Barajas-Barbosa et al. (2022) found that non-endemic species increased functional diversity, as they were more functionally distinct than species that originated from cladogenesis, which functionally converged around similar trait values. The relationship of each of these groups' diversity with island ontogeny might help bring to light the mechanisms underpinning island assembly.

Here, we aim at: i) investigating the trait space and functional composition of oceanic islands' floras; and ii) testing GDM-derived predictions. In order to better understand the functional assembly of islands' floras, we use two components of functional diversity: Functional dispersion, measured as the mean distance of all species to the trait space centroid of the assemblage community (Laliberté et al., 2010), and functional evenness, measured as the regularity of species distributions within the trait space (Carmona et al., 2016; Mammola et al., 2020). Using six model archipelagos (Canary Islands, Cook Islands, Galapagos, Hawaii, Juan Fernandez, Madeira), we test four predictions of functional diversity accumulation on volcanic oceanic islands over island ontogeny. Following Borregaard et al., (2017), we assume that at the early stages of an island's ontogeny, islands are colonized by a subset of species with strong dispersal abilities (Vargas et al., 2014), likely resulting in a limited combination of traits. Further island topographic development leading to higher habitat heterogeneity, will bring more colonists, and together with in-situ evolved species, they would then add new traits to the island's trait space. As islands age and lose their area and consequently, some of their habitats, species carrying traits that allow them to persist in a given environment, would be lost, leading to a smaller trait space. We predict that: a) Functional dispersion will broadly mirror species richness showing a hump-shaped relationship with the island's age, consequently, functional evenness will show a "u-shaped" curve; b)

Functional dispersion will peak before islands reach their maximum carrying capacity (peak of species richness); c) Endemic species drive an island's trait space to be more dispersed by adding novel traits; and d) Native non-endemic functional dispersion will be the highest before endemic species reach their maximum functional dispersion, as both groups might compete for similar resources (Figure 1.1)

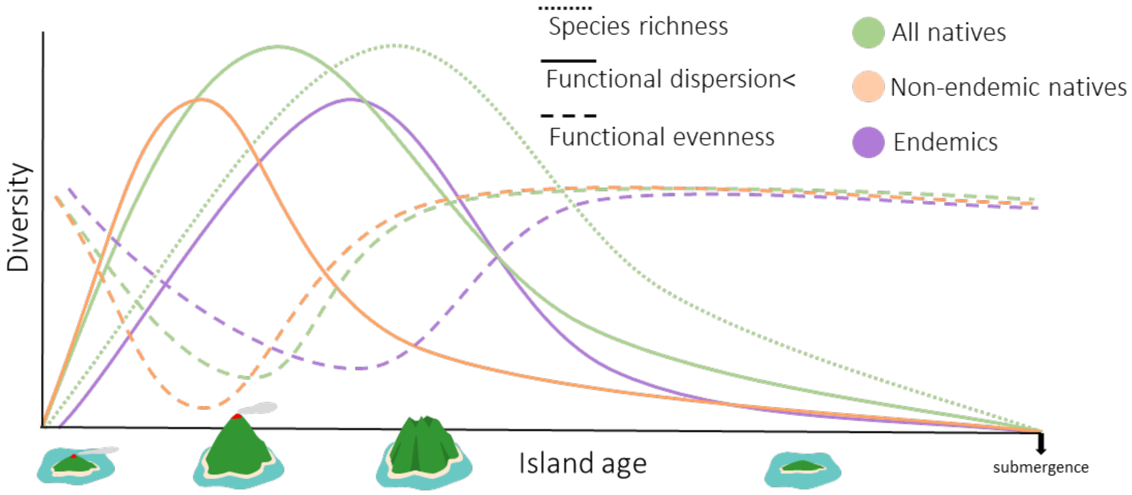

Figure 1.1.Graphical representation of the relationship between species richness, functional dispersion, and functional evenness in response to island ontogeny, grouped by species type. In the early stages of island development, the first species to colonize are highly dispersive with similar traits, leading to low functional dispersion and high Functional evenness. Further colonization by non-endemic natives and in-situ speciation bring new traits to the island, increasing functional dispersion and reducing functional evenness. New colonist and endemic species with similar traits fill the trait space, decreasing functional dispersion and increasing functional evenness, reaching the maximum species richness. As the island ages and habitats are lost, specialized species become extinct, reducing functional dispersion and species richness while increasing Functional evenness. Both non-endemic and endemic functional dispersion follow a hump-shaped curve, with non-endemic functional dispersion peaking earlier and decreasing as endemics emerge and compete for similar resource

1.2 Material and Methods

1.2.1 Species distribution and trait data

We assembled species composition and functional trait data for a total of 62 oceanic volcanic islands belonging to six archipelagos, plus New Zealand, spread across the globe: Canary Islands, Cook Islands, Galapagos, Hawaii, and San Juan Fernandez. From New Zealand, only islands of volcanic origin were included, namely Chatham Islands, Kermadec Islands, Mayor Island, and Norfolk Island (Figure 1.2). We extracted information regarding species distribution and functional traits from published scientific floras (Autrey et al., 1978-2008; Muer et al., 2016; Penneckamp Furniel, 2018; Press et al., 2016; Sykes, 2016; Wiggins et al., 1971), online databases (Herring et al., 2003; Kattege et al., 2011; Kattge et al., 2020; Lavorel et al., 2011; Weigelt et al., 2020) and field data (Barajas-Barbosa et al., 2022). The largest trait database for plants, TRY (Kattge et al., 2020), still has a large gap regarding island species, but floras have been identified to be a reliable source of trait information for islands' floras (Cutts et al., 2021; Hanz et al., 2022). We chose four traits that capture different ecologically relevant life history dimensions: i) maximum plant height (m) as a measure of light interception and seed dispersal facilitation (Westoby et al., 2002; Moles et al., 2009; Garnier et al., 2016), ii) leaf size (leaf length and width in mm^2) to assess leaf energy production and water balance (I. J. Wright et al., 2017), and iii) seed length (mm) as a measure of dispersal ability and seedling survival (Thompson et al., 1993; Moles et al., 2004; Wyse & Hulme, 2021). We chose to work with seed length instead of the more commonly used seed mass because both measures are highly correlated, reflecting similar ecological axes of variation, and seed length had a higher proportional (per island) coverage.

We did taxonomic harmonization and trait standardization according to the Global Inventory of Floras and Traits (GIFT) database version 2.2 (Weigelt et al., 2020) workflow. Genus names were first manually checked for spelling mistakes and further automatically compared to all available names per genus in The Plant List 1.1 (TPL) (The Plant List, 2010) using orthographic distances. We then selected the best-matching species epithets, and in cases with multiple matches, we used the ones with the best-matching author names. Synonyms were linked to their accepted species names according to TPL. To standardize the trait information, we first transformed all trait values to the same unit of measurement (Garnier et al., 2017; Pérez-Harguindeguy et al., 2013). When more than one trait value was available for a given species, we summarized the original values to mean, maximum, and minimum. For the analyses, presented here we used maximum values for all the traits, as maximum trait values were the more common measurement found in published floras.

Figure 1.2. Map of the studied archipelagos, including oceanic islands belonging to New Zealand (Norfolk, Mayor, Kermadec, and Chatham), which were used for the construction of the trait space.

We considered only native seed plant species for each archipelago, summing up to a total of 3821 species. Then, we selected only those species with data for at least one out of three traits, resulting in a total of 2834 species (74 %) in our dataset. Since data for all three traits were not available for all the species in our data set, we imputed the missing trait values (9% plant height, 52% seed length,22% leaf width, 30% leaf length) using the "missForest" function in the missForest package (Stekhoven et al., 2012). This function imputes missing values by fitting a random forest model (Breiman, 2001) on the observed part of each functional trait. It uses phylogenetic eigenvectors (n=1–30) to improve the predictive power, by selecting the number of phylogenetic eigenvectors that had the minimum imputation error for each trait. For the phylogenetic information, we used the phylogenetic tree by S. A. Smith et al., (2018) and a total of 2410 species could be matched to the tree, and other 396 were conservatively added at the genus level using the "congeneric.merge" function from the R package pez (Pearse et al., 2015), and 29 could not be matched the tree at all, and were left out of the analyses. To further improve the performance of the random forest algorithm, we included in the observed dataset 13 other traits that highly correlated ($p>0.0001$) with the main three traits we used (Appendix Table S1.1). Those additional traits were not used in the main analyses because they either did not have enough coverage or they offered redundant ecological information (e.g. minimum seed length). We used data imputation because imputed data introduces fewer errors compared with removing species that do not have information for all traits (Penone et al., 2014). We estimated imputation error as the root mean squared error (RSME) normalized by standard deviation. We found 1.4 for plant height, 1.08 for seed length, 1.75 for leaf width, and 2.92 for leaf length. Our imputed trait data also presented similar distributions and mean values as our observed data (Appendix Figure S1.3)

1.2.2 Islands features

To test our hypotheses, we related different indexes of taxonomical and functional diversity to island age (ref at Appendix S1.2) and area (Weigelt et al., 2020). Additionally, we considered four island features previously shown to influence insular plant species richness and the variation of their trait values: mean annual precipitation, mean annual temperature, maximum elevation, and geographical isolation (Irl et al., 2015; Jacquet et al., 2017; Kreft et al., 2008; Taylor et al., 2021). Mean annual precipitation, mean annual temperature, and maximum elevation was extracted at a resolution of 30 arc seconds and aggregated as the mean per island for climatic variables and as maximum for elevation (Fick et al., 2017; Hijmans et al., 2005). As isolation plays an important role in the assembly of island floras (MacArthur et al., 1963) we included the surrounding land mass proportion (hereafter SLMP), as the log of the sum of landmass proportions in 100, 1000, and 10000 km buffer distances. SLMP accounts for stepping stone islands and variations on coastlines by considering the amount of landmass surrounding each island (Weigelt & Kreft, 2013).

1.2.3 Functional trait space and functional diversity

To assess the functional trait space, we performed a Principal Coordinates Analysis (PCoA) on three different subsets of our data: all species, non-endemic native species, and endemic species. To perform the PCoA, we first produced a dissimilarity matrix using the methodology proposed by (de Bello, Botta-Dukát, et al., 2021) using the "gawdis" function of the gawdis R-package (de Bello, Botta-Dukát, et al., 2021). This approach allowed us to group traits that reflect the same ecological strategies, thus accounting for an unbalanced contribution of traits to the dissimilarity matrix. The "gawdis" approach finds optimal weights for each trait or group of traits so they have a comparable influence on the dissimilarity matrix (Bello et al., 2021). Here, we grouped leaf length and leaf width, so the whole group was weighted to have a similar contribution to multi-trait dissimilarity as the other remaining traits. We then used the PCoA coordinates to calculate hypervolumes using three dimensions and kernel density of the hypervolumes (Mammola et al., 2020) to quantify functional diversity as functional dispersion and functional evenness (Laliberté et al., 2010), using the functions "kernel.dispersion" and "kernel.evenness" in the BAT package (Cardoso et al., 2015). Only islands with more than seven species in each biogeographical group were considered to have reliable results from the hypervolume calculations (52 out of 62).

1.2.4 Statistical Analyses

To investigate the uneven representation of growth forms between native and endemic island floras, we calculated the proportion of herbs, shrubs, and trees as well as the proportion of woody and non-wood species of each archipelago. We then conducted a two-proportions z-test (E. B. Wilson, 1927) for each growth form and woodiness group to test whether they were over- or under-represented among endemic species compared to non-endemic natives.

We modeled each diversity metric in response to area and age by using linear mixed models. For species richness, we considered the complete species checklist of each island while for functional diversity metrics, we used a subset with only the species we had trait data for. We used the GDM formula as proposed by (Steinbauer et al., 2013), using log-transformed island age to account for an early diversity peak. We included the archipelago as a random effect to account for the shared geological histories of individual islands within each archipelago (Borregaard et al., 2017; Bunnefeld et al., 2012). Thus, the GDM formula we used consisted of: $diversity\,metrics \sim log(Area) + log(Age) + log(Age^2) + (1|Archipelago)$. We modeled all native species, non-endemic natives and endemic species leading to nine models with different response variables. Further, we used the models to predict diversity over time using the function "ggpredict" from the ggeffects package (Lüdecke, 2018). Using the same set of response variables as used for the GDM models, we fitted multiple linear mixed-effects models additionally including other potential drivers of diversity on islands: precipitation, temperature, elevation, and isolation. Using all native species, we checked the correlation among diversity indexes using Pearson correlation tests and found that none of the functional diversity indices was correlated with species richness ($p>0.1$, (Appendix Figure S1.2).

1.3 Results

Across archipelagos, non-endemic native plant species showed a significantly greater representation of non-woody species ($p< 0.001$; Figure 1.3), which accounted for 69% of the non-endemic species, in contrast to only 19% of non-woody within endemic species.

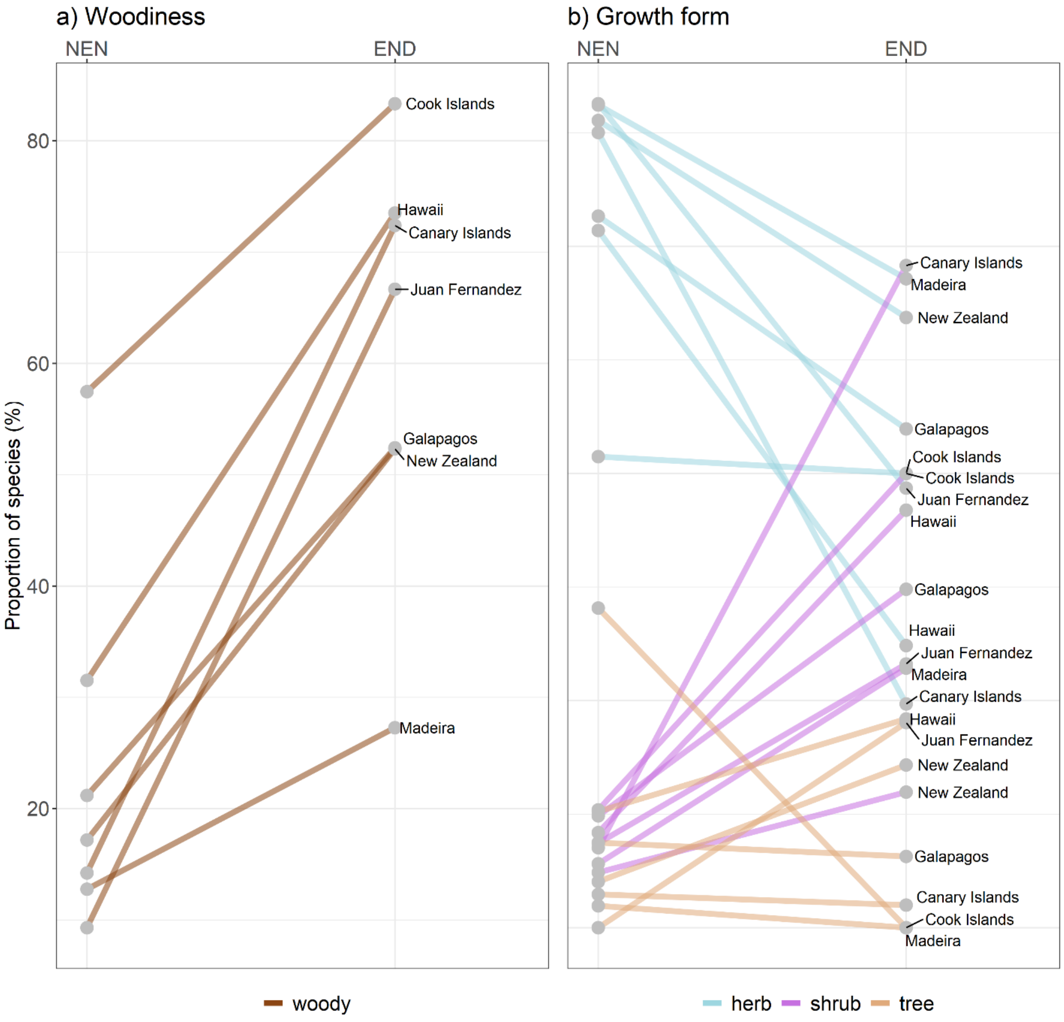

Figure 1.3 Relative proportion of woody species and growth form, among non-endemic natives (NEN) and endemics (END) on seven oceanic archipelagos.

Non-endemic species showed a significant (p<0.001) overrepresentation of herbs, with herbs accounting for 86% of the growth form in this group, while only 33% of endemic species were herbs. Endemic species showed a significantly (p<0.001) higher proportion of shrubs (51%) than non-endemic natives (8%). Trees also showed significant (p<0.001), but greater representation among endemic species, accounting for 15%, compared with 6% among the native non-endemics.

The first two PCoA axes explained 52.5% and 31.9% of the variation in the functional trait space, respectively. The first axis reflected species resource acquisition abilities, as the leaf traits and plant height were strongly associated with it, while axis two mainly represented variation in seed length. The PCoA analysis, including all native species (Figure 1.4, A), shows that the majority of species cluster towards the center of the trait space, indicating that they are smaller in size and have smaller seeds. However, some species, mostly trees, are located towards the edges and are characterized by larger seeds and taller stature.

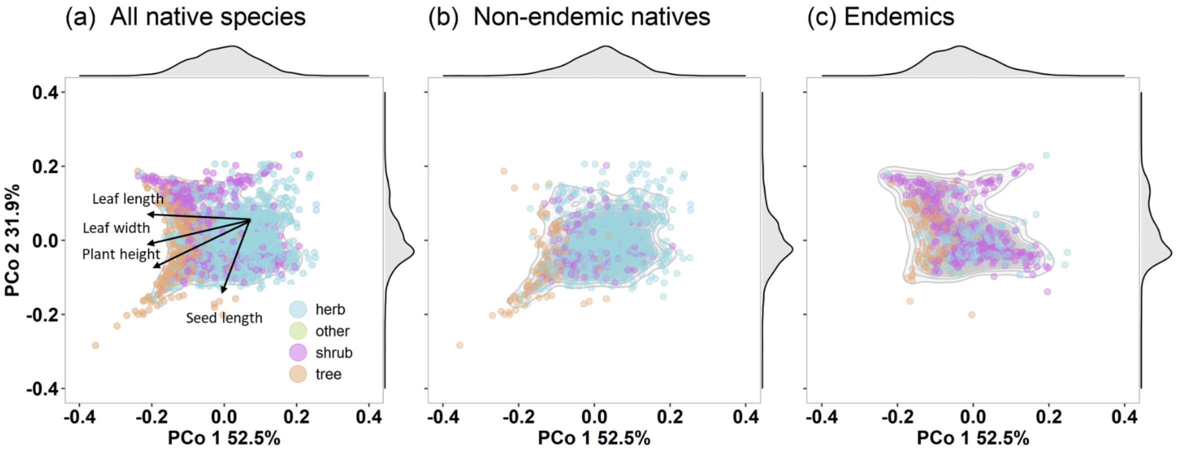

Figure 1.4. Trait spaces for the native flora (a) of 2806 species belonging to seven oceanic archipelagos (Canary Islands, Cook Islands, Galapagos, Hawaii, Madeira, New Zealand, and Juan Fernandez) and divided into (b) non-endemic-natives (n = 1597) and (c) endemics species (n = 1231). Traits included are plant height (m), seed length (mm), leaf width (mm), and leaf length (mm). Projections are of the two first dimensions of variation from the principal component analysis.

When dissecting native floras into different biogeographical groups, non-endemic native species (Figure 1.4, B) were made up mostly of herbs with smaller leaves and seeds. However, the tallest trees of our dataset and the ones with bigger leaves were also present in this group. The endemic species group (Figure 1.4, C) consisted mostly of shrubs that occupied different parts within the range of each trait as well as shorter trees and presented smaller seeds and leaves.

We found a hump-shaped relationship between species richness and island age across all three biogeographical species groups. Functional dispersion showed a u-shaped relationship with age for all native species (Figure 1.5, A) and endemic species (Figure 1.5, c) while presenting a hump-shape for non-endemic natives (Figure 1.5, B). However, both functional diversity metrics showed wide confidence intervals, since they were not significantly correlated with island ages, except all natives functional evenness (Figure 1.6, A, B, C). Functional evenness mirrored the trend of species richness for all the native plants and endemic species while showing a u-shaped form for the non-endemic natives.

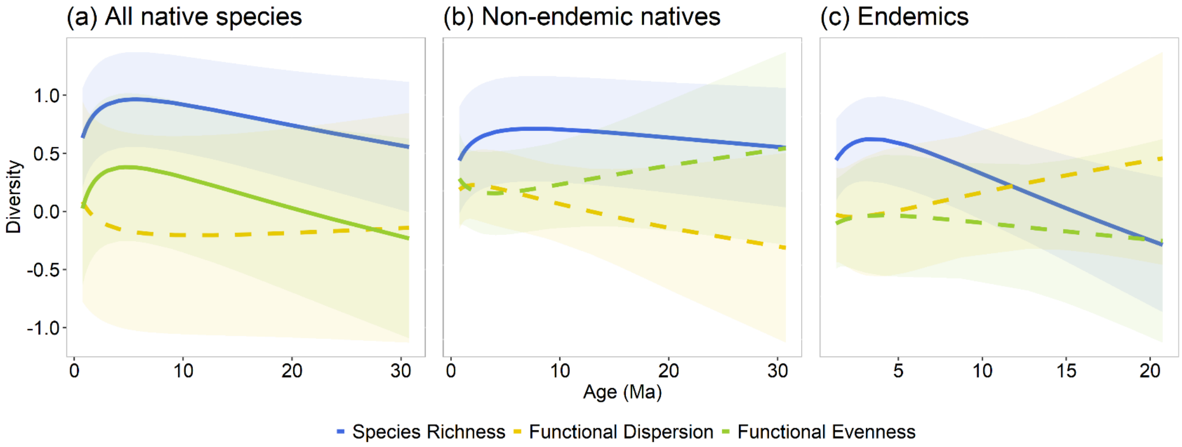

Figure 1.5. Temporal trends of species Richness, functional dispersion and functional evenness over island age (in millions of years, i.e., Ma) estimated from 52 oceanic islands belonging to six archipelagos. Predictions were extracted from generalized linear mixed effect models of the form 'Diversity Metric ~ log(Area) + log(Age) + log(Age^2) + (1|Archipelago). Diversity metrics values were scaled (zero means, unit variance) to simplify comparisons among them.

Our models including additional island features showed significant ($p<0.001$) relationships between diversity indices of native species and area, with functional evenness being positively correlated with age and elevation, while functional dispersion was correlated with annual precipitation (Figure 1.6, D). Non-endemic native species functional diversity indices were not significantly correlated with any of our variables, while species richness was positively correlated with age and area (Figure 1.6, E). Endemic species showed significant relationships between species richness, area, and elevation (Figure 1.6, F).

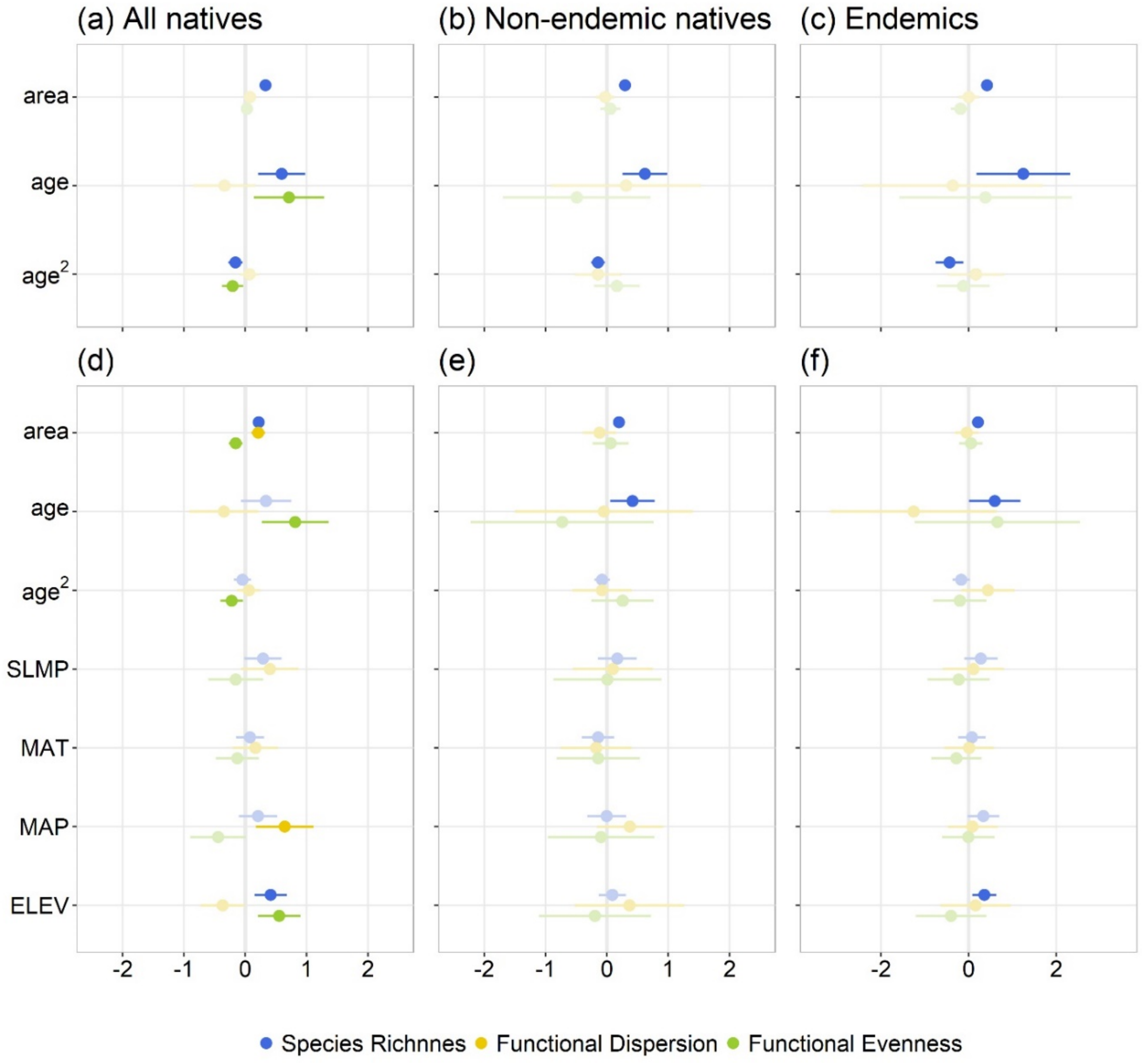

Figure 1.6. Standardized coefficient plots showing the effect of island area (km²), age (age and age quadric term = age², in millions of years), surrounding land mass proportion (SLMP), mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm/a) and maximum elevation (ELEV, m), on all native species (A,D) non-endemic natives (B,E) and endemics (C,F). Semi-transparent dots are non-significant relationships.

1.4 Discussion

In this study, we test how island geological ontogeny might influence the assembly and maintenance of the functional diversity of islands' plants. Our results show that the relationships between functional diversity and island ontogeny are much more complex than those between species richness and island ontogeny (Kraemer et al., 2022; Otto et al., 2016; Steinbauer et al., 2013). Contrary to our initial hypothesis, our models showed island age not to be a significant predictor of functional diversity. We also found that different biogeographical groups show different relationships between functional diversity and island age and environmental drivers. Our findings show that a majority of species, belonging to both biogeographical groups, occupy similar resource space. However, endemic species had a larger variation of traits than non-endemic species, despite the over-representation of one growth form (shrub) in this group. This larger variation suggests that endemic species indeed expand the trait space by adding novel trait combinations

1.4.1 Plant functional strategies on oceanic islands

Our results of a high proportion of shrubs within the endemic group are in line with patterns reported in Tenerife (Barajas-Barbosa et al., 2022). In Tenerife, the predominance of shrubbiness among species originated from cladogenesis, which could be a consequence of strong environmental filters leading to functional convergence (Barajas-Barbosa et al., 2022). However, the high proportion of woody species on islands has been addressed by several studies (Böhle et al., 1996; Burns, 2019; Dulin et al., 2010; Lens et al., 2013; Zizka et al., 2022), and there is not yet one unifying explanation for this pattern (Zizka et al., 2022). The overrepresentation of woody species could be explained by herbaceous species that evolved into woodiness (i.e. secondary woodiness), or woody colonizers that diversified. Secondary woodiness has frequently been reported from oceanic islands (e.g. in *Lobelioid* on Hawaii or *Sonchus* on the Macaronesian islands). Alternatively, diversification rates could also be higher among woody colonizers due to more ecological opportunities under lower competition from other colonizers. There are also cases where endemic woody species are relics of once-widespread woody species (Cronk, 1987; Pasta et al., 2022; Poncet et al., 2013). Higher insular woodiness may be a result of the combination of those three processes.

1.4.2 The GDM through the lenses of functional ecology

In line with the GDM predictions and previous empirical studies (Cameron et al., 2013; Lenzner et al., 2017; Steinbauer et al., 2013) we found a significant hump-shaped relationship between species richness and island age, across all three biogeographic groups. However, this correlation does not translate to all functional diversity indices, and surprisingly only holds true for the functional evenness of all native species. Contrasting with our hypothesis, the synchrony between functional evenness and species richness of all native species suggests high levels of functional redundancy, where newly added species are packing the trait space, instead of expanding it by exploiting new functional strategies. This pattern has been previously observed in plants from the Canary Islands (Barajas-Barbosa et al., 2022; Hanz et al., 2022) and in other systems, where the organisms are constrained to the same resource space (Hiraiwa et al., 2017; Klopfer et al., 1961). However, when evaluated separately, the non-endemic natives showed the expected patterns, while endemic species presented the opposite trend. High levels of the functional evenness of non-endemic native species during early island stages seem to point to a strong dispersal filter acting on this biogeographic group. The effects of dispersal filtering on non-endemic native species are not surprising and expected, as the isolated nature of the islands here investigated, might constrain species with less dispersive traits from reaching these islands leading to similar traits among the colonizers (Whittaker et al., 1997). Dispersal filtering might be a stronger constraint on early stages islands, because on older islands, enough time has passed that even the less dispersive species would, eventually, have had a colonization opportunity (Carvajal-Endara et al., 2017). This is in contrast to Karadimou et al., 2015 who found stochastic processes to be a dominant force on young volcanic islands since they could not pin down one common assembly mechanism for the different communities studied. This divergence might be related to the different observational scales, as they studied much finer scales and previous research has shown scale-dependency of assembly mechanisms (Kraft et al., 2008; Silvertown et al., 2006).

The hump shape of functional dispersion of non-endemic natives coincides with the opposite trend of endemic species, indicating that when endemic species start to emerge, they also occupy the resources space of non-endemic natives, bringing down functional dispersion of non-endemic natives even when this groups' species richness continues to rise. More interestingly, functional dispersion of endemic species continues to increase until the late stages of islands, suggesting that trait space remains unsaturated and that there are unexploited ecological opportunities until, at least, very late stages of the island life cycle. Our findings of a lack of functional saturation align with other studies using similar periods, of tens of millions of years (Kraemer et al., 2022; Price et al., 2002) The opposite patterns of endemics and functional dispersion of non-endemic natives point to endemic species indeed adding novel traits to the trait space, and without endemic species, the fall of functional dispersion of all natives would be faster and steeper.

1.4.3 Moving beyond the GDM to understand functional diversity on oceanic islands

Species richness is a well-studied dimension of the biodiversity of island floras, and studies have shown the influence of island features, such as climate, environmental heterogeneity, age, area, isolation, and disturbance history (Barajas-Barbosa et al., 2020; Cardoso et al., 2010; Irl et al., 2015; Kreft et al., 2008; Weigelt et al., 2016; Weigelt & Kreft, 2013). However, our understanding of the drivers of insular functional diversity at the global scale is still limited (Ottaviani et al., 2020; Schrader, Wright, et al., 2021). Here, we found that functional diversity could not be well explained by environmental island features. Remarkably, we could only find significant drivers of functional diversity when investigating all species, indicating that non-endemic natives and endemics show contrasting patterns and complementary information about the drivers of the taxonomic and functional composition of island floras. We found that the functional dispersion of all natives increases with mean annual precipitation, which agrees with previous studies showing that more available resources increase the viability of different plant strategies (Schellenberger Costa et al., 2017; Zuo et al., 2021). Specifically, for our islands, higher precipitation rates can be associated with habitats such as rainforests, that harbor many different growth forms, leading to higher functional dispersion. Conversely, dryer islands might provide harsher environments and thus require a more specific set of functional traits, decreasing functional dispersion (Weiher et al., 1995). Finally, we found that the functional evenness of all natives increases with island elevation, following the trend of species richness, supporting our earlier findings that island floras have high functional redundancy, as species richness increases it fills the trait space without expanding it.

1.4.4 Limitations

We used four traits that provide information on plant form and function. Yet, it is likely that we are not capturing the diversity of plant strategies, and consequently the full range of functional diversity of islands' floras. Other traits such as leaf mass per area, stem-specific density, and dispersal syndrome may play a key role in species colonization and persistence capacity as well as how species interact with each other. Yet, due to low trait coverage, they were not included in the study. While we cover 74% of the island's floras (seed plants), the missing species as well as the contribution of other functionally distinct plants (e.g. ferns and mosses) – not considered in the current study – may lead to changes in our understanding of the island's functional trait space.

1.4.5 Conclusion

Our results indicate that island ontogeny has only a small effect on functional diversity, as only functional evenness follows the expected hump-shape trend of along island age. However, we attribute that similar trend between functional evenness and species richness, to oceanic island floras being functionally highly redundant. Although endemic species seem to add some novelty to the trait space, species mostly occupy similar resource space, and further ecological strategies remain unexploited. The continuous increase of functional dispersion of all native species, suggests that there is no saturation of the trait space. Moreover, our study adds to a growing body of literature on global functional island biogeography studies and consequently the underlying mechanism of the functional assembly of island floras. Future studies including additional traits that relate to other ecological aspects of species, as well as better trait coverage are needed to more accurately assess the generality of the GDM for other diversity facets.

2 Island area and historical geomorphological dynamics shape multifaceted diversity of barrier island floras

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Abstract

The influence of island dynamics and characteristics on taxonomic diversity, particularly species richness, are well studied. Yet, our knowledge on the influence of island dynamics and characteristics on other facets of diversity, namely functional and phylogenetic diversity, is limited, constraining our understanding of assembly processes on islands (e.g., biogeographic history, dispersal and environmental filtering, and species interactions). Using barrier islands, a highly dynamic and so far, understudied island type, we investigate how multiple facets of vascular plant diversity (functional, phylogenetic and taxonomic diversity) are shaped by island geomorphology, modern area and historic area, and habitat heterogeneity. In line with our expectation, historical dynamics in island geomorphology affected phylogenetic and taxonomic diversity via habitat heterogeneity. However, island area was the best predictor across all facets of diversity. Specifically, larger islands had higher functional and phylogenetic diversity than expected by chance while most of the smaller islands had lower diversity. The influence of area on functional diversity acted via habitat heterogeneity, with habitat heterogeneity influencing negatively functional diversity. Our results suggest that larger islands accumulate functionally and phylogenetically unique species. Further, results for functional diversity pointed towards potential area-heterogeneity trade-offs, with these trade-offs likely resulting from increased interspecific competition favoring a specific set of trait values (of stronger competitors), particularly on smaller islands. Together, these results demonstrate that going beyond taxonomic diversity contributes to identifying underlying processes shaping diversity-area relationships.

2.1 Introduction

In search of answers to complex ecological and biogeographical questions, scientists have long turned to islands as model systems (Warren et al., 2015) due to their comparatively small size, distinct spatial boundaries and their striking examples of evolutionary diversification (e.g. Mayr (1963) and Losos et al. (2010)). Island research has advanced our general understanding of evolutionary and ecological patterns and processes reaching far beyond islands, including the species-area relationship (Rosenzweig, 1995; Triantis et al., 2012), the role of immigration and extinction (MacArthur & Wilson, 1967) and adaptive radiation (Gillespie et al., 2002; Kisel et al., 2010). One of the most prominent outcomes of island research, the equilibrium theory of island biogeography (ETIB) by MacArthur et al. (1967), points to area and isolation as the major aspects influencing species richness on islands. However, test of ETIB found that other aspects such as climate (Kreft et al., 2008), environmental heterogeneity (Barajas-Barbosa et al., 2020), geodynamics and disturbance history (Fahrig et al., 1993; Weigelt et al., 2016) as well as island age (Whittaker et al., 2008) also greatly influences insular plant diversity.

Island area is probably the most well studied abiotic island feature and its relationship with species richness is well known as the species-area relationships (SAR), (Triantis et al., 2012; Turner & Tjørve, 2005). Beyond being influenced by factors such as spatial scale, sampling, minimum area effects and geographical location (Turner, Tjørve, & Hillebrand, 2005), the SAR also reflects underlying ecological processes, as higher habitat heterogeneity and increasing immigration and speciation rates (Connor et al., 2001; He et al., 2002). Habitat heterogeneity is, arguably, the most consistent factor influencing SAR, from local to global scale (Rosenzweig, 1995; Turner, Tjørve, & Hillebrand, 2005). However, the relationship between area and habitat heterogeneity is not always straightforward. When heterogeneity increases for a given area, the effective area available for species is reduced which in turn may lead to declines in population size (Allouche et al., 2012; Ben-Hur et al., 2020). However, such a hump-shaped relationship between species richness and habitat heterogeneity might not apply to island systems (Hortal et al., 2009). Despite extensive research, disentangling the effects of area and habitat heterogeneity on biodiversity remains an important task, and going beyond species taxonomic identity might shed light on how those two aspects are intertwined.

Although area and habitat heterogeneity are paramount for our understanding about island biodiversity, they do not capture island dynamics. Recent models in island biogeography highlight the importance of geo-environmental dynamics for key ecological processes like immigration, speciation and extinction and ultimately biodiversity dynamics on islands (Heaney, 2000; Whittaker et al., 2008). Such non-equilibrium models stress that island age and geological ontogeny affect the carrying capacity of islands through time (Whittaker et al., 2008). Island dynamics are present across a wide range of spatial-temporal scales, and range from tidal dynamics that shape island coastlines and coastal communities on a daily basis, wave action and sedimentation that change island area at the scale of decades and centuries (Ernstsen et al., 2006; Fitzgerald et al., 1984) as well as changes in climate and sea levels due to glacial cycles over tens of thousands of years (Weigelt et al., 2016) and geological dynamics over millions of years affecting species turnover, immigration and extinction rates (Whittaker et al., 2008). The effects of area, habitat heterogeneity and island dynamics on other biodiversity facets than species richness is poorly understood (Matthews et al., 2015; Matthews et al., 2020; Negoita et al., 2016). For a more mechanistic understanding of community assembly processes and how they influence biodiversity patterns at different scales (Leibold et al., 2018), we should consider the interrelationships between the three primary facets of biodiversity: taxonomic, functional, and phylogenetic diversity (Bauer et al., 2021; Latham et al., 1993; Swenson, 2011, 2014a). Functional diversity represents the variation in morphological, physiological and ecological traits that affect individual performance and fitness (Garnier et al., 2016), which in turn can help explain ecological strategies and assembly processes (Tilman, 2013). Studying traits variation related to species dispersal and resource acquisition strategies may unveil the main dispersal and environmental filters (de Bello, 2021; Kraft, Adler, et al., 2015). Phylogenetic diversity represents the phylogenetic relatedness among species in a community that can be used to investigate assembly processes and the role of species interactions (Faith, 1992; Webb et al., 2002).

Research on the influence of spatial features on functional and phylogenetic diversity has found highly context-dependent relationships. For instance, Mazel et al., (2014) and Jarzyna et al. (2018) showed that richness-based metrics of functional and phylogenetic diversity produce a similar pattern as taxonomic diversity. However, the functional diversity-area relationship (FDAR) has a lower saturation point (i.e. when functional diversity stops increasing with area and the FDAR curve stabilizes) than SAR, indicating functional redundancy, i.e. several species with similar trait values, while the number of species still increases. In contrast, Karadimou et al., (2016) did not find evidence of a saturation point of FDAR. Wang et al., (2013) found that FDAR as well as phylogenetic diversity-area relationship (PDAR) closely mirrored SAR, but FDAR and PDAR did show scale dependency, indicating competitive exclusion at small scales and habitat filtering at larger scales. Zhang et al., (2021) showed an area threshold requirement to maintain functional diversity of woody plants. Overall, there is still a knowledge gap when it comes to understanding the scale dependency of functional and phylogenetic diversity.

A large proportion of studies in island biogeography focuses on oceanic islands (e.g. islands of volcanic origin such as the Hawaiian and Canary Islands or Galápagos), but other island types with different ontogenies and geo-environmental dynamics can offer fresh perspectives in island biogeography (Ali, 2017). Barrier islands, for instance, have highly dynamic landscapes composed mainly of unconsolidated sediments (Davis, 1994a; Wang et al., 2015). These highly dynamic landscapes suffer from plant biomass destruction by stochastic disturbances in addition to large variation in resource availability over a short period of time; processes that may break established environment-plant-ecosystem relationships (Kleyer et al., 2014). Studies on rivers and wetlands found that neutral processes and dispersal limitation better explain species diversity in highly dynamic ecosystems than environmental filtering (Isabwe et al., 2019; Schöpke et al., 2019).

Barrier islands occur along about 15 percent of the world's coasts and are present on almost all continents (Davis, 1994a). Constant geomorphological activity caused by wind and water are changing barrier islands by destroying and renewing features across various temporal and spatial scales. While past geographical conditions and temporal changes in environmental conditions are increasingly recognized to greatly influence present plant diversity on oceanic islands (Warren et al., 2015; Weigelt et al., 2016; Whittaker et al., 2008), their role in determining plant diversity of barrier islands remains largely unexplored. Water-related mechanisms shaping barrier islands can be explained by inlet sediment bypassing, where sand is carried out from the beach by longshore drift and deposited at the upstream, as the inlet erodes the downstream causing the islands to move (Fitzgerald et al., 1984). Therefore, all barrier islands share 'head' and 'tail' as common elements (Oost et al., 2012). In the Frisian islands, this process happens mainly from west to east following the direction of the sea tides and strong wind; that way the western parts of the islands (representing the 'head') consist of older, more consolidated sediment, while the islands' 'tail' in the east are the younger parts of the islands, made up of newer sediments. The island tail mainly consists of salt-marshes and dunes and their extent vary widely from island to island (Groot et al., 2017). The West and East Frisian are much younger than most oceanic islands and thus lack in-situ diversification and endemic species (Niedringhaus et al., 2008).

Here, we investigate how different facets of plant diversity are affected by area (modern and historic), habitat heterogeneity and island geomorphological dynamics. The Frisian Islands are a particularly interesting model system to study the impact of island features on multifaceted diversity, because of their fast-changing geomorphology and constant environmental disturbances. They offer an opportunity to gain insights into patterns and drivers of biodiversity in a highly dynamic island system with geomorphological dynamics acting at the decadal to centennial time spans. The geomorphology of the Frisian islands causes them to grow by increasing the island's ‘tails ‘, where habitats are mainly salt marshes and dunes. Therefore, we expect that the increase in island area will not necessarily amount to the increase in habitat heterogeneity. Consequently, larger islands can have a larger number of species, but species will remain highly similar in their functional traits. We hypothesize that (1) habitat heterogeneity positively affects functional and phylogenetic diversity, and that it is a stronger predictor than area per se. Considering the constant disturbances naturally present in the barrier island system, we also hypothesize that (2) the temporal geomorphological dynamics negatively impact functional, phylogenetic and taxonomic diversity either directly or via changes in area and habitat heterogeneity.

2.2 Material and methods

2.2.1 Study site

The West and East Frisian Islands are located at the coastline of Germany and the Netherlands in the North Sea (53°02′05″N, 4°43′35″E–53°47′08″N, 8°00′20″E) (Figure 2.1). This chain of barrier islands comprises seventeen islands, all of which originated from sedimentation and erosion processes (Homeier et al., 2010; Streif, 1989) with the exception of Texel which got disconnected from the mainland in the 12th century by the “All Saints" flood (Eisma et al., 1980). The islands vary in size (

Table 2.1) and usually have an elongated shape, oriented parallel to the shore line; they are of similar age and similar distance from the shore (7 km on average). Most of the Frisian islands have formed approx. 7000 thousand years ago when large amounts of sand were accumulated along the seashores by tidal action creating dune ridges. Subsequently, plant colonization led to the stabilization of those dunes and the formation of salt marshes (Davis, 1994a; Streif, 1989).

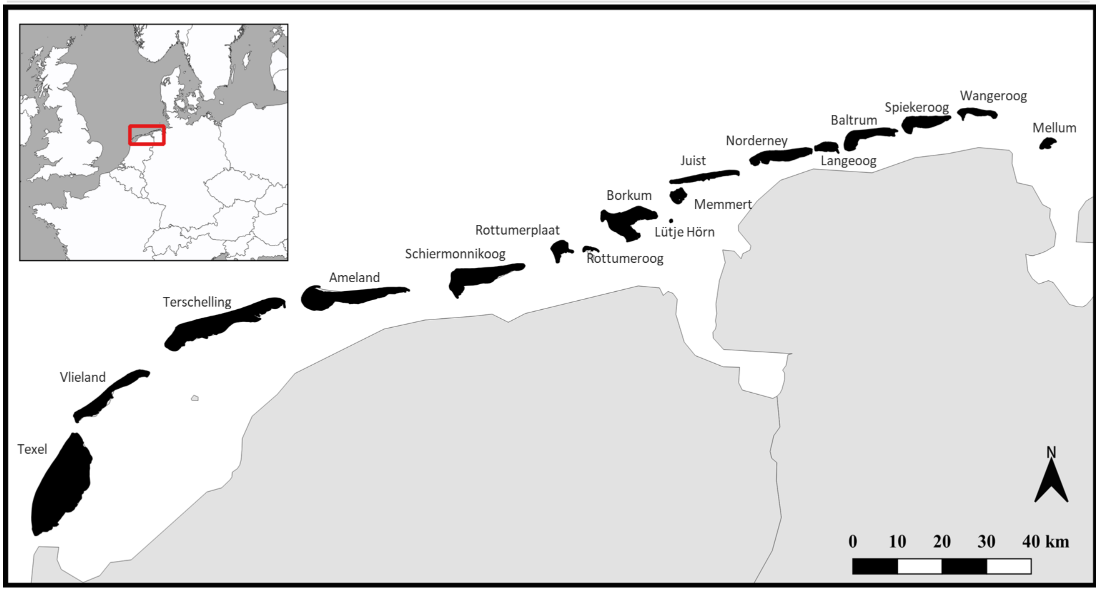

Figure 2.1 Map of the Study area showing the 17 West and East Frisian Islands located off the German and Dutch coastline in the North Sea.

2.2.2 Species distribution

We extracted species distributions of vascular plants for each island from two different sources: Niedringhaus et al. (2008) for the East Frisian Islands and the Nationale Databank Flora en Fauna, (2015) for the West Frisian Islands. The East Frisian comprised a group of ten islands with 1004 species, the West Frisian had a total of seven islands and 1368 species. We first standardized species' names according to The Plant List, (2010). Hybrids and infra-specific ranks were excluded. During name standardization, 69 species names were changed in the East Frisian dataset and 161 in the West Frisian dataset. Since all Frisian Islands are modified by human land use, we filtered out non-native species (Niedringhaus et al., 2008; Tamis et al., 2004) to best represent natural patterns. We then filtered out species known to only occur in human-dominated habitats as classified by Klotz et al. (2002) and Niedringhaus et al., (2008), assuming that even though native, these species would not be capable of colonizing the islands without human interference. From that we obtained a total of 938 species on East Frisian and West Frisian.

2.2.3 Functional traits and phylogenetic information

We selected four traits that represent different ecological strategies (Díaz et al., 2016) i) Maximum plant height (m), is connected to light interception and seed dispersal facilitation (Díaz et al., 2016; Moles et al., 2009); ii) Seed mass (mg) is linked to colonization capacity and seedling survival (Moles et al., 2004; Thompson et al., 1993; Wyse et al., 2021); iii) Leaf mass per area (g/cm^2) is related to carbon gain and leaf life span (Poorter et al., 2009; I. J. Wright et al., 2004); iv) Leaf area (mm^2) is linked to leaf energy production and water balance (Ackerly et al., 1998; Farquhar et al., 2002). We obtained trait data primarily from the LEDA Traitbase (Kleyer et al., 2008), as the trait data salt marshes and dunes were collected in the East Frisian islands and further complemented them with data from Minden et al., (2012), Minden et al., (2019). Further missing trait information was extracted from the GIFT (Weigelt et al., 2020) and TRY databases (Kattge et al., 2020). We standardized trait values to the same units of measurement and if species had more than one measurement for the same trait, we took the mean, except for maximum plant height where we took the 90th percentile, in order to preserve the highest values. We only considered species with data for at least three out of the four traits, reducing our data set to a total of 712 species. From the 712 species, 99% had available data for maximum plant height, seed mass, and leaf mass per area, while only 79% had data for leaf area. We imputed the remaining missing trait values using the missForest function in the missForest package (Stekhoven et al., 2012) which imputes missing values by repeatedly fitting a random forest (Breiman, 2001) on the observed part of each plant trait. It uses phylogenetic eigenvectors ($n = 1 - 30$) to reduce prediction error, by selecting the number of phylogenetic eigenvectors that had the minimum imputation error for each trait. For the phylogenetic information we used the Daphne phylogenetic tree by Durka et al., (2012).

2.2.4 Multifaceted diversity

Taxonomic diversity is defined by species richness of each island. We assessed functional diversity as functional richness, using the hypervolume approach proposed by Blonder (2018), which places each species of an island within a multidimensional trait space and quantifies functional richness as the total volume created by all species in the trait space. Hypervolumes rely on kernel density estimations based on the distributions of the observations which returns a volume in a multidimensional space accounting for holes, i.e. missing trait combinations. To make sure the hypervolume for each island was comparable among each other and to identify structuring axes that segregate species, we performed Principal Component Analysis (PCA) of the traits for the total species pool and used the first three axes of this PCA as our dimensions for the calculation of hypervolume and kernel bandwidth estimation, using Silverman's rule (Silverman, 1986). Kernel bandwidth and hypervolume were calculated using the functions estimate_bandwith and hypervolume from the R package hypervolume (Blonder et al., 2014).

To assess phylogenetic diversity, we used the richness-based metric Faith's Phylogenetic diversity (Faith, 1992), calculated by summing up the branch lengths of the species (Tucker et al., 2017). We calculated Faith's Phylogenetic diversity based on a matrix containing presence and absences of native species in each island and in our constructed tree using the function pd from the package picante (Kembel et al., 2010). Because functional and phylogenetic diversity systematically increase with species richness we standardized both values for effect size (SES). SES control for species richness by testing for significant deviation between observed and random communities. Therefore, SES can inform if functional and phylogenetic diversity are higher or lower than expected by chance for a given species richness. We ran 100 null models, reshuffling the species list of each island from the total species pool, and then calculated the standardized effect sizes (SES) for functional and phylogenetic diversity, using the formula as follows: SES = (Obs. value –Null mean)/ Null Standard Deviation; where "SES" is standardized diversity index; "Obs. Value" is the observed diversity index, while "Null mean" and "Null Standard Deviation" are the mean value and standard deviation of the null distribution of diversity index values generated for each island (Gotelli et al., 1996). SES values lower than zero indicate less diversity than expected by chance, given species richness, while positive values indicate higher diversity than expected. However, since SES usually leads to a normal distribution of data, significance starts at the 5% margin (above and below (-)1.96) (de Bello, 2021). Functional and phylogenetic diversity were highly correlated with taxonomic diversity (r = 0.77 and r= 0.97, respectively). Null model standardization reduced the correlation among functional and phylogenetic diversity with taxonomic diversity to r = 0.26 and r= 0.75, respectively (Appendix Figure S2.7)

2.2.5 Abiotic island features

We extracted habitat heterogeneity from raster files at 100 m resolution from the Ecosystem Types of Europe dataset (Weiss et al., 2018) (Appendix Figure S2.5) which maps 18 different habitats on the Frisian Islands. We excluded habitats classified as urban or anthropogenic (n = 6 habitats). Then, we calculated the effective number of habitats based on their area using the Hill number approach (Chao et al., 2014), with total number of habitats (Hill number q = 0), Shannon diversity (Hill number q = 1) more strongly weighting rare habitats, and Simpson diversity (Hill number q = 2) more strongly weighting common habitats. Patterns were consistent when including total number of habitats, Shannon or Simpson diversity; we thus focus on results for the effective number of habitats with q = 2 (Simpson diversity). We calculated the effective number of habitats for each island except Lütje Hörn for which no data were available regarding its habitat types. Island area was assessed in two different ways: First, modern island area (hereafter area) was quantified by summing the area of natural and semi-natural habitats occurring for each island. Second, historic area was based on the year 1700 for all islands except Rottumerplaat (with the oldest record from 1900). To assess temporal geomorphological dynamics, we followed the approach by (Scherber et al., 2018) using temporal area variation as a proxy for geomorphological dynamics. Temporal area variation serves as a proxy for the geomorphological dynamics of the islands because the changes in area are a consequence of the geomorphological processes of sedimentation and erosion caused by the tides and strong winds as well as big catastrophic events like floods and storms. We retrieved past island area from different points in time ranging from 1700 to 2008 (Appendix Figure S2.6) from georeferenced historical maps (Homeier et al., 2010; van Egmong, 2013) using QGIS (QGIS Development Team, 2020) and calculated the coefficient of variation (standard deviation divided by the mean) (Table 1).

2.2.6 Statistical analyses

Due to the lack of consensus on which model form provides the best fit to FDAR and PDAR, we fitted 12 different models and averaged them (Mazel et al., 2020). The models were weighted according to their AIC values and we further derived the average SAR, and standardized FDAR and PDAR. Using the R package "sars" (Matthews et al., 2019), we started with the 20 models available in the package and evaluated the model's normality of the residuals by Shapiro-Wilk tests and used Pearson correlation between squared residuals and area to test for homoscedasticity. The models that passed the tests were used for the final averaged diversity-area curves.

To assess the influence of island dynamics, area, and habitat heterogeneity on the diversity facets, we used piecewise structural equation models (SEM) using the approach proposed by Lefcheck, (2016). SEMs link multiple response and predictors variables in a single causal network, relying on pre-existing knowledge of the system to make educated hypotheses on the causal relationships between variables (Shipley, 2016). It allowed us to test a hypothetical causal model based on a priori knowledge related to the relationships between island dynamics, area, and habitat heterogeneity. We established two alternative SEM, one using area and another using historic area (Figure 2.2. A and B, respectively). For the SEM using area, direct paths between geomorphological dynamics and area, geomorphological dynamics and habitat heterogeneity, and island dynamics and diversity facets were included in the initial model. Alternative paths to the initial model between area and habitat heterogeneity as well as them and the biodiversity facets were added, if this improved the model fit (based on modification indices, p-value <0.05, Figure 2.2. A). For the SEM using historic area, direct paths between historic area and geomorphological dynamics, historic area and habitat heterogeneity, and historic area and diversity facets were included in the initial model. Alternative paths to the initial model between geomorphological dynamics and habitat heterogeneity as well as them and the biodiversity facets were added, if this improved the model fit (based on modification indices, p-value <0.05, Figure 2.2. B). Area (and historic area) and habitat heterogeneity were both log-transformed to fit normal distribution. Model fits were assessed using Fisher's C statistic based on the test of directed separation. Therefore, if the p-value of the test was > 0.05, we considered the data to fit the hypothetical causal network (Lefcheck, 2016). To calculate the piecewise SEM, we used the function psem from the piecewiseSEM package (Lefcheck, 2016). We also did a sensitive analysis on a data subset using two more traits, stem specific density to assess growth strategy and mechanical resistance (Díaz et al., 2016) and leaf nitrogen per leaf area, an indicator of the photosynthetic potential and herbivory resistance (Chapin, 1980; Díaz et al., 2004).

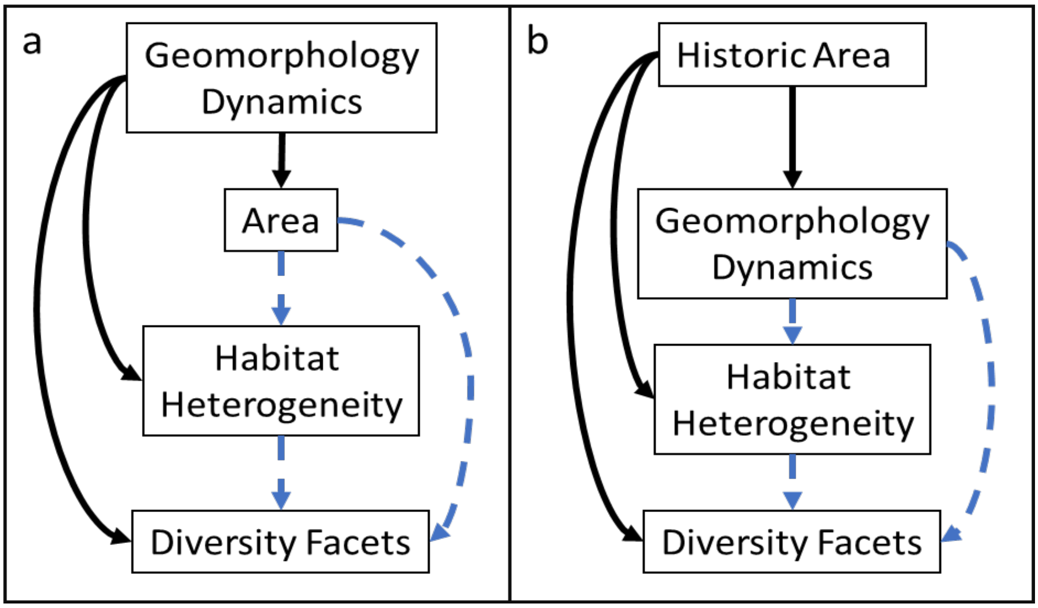

Figure 2.2 Conceptual figure of two alternative structure equation models on how modern and past island characteristics might affect different facets of insular plant diversity. Solid lines are the initial path added in the model while dotted blue lines were added in the model while dotted blue lines were added only if this improved the model fit (based on modification indices, p-value <0.05). In panel A, geomorphological dynamics are hypothesized to influence diversity facets directly or indirectly via area and/or habitat heterogeneity. Alternatively, in panel B, historic area is hypothesized to influence diversity facets directly or indirectly via geomorphological dynamics and/or habitat heterogeneity.

2.3 Results

PCA of species traits revealed two independent main components that together accounted for 68% of the variation in the four-dimensional trait space. Plant height and seed mass were mostly associated with PC1 (42.6%) while leaf traits contributed mostly to PC2 (24.8%) (Appendix Figure S2.8). Most species were short stature, had small seeds and relatively acquisitive leaf strategy, i.e. low leaf mass per area. Most of the islands showed underdispersion (negative values) for standardized functional diversity (hereafter FD.ses) and standardized phylogenetic diversity (hereafter PD.ses) (Table 2.1). Larger islands had FD.ses values close to zero, indicating randomness, or above it, indicating overdispersion of traits. Underdispersion in FD.ses was more pronounced in islands with area size below 30 km2. Texel, the largest island with the highest taxonomic diversity, had lower FD.ses than Terschelling and Ameland, that are considerably smaller and have less habitat heterogeneity. In the case of PD.ses, all islands showed values departing from the null expectations, however only three islands showed PD.ses values above zero (Texel, Vlieland and Ameland). Contrary to FD.ses, PD.ses does not show an area threshold, where the patterns change from underdispersion to overdispersion. The FDAR curve (Figure 2.3. A) showed a linear form, while he PDAR (Figure 2.3. B) curve mirrored the one of SAR (Figure 2.3. C).

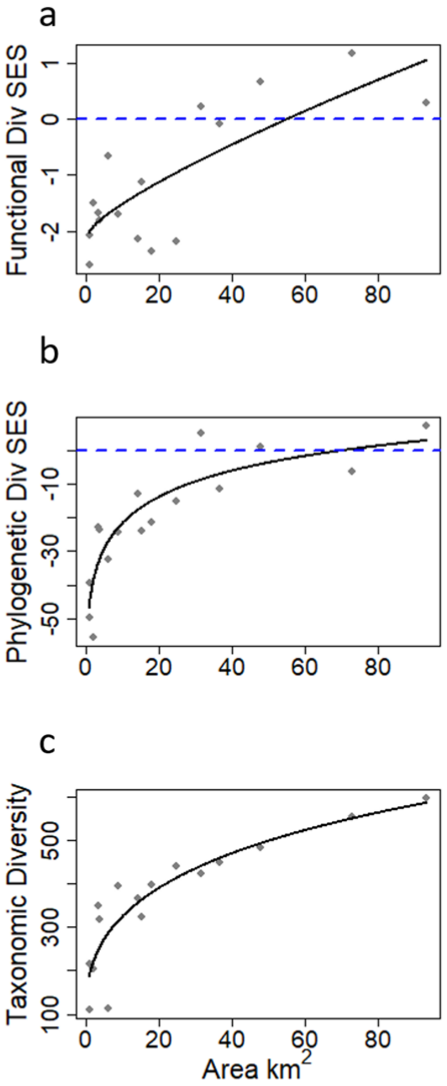

Figure 2.3 The three facets of diversity and their area relationship. Dashed blue lines on a) and b) mark the 0-point value. Where values below 0 indicate functional and phylogenetic diversity lower than expected by chance (underdispersion) and above 0 it indicates higher than expected by chance (overdispersion).

Table 2.1 Island names and their respective Geomorphological Dynamics defined by the coefficient of variation of island area between 1700 and 2008. Habitat Heterogeneity calculated as the Shannon index of different habitat area proportions. The total Area and Historic Area in km^2. Functional iv. shown as observed values and standardized as (SES). Phylogenetic Div. shown as observed (OBS) values and standardized (SES). Taxonomic Div. refers to the absolute number of species on each island. Note that Lütje Hörn does not have data for its habitats in the Ecosystems types of Europe database, hence a value of habitat heterogeneity is missing.

Island	**Island characteristics**				**Plant diversity**				
	Geomorphological Dynamics	**Habitat Heterogeneity**	**Area**	**Historic Area**	**Functional**		**Phylogenetic**		**Taxonomic**
					Obs.	**SES**	**Obs.**	**SES**	**Obs.**
Ameland	0.29	2.97	47.7	55.1	22.6	0.7	484	1.1	484
Baltrum	0.49	2.79	3.72	7.36	17.9	-1.8	317	-23.7	317
Borkum	0.27	4.15	24.83	19.04	19.1	-2.2	442	-15.2	442
Juist	0.17	3.3	8.83	11.7	19.4	-1.7	394	-24.3	394
Langeoog	0.33	5.17	14.18	9.83	18.7	-2.1	367	-13.1	367
Lütje Hörn	0.22	-	0.06	1.62	12.5	-0.7	44	-46.6	44
Mellum	0.43	1.37	2.11	2.78	17.2	-1.5	205	-55.6	205
Memmert	0.44	1	1.06	3.62	15.3	-2.6	217	-39.3	217
Norderney	0.33	4.4	18.06	11.98	18.2	-2.4	397	-21.4	397
Rottumeroog	0.59	1.14	1.06	8.57	13.3	-2.1	110	-49.7	110
Rottumerplaat	0.25	2.03	6.34	6.22	16.8	-0.7	114	-32.2	114
Schiermonnikoog	0.40	3.45	36.62	18.74	21.8	-0.1	449	-11.6	449
Spiekeroog	0.05	3.21	15.35	7.44	19.4	-1.1	323	-24.1	323
Terschelling	0.28	3.48	72.97	65.71	23.2	1.2	555	-6.2	555
Texel	0.35	2.75	92.97	99.13	22.4	0.3	597	7.1	597
Vlieland	0.23	3.72	31.59	59.35	22.1	0.2	424	5.2	424
Wangerooge	0.09	2.9	3.50	8.28	18.6	-1.7	351	-22.7	351

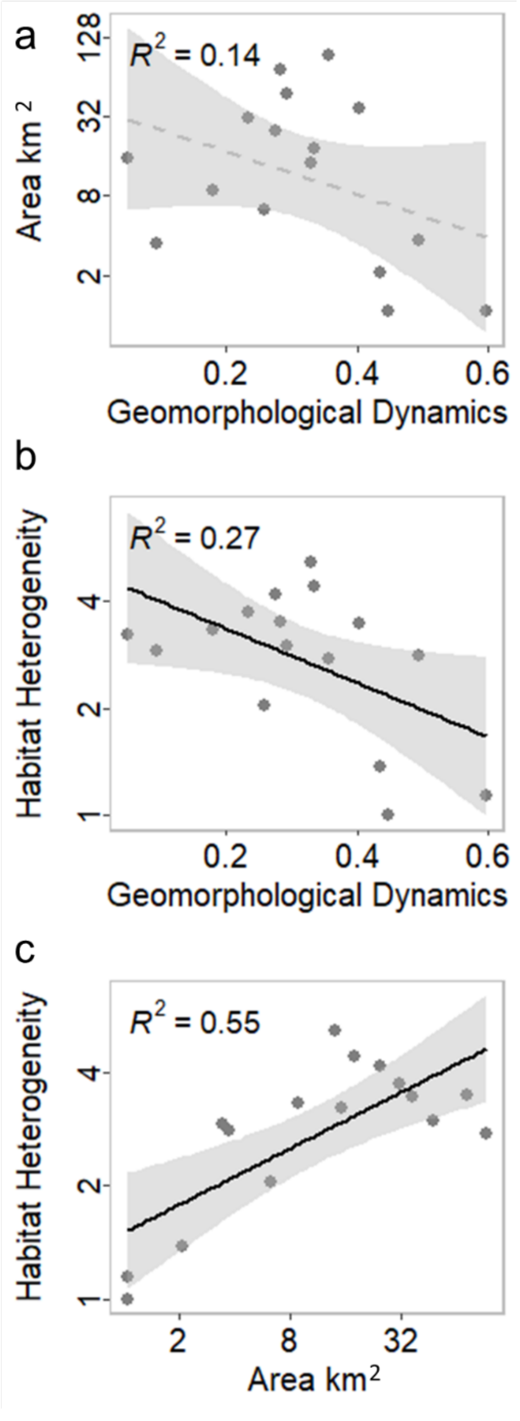

Figure 2.4 The three abiotic factors and their relationships. Solid lines indicate significant relationships (p< 0.05) and dashed lines show non-significant ones. Confidence intervals are shown as gray contours. When analyzed individually Geomorphological dynamics presented no significant relationship with area but a negative relationship with habitat heterogeneity.

Geomorphological dynamics measured as the coefficient of variation in island area varied from 0.05 to 0.59, Moreover, geomorphological dynamics were unrelated to island area with the whole range of values of geomorphological dynamics covered in smaller islands, (Figure 2.4 A). In contrast, geomorphological dynamics negatively influenced habitat heterogeneity, as islands with lower geomorphological dynamics presented higher habitat heterogeneity (Fig. 4 B). Further, larger islands were associated with higher habitat heterogeneity (Figure 2.4 C).

Additionally, linear models result showed that standardized FD.ses was neither influenced by habitat heterogeneity (Figure 2.5 A) nor by geomorphological dynamics (Figure 2.5 B), PD.ses was positively influenced by habitat heterogeneity (P<0.0001, r2= 0.51) (Figure 2.5 C) but not by geomorphological dynamics (Figure 2.5 D). Taxonomic diversity was positively influenced by habitat heterogeneity (P<0.0001, r2= 0.47) (Figure 2.5 E) but not by geomorphological dynamics (Figure 2.5 F).

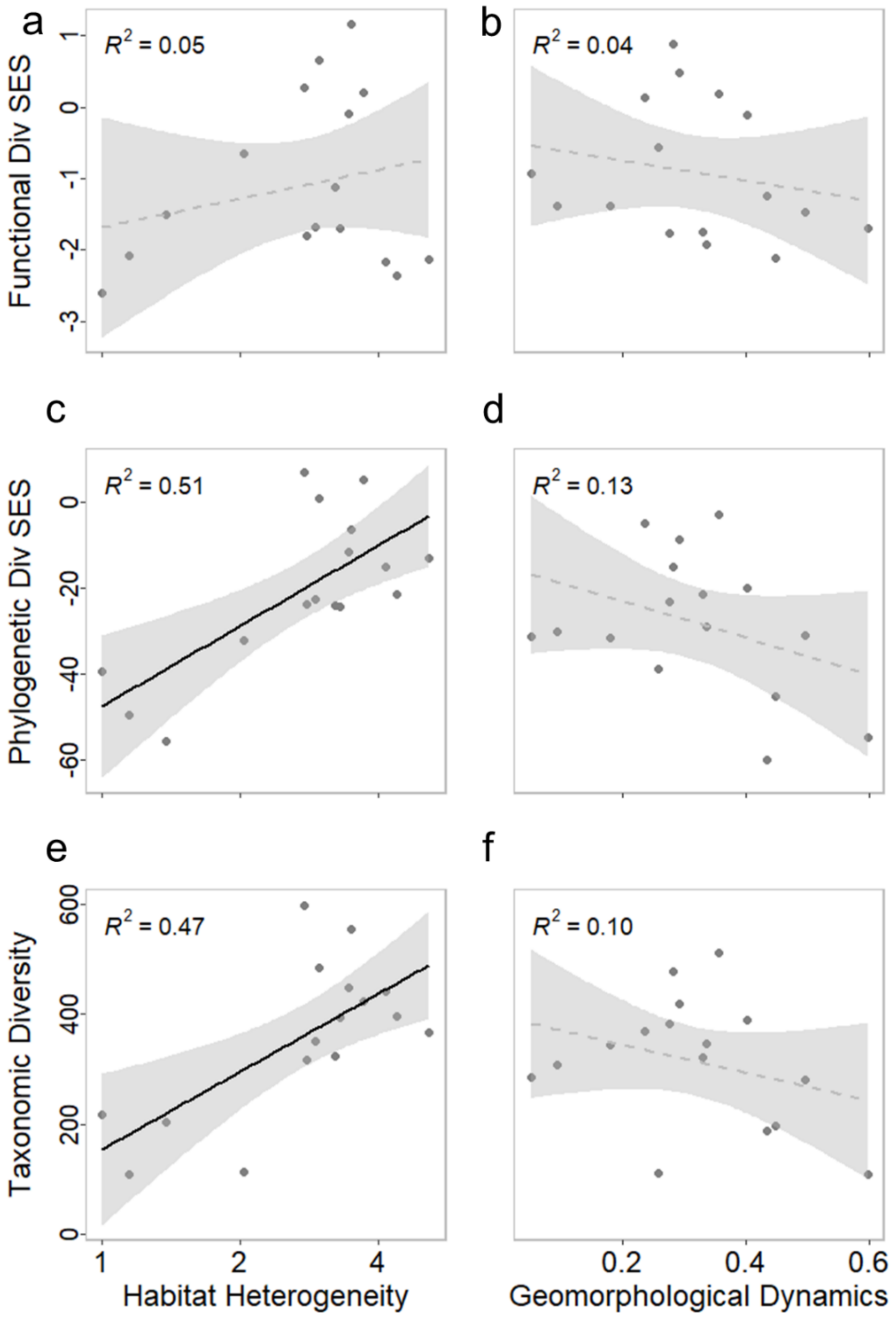

Figure 2.5 The three facets of diversity and their correlation with habitat heterogeneity and geomorphological dynamics. Solid lines indicate significant relationships ($p< 0.05$) and dashed lines show non-significant ones. Confidence intervals are shown as gray contours. When analyzed individually neither habitat heterogeneity nor geomorphological dynamics showed correlation with FD.ses (A, B). Habitat heterogeneity was positively correlated with PD.ses and taxonomic diversity (C,E) while geomorphological dynamics did not present any significant correlation with any of the diversity facets (D,F)

When analyzing the relationships by piecewise SEMs, area explained 74%, 80% and 78% of the variance for FD.ses, PD.ses and taxonomic diversity, respectively; with area driving the variation across diversity facets either directly (standardized effects = 1.2, 0.88 and 0.78 for FD.ses, PD.ses and taxonomic diversity, respectively) or via habitat heterogeneity (standardized effect via habitat heterogeneity = -0.47 for FD.ses, Figure 2.6 A). In other words, overall, larger islands had higher FD.ses, despite a negative effect of habitat heterogeneity on FD.ses. In addition, we found that geomorphological dynamics did not significantly affect - neither directly nor via area and habitat heterogeneity - any of the diversity facets. The model using historic area (Figure 2.6 B) explained 59%, 89% and 79% of the variance for FD.ses, PD.ses and taxonomic diversity. Historic area emerged as the main driver of all diversity facets (standardized effects = 0.77, 0.71 and 0.65 for FD.ses, PD.ses and taxonomic diversity, respectively). However, this model unveiled an indirect effect of geomorphological dynamics on phylogenetic and taxonomic diversity via habitat heterogeneity (standardized effect via habitat heterogeneity = -0.16 for PD.ses and taxonomic diversity). In contrast, no significant relationship between historic area and habitat heterogeneity was found.

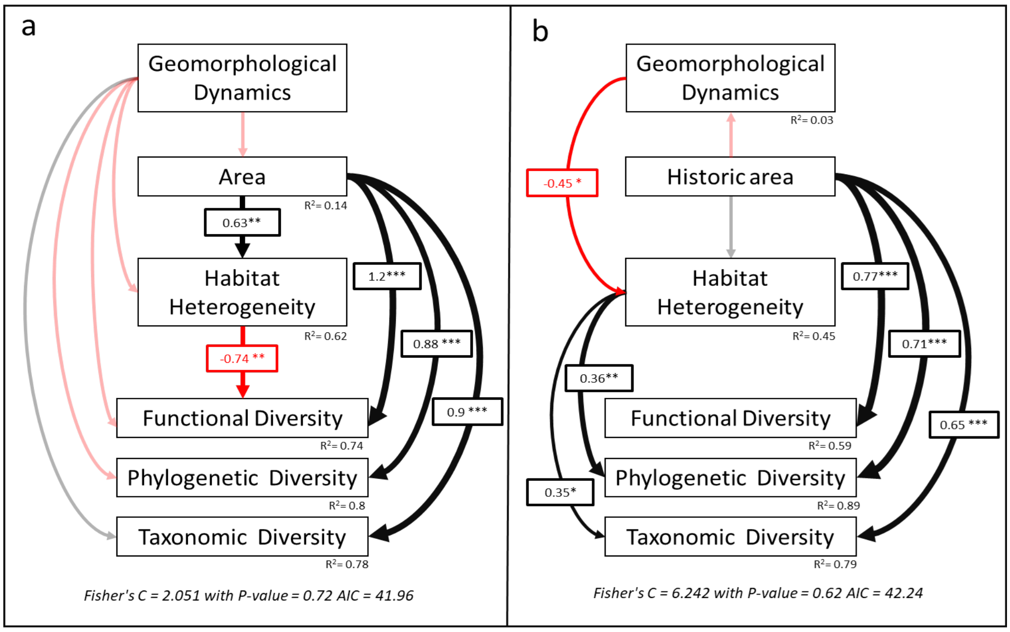

Figure 2.6 Piecewise structure equation models with black arrows denote positive relationships, and red arrows negative ones. Arrows for non-significant paths (P ≥ 005) are semi-transparent and stars represent level of significance: 0 '***' 0.001 '**' 0.01 '*' 0.05. The thickness of the significant paths has been scaled based on the magnitude of the standardized regression coefficient Model A quantifies modern island area as the sum of all natural and semi-natural habitats on each island, while model B uses historic area from the baseline year 1700 (with the exception of Rottumerplaat island which is from 1900).

2.4 Discussion

The West and East Frisian Islands are a comparatively young and highly dynamic island system. They are characterized by a large range of island sizes and different degrees of habitat diversity. Typical geomorphological dynamics of a barrier island system puts island plant communities under constant disturbances, such as storm surges, tidal floods and erosion and sedimentation caused by wind and water action. Yet, our results revealed that while geomorphological dynamics did play a role shaping multifaceted diversity via influencing habitat heterogeneity, area was the most important driver of all three facets of diversity. Area was also closely related to habitat heterogeneity, showing that they are both relevant and not independent of each other. Most islands showed lower FD.ses and PD.ses than expected by chance (underdispersed) but the few islands larger than 30 km^2 showed closer to random or higher than expected (overdispersed) patterns for FD.ses. Even though we accounted for differences in species richness, FD.ses and PD.ses showed a strong relationship with area, suggesting that functionally and phylogenetically unique species are accumulating on larger islands. The influence of area via habitat heterogeneity, while weaker, was significant, with an unexpected negative effect on FD.ses.

Functional underdispersion occurred on islands smaller than 30 km2, while functional diversity increased on larger islands. On the one hand, functional underdispersion is commonly attributed to environmental filtering (Mazel & Thuiller, 2020). The Frisian islands are constantly exposed to disturbances caused by wave and wind action, as well as storm surges, which are even more pronounced on smaller islands due their lack of taller dunes and more consolidated sediment. Therefore, the harsh environment of these islands may narrow the range in suitable trait values. On the other hand, competitive exclusion can also lead to underdispersion, depending on the trait being analyzed (Kraft, Godoy, & Levine, 2015; Mayfield et al., 2010). Yet, disentangling abiotic from biotic filtering processes based solely on FD.ses patterns is an intricate task or even impossible (Mazel & Thuiller, 2020).

The indication that plants on the Frisian islands are functionally highly similar is further supported by PD.ses, which also shows underdispersion for most of the islands. Given that the description of a functional role might involve an unknown combination of traits, functional diversity has been used as proxy of functional diversity (Cadotte et al., 2009; Cavender-Bares et al., 2009; Prinzing et al., 2001), based on the assumption that phylogenetically closer species are functionally more similar due to phylogenetic trait conservatism.

The shape of FDAR and PDAR curves are in line with previous studies that showed generally underdispersion, which decreases as area increases (Carvajal-Endara et al., 2017; A. B. Smith et al., 2013; Zhang et al., 2021). In our study, the difference between the shape of FDAR and SAR curves can be explained by the influence that underlying functional data have on FDAR. Underdispersed functional diversity causes FDAR curves to depart from SAR curves, instead of mirroring it (Mazel & Thuiller, 2020). As FD.ses scales with area, islands larger than 30 km2 turn from underdispersed to overdispersed or random, which is a pattern that could be influenced by anthropogenic activities. Larger islands with bigger populations are more subject to human modifications (e.g. fixation of dunes, grazing) which interfere with the natural habitats (e.g. dunes and salt marshes). These interferences can artificially create opportunities for new species to come in, which will potentially increase the range of trait values that are represented. Additionally, some species require a minimum area for maintaining viable populations and are filtered out on smaller islands (Zhang et al., 2021). The similarity in the shape of the PDAR and SAR curves can be attributed to the high correlation between PD.ses and taxonomic diversity; this correlation shows that the increase in number of species comes from species of different families (and different traits), reflecting the habitat heterogeneity correlation with PD.ses. This relationship, however, disappears or becomes weaker once we take area (or historic area) into consideration in the SEMs, as PD.ses is greatly influenced by area (or historic area). The influence of area on FD.ses via negative effects of habitat heterogeneity on FD.ses is unexpected and differs from other diversity facets. This unexpected relationship may emerge because, high habitat heterogeneity in a limited space, such as on the islands of Baltrum, Norderney and Langeoog, causes a reduction in the amount of effective area available per habitat, also known as area-heterogeneity trade-off (Allouche et al., 2012). This could lead to (1) stochastic extinctions or (2) increased competition pressure favoring a specific set of traits of stronger competitors, reducing trait variation. The area-heterogeneity trade-off diminishes as island area grows or habitat heterogeneity declines, like on Texel and Terschelling and Ameland, which will in turn increase FD.ses. However, this effect was no longer present in the SEM using historic area. This can be explained by historic area being not directly correlated with habitat heterogeneity, which in turn diminishes the influence of habitat heterogeneity on FD.ses. Additionally, this difference among the SEMs could also be influenced by how we measured area, excluding urban habitats, while historic area accounts for the complete island. The contrast between the two SEMs also highlights how area and habitat heterogeneity are intertwined, which makes it notoriously challenging to disentangle their relative effects on diversity (Hortal et al., 2009).

Despite area being the best predictor of habitat heterogeneity and multifaceted diversity, linear models and the SEM using historic area highlight the underlying role of geomorphological dynamics influencing habitat heterogeneity and subsequently, PD.ses and taxonomic diversity. A higher degree of geomorphological dynamics and repeated disturbances makes it more difficult for some habitats to be formed and maintained. This includes habitats such as high marshes and gray dunes, which provide a less disturbed environment and harbor higher number of species (Leuschner et al., 2018). One possible explanation for the absence, weak or inconsistent effects of geomorphological dynamics on multifaceted diversity is that in highly dynamic systems, such as barrier islands, geomorphological dynamics affect island plants on smaller time scales. For instance, processes including daily tide changes and seasonal storms may influence island composition, making it hard for the long-term metrics to capture the influence of geomorphology dynamics on plant diversity. Alternatively, one may argue that since the geomorphological dynamics of the islands have a direct impact on the abundance of species on the islands (e.g. by breaking monospecies communities of mature saltmarshes (Dijkema & Wolff, 2010)), the diversity metrics we used, which are richness based, might been unable to fully capture the variations caused by the long-term geomorphological dynamics of the Frisian islands.

Our results on the influence of islands characteristics (geomorphological dynamics, area and habitat heterogeneity) on taxonomic diversity of plants contrast with those found by Scherber et al., (2018), which in a study on the East Frisian islands found that habitat heterogeneity and geomorphological dynamics were the best predictors to plant taxonomic diversity. This difference might at least partly arise from differences in the underlying data and statistical approach used. For instance, our study considered seven additional islands in the Western part (on top of the ten East Frisian islands) which increased the range of island area size as the West Frisian islands are considerably larger than the East Frisian ones. Furthermore, our study could greatly benefit from data on species abundances, which would make it possible to better assess the impact of the geomorphological dynamics and abundance weighted measure of functional and phylogenetic diversity. Another caveat is the assumption that habitats are independent entities, which most of the cases is not met, since different habitats often share the same species. Therefore, if the proportion of shared species by habitat is not included, habitat heterogeneity may fall short to capture the real heterogeneity.

Finally, our study adds to a growing body of literature on the scale dependency of functional and phylogenetic diversity. Our results also demonstrate that looking at multifaceted diversity can yield relevant information on the drivers and underlying mechanisms of insular plant diversity. Our research also contributes to the general understanding of island dynamics and their temporal scale. Using barrier islands as a study system, we show that for this highly dynamic system, although historical dynamics in island geomorphology influence plant diversity, area is still the strongest driver.

3 Functional diversity and trait changes along maturity gradients in coastal habitats

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Abstract:

Understanding the mechanisms of community assembly and maintenance of biodiversity in dynamic ecosystems is crucial, but the context-dependency nature of habitat maturation changes makes it difficult for ecologists to develop a comprehensive theory on its occurrences. To better understand these processes, it's important to go beyond species' taxonomic identity and also consider their functional traits. Here, we investigate changes in functional and taxonomic diversity, and of community-weighted mean of trait (plant height, specific leaf area, leaf dry matter content, seed mass, seed buoyancy, and salt tolerance) across different stages of habitat maturity. We investigate three coastal habitat types (dunes, dune slacks, and salt marshes) that share similar geomorphological dynamics. We found that both taxonomic and functional diversity followed the same directional but functional diversity remains relatively similar within each habitat, while taxonomic diversity shows significant changes. We found a consistent increase in plant height and leaf dry matter content, as habitats become more mature, indicating a shift towards a higher competitive ability and more conservative ecological strategy as habitats mature. Our results suggest that the links between plant diversity, disturbance, and competition are complex and do not always follow a predictable pattern. This could be due to stochastic processes excerpting stronger influence on community assembly. Our results highlight the importance of using both taxonomic and functional diversity in understanding the dynamics of plant communities, as they provide complementary information.

3.1 Introduction

Worldwide, the composition and diversity of ecological communities are increasingly affected by environmental changes, either because of direct or indirect human impact (Loreau et al., 2001). Therefore, there is an urgent need to better understand the mechanisms shaping community assembly and maintaining biodiversity, particularly in highly dynamic natural ecosystems undergoing changes in species composition over time. Understanding the mechanisms of community assembly might be challenging, as it is hard to disentangle the contribution of deterministic and neutral processes.

Niche theory assumes that community composition is deterministic and results from environmental and biotic filtering (e.g. environmental conditions, inter-specific competition, mutualistic and trophic interactions, Tokeshi, 1990). In contrast, the neutral theory expects community composition to result from demographic and stochastic processes (Hubbell, 2000). Niche theory predicts that strong environmental filtering generates ecological similarity in community composition. However, ecological communities under strong biotic filtering might yield different outcomes, either promoting the distinctiveness of communities through limiting similarity or their homogenization in case of competitive hierarchy, where stronger competitors become more dominant (Kraft, Adler, et al., 2015; Mayfield et al., 2010). For example, theory predicts that environmental filtering is the dominant driver in the early stages of habitat maturation and, as maturation proceeds, biotic filtering becomes a more important force (Connell et al., 1977).

However, changes in species composition over time are likely shaped by a combination of both, niche and neutral processes. Furthermore, species composition changes in habitat maturation are highly site-dependent, making it harder for ecologists to develop a general and unifying theory on how these changes work (Glenn-Lewin et al., 1992). To unveil the mechanisms underlying habitat maturation and their context-dependency, there is the need of going beyond species' taxonomical identity and incorporating species' functional traits. Functional traits are morphological and physiological features that affect species' performance and fitness (Garnier et al., 2016; Violle et al., 2007). Functional traits can help reveal ecological strategies and assembly processes (Tilman, 2013) and have also been successfully applied to shed light on processes underpinning habitat maturation (Chun et al., 2019; Purschke et al., 2013). Furthermore, functional traits provide the grounds to compare different vegetation types and communities composed of different species. For instance, understanding the role of species' functional traits in habitat maturation is key when studying highly dynamic ecosystems, such as coastal vegetation, where disturbance levels are constantly high due to wave action, strong winds, and erosion (Corenblit et al., 2015; Minden et al., 2012).

In highly dynamic ecosystems, environmental filtering is generally considered the main driver of biodiversity (Chase, 2007; Lepori et al., 2009). However, concerning functional traits, environmental filtering is more likely to strongly influence traits related to tolerance as opposed to traits related to dispersal (*sensu* Bauer et al. 2021). Additionally, the environment, and subsequently, the strength of environmental filtering might also be modified by functional traits and species interactions, due to processes such as biogenic niche construction (Bauer et al., 2021; Jones et al., 1994). Coastal plant communities are considered as good examples of how this feedback between plant traits and the environment modifies the landscape, as they are crucial to the formation and development of different habitats, which follow contrasting maturity stages such as dunes, dune slacks, and salt marshes (Doing, 1982). The formation process of dunes and salt marshes are typical forms of biogeomorphic ecosystems that are dominated by biota that strongly influence geomorphology (Groot et al., 2017).

Early stages of habitat maturation are expected to harbor species that have similar trait values, which optimize their fitness for places exposed to high levels of stress and disturbance such as high salinity, frequent inundation, and strong winds (Corenblit et al., 2015). As more species are established and modify the initial habitat, other species are able to establish themselves and as habitats mature. Trait values change and species are no longer subjected to the harshness of early-stage habitat maturation and need to optimize resource acquisition as competition increases. As a result, mature habitats would mainly harbor species with similarly competitive trait values. However, to what extent these trait changes with habitat maturity are consistent across habitats remains uncertain.

Barrier islands are coastal islands composed mainly of unconsolidated sediments (Davis, 1994b; Wang et al., 2015) and arbor coastal vegetation that is made up mostly of ecosystems influenced by biogeomorphic processes, specifically dunes and salt marshes (Groot et al., 2017). In the East Frisian islands, the biogeomorphic habitat maturation starts with bare strand lines when the first pioneer species establish themselves and start forming salt marshes or green dunes or dune slacks. With the facilitation of the established plants, more species will be able to colonize these habitats, until stronger competitors dominate those habitats (Groot et al., 2017). However, the East Frisian islands are often exposed to strong wave action and winds and are occasionally hit by storms (Oost et al., 2012), making them highly dynamic landscapes. Barrier islands undergo processes, such as plant biomass loss and spatial-temporal variations in resource availability, that can disrupt established environment-plant-ecosystem relationships in relatively short periods of time (Kleyer et al., 2014). Additionally, the East Frisian islands are subject to anthropogenic pressure. Starting already 5000 years ago with livestock farming and the construction of small mounds, by early settlers. More recently, the pressure from livestock farming has been reduced but new ones have been added, such as dyke constructions and dune stabilization (Reise, 2013).

Here, we study taxonomic and functional diversity, calculated using multiple traits, as well as changes in individual traits throughout habitat maturation. We build on the model of biogeomorphic succession proposed by Corenblit (2015) and hypothesize that functional diversity will be highest in intermediate stages of habitat maturity, where disturbance is no longer the dominant force and competition is not yet at its highest, enabling different ecological strategies to coexist (Fig. 1a).

To test this hypothesis, we use 427 vegetation plots located on 11 East Frisian Islands, which comprise three different habitats (i.e., dunes, dune slacks, and salt marshes), and establish links between the vegetation data and species-specific traits. We use six traits that are fundamentally linked to species dispersal and establishment capabilities as well as species fitness to highly dynamic environments such as the East Frisian Islands; specific leaf area, to inform on the speed of acquisition of carbon gain and leaf life span (Poorter et al., 2009; I. J. Wright et al., 2004), leaf dry matter content as a measure of leaf abrasion resistance (Onoda et al., 2011; Tan et al., 2021), maximum plant height to assess light interception and seed dispersal distance (Garnier et al., 2016; Moles et al., 2009; Westoby et al., 2002) seed buoyancy to account for dispersal capacity in flooded environments (Moles et al., 2004; Thompson et al., 1993; Wyse et al., 2021), seed mass reflecting dispersal capacity and seedling survival (Moles et al., 2004) and species salt tolerance.

Moreover, we hypothesize that species traits will follow similar patterns of change across all habitat types, as species strategies change from investing more in tolerance related traits to investing in resource acquisition traits. Specific leaf area and plant height will increase with habitat maturity, as the need to optimize resource acquisition increases with the competition; leaf dry matter content will decrease over habitat maturity as the exposition of plants to strong winds and sand abrasion diminishes the more mature habitats are; seed buoyancy will also decrease as habitat matures, given that mature habitat are less exposed to floods diminishing the dependence of water for seed dispersal; seed mass is expected increase with habitat maturity, following an allometric relationship with plant height and higher investment in seedling survival; salt tolerance will become less prevalent as habitat matures and become less exposed to floods (Figure 3.1).

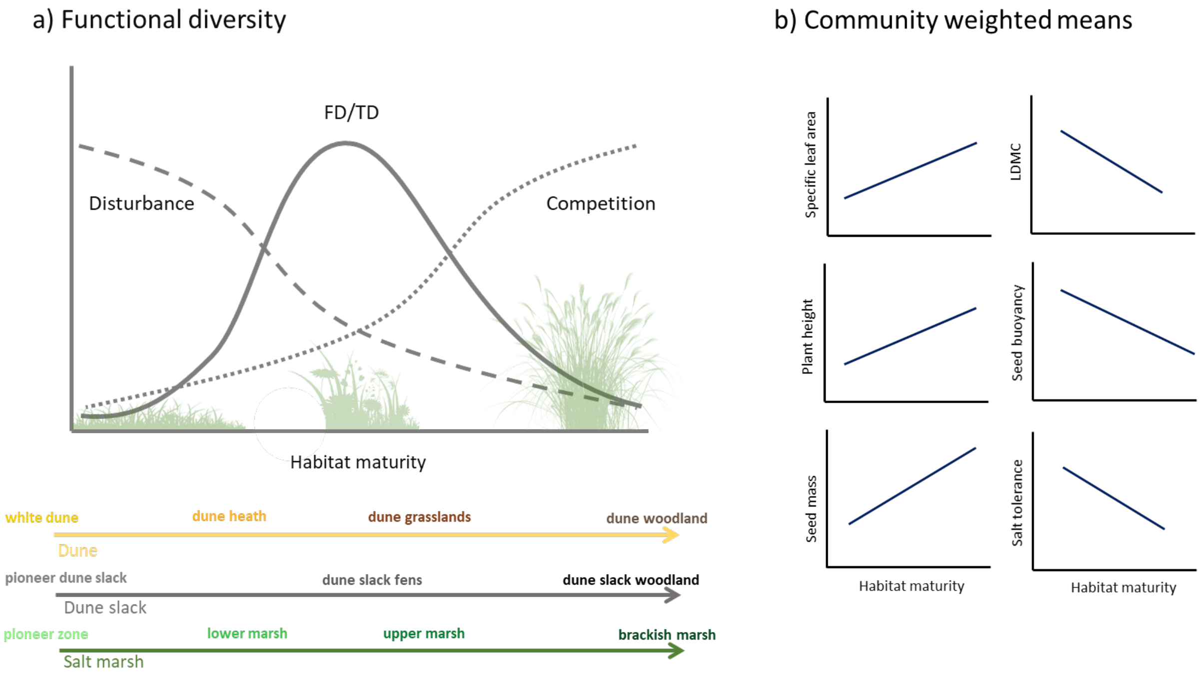

Figure 3.1. Conceptual figure of habitat maturity gradient across three different habitats of the East Frisian islands (a) and expected changes in community weighted means of traits over habitat maturation (b). (a) Early stages of habitat maturation are expected to have the lowest levels of taxonomic (TD) and functional (FD) diversity, as the high levels of disturbance would only allow or few pioneer species with similar trait values to establish. With the facilitation of the established plants, more species will be able to colonize these habitats, increasing TD and FD until stronger competitors completely dominate those habitats and diversity levels decrease again. (b) Specific leaf area and height increase to optimize resource acquisition, as competition increases. Seed mass increases with habitat maturity, following the allometric relationship with plant height higher investment in seedling survival. Leaf dry matter content decreases with wind and sand abrasion in mature habitats. Seed buoyancy and salt tolerance decrease as exposure to floods decrease in mature habitats.

3.2 Methodology

3.2.1 Study site

The East Frisian Islands are located at the coastline of Germany in the North Sea (53°02′05″N, 4°43′35″E – 53°47′08″N, 8°00′20″E) (Fig. 2). These barrier islands usually have an elongated shape, broadly oriented parallel to the shoreline and are shaped by an inlet sediment bypassing process. This process consists of sand being carried out from the beach by longshore drifts and deposited at the upstream side of the inlet, as the tides erode the downstream side, moving the islands as time passes (Fitzgerald et al., 1984). Therefore, all barrier islands share ‘head’ and ‘tail’ as common elements (Oost et al., 2012). The 'head' consist of older, more consolidated sediment, while the island's 'tail' is the younger part of the island, made up of newer sediments. Specifically, in the East Frisian Islands, this process happens eastwards along with the direction of the sea tides and strong wind. The East Frisians have formed approximately 7000 years ago when large amounts of sand were accumulated along the seashores by tidal action creating dune ridges, which were subsequently colonized by plants, leading to the stabilization of those dunes and the formation of salt marshes (Davis, 1994b; Streif, 1989). They are located within the Lower Saxon Wadden Sea National Park, which is part of the trilateral Wadden Sea cooperation conservation plan, a joint effort of Denmark, Germany, and the Netherlands to protect the Wadden Sea islands. The National Park authorities maintain georeferenced long-term monitoring plots on all East Frisian islands across different habitat types and stages of habitat maturation (Figure 3.2).

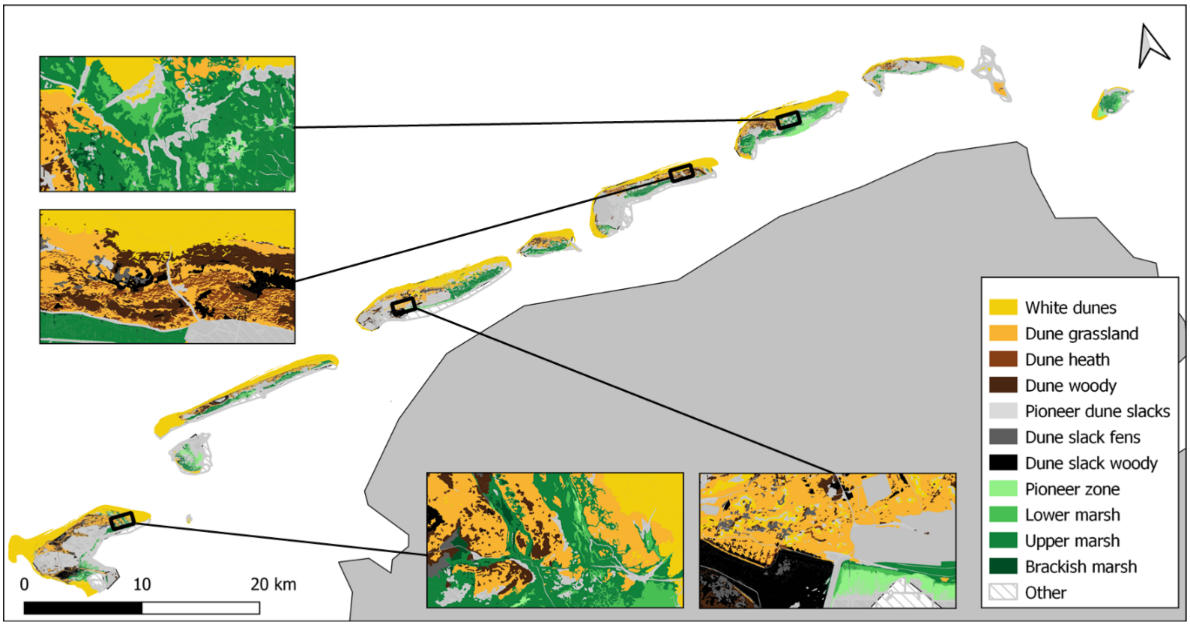

Figure 3.2. Study site map showing the East Frisian Islands off the coast of Germany. Overview maps show the geographical distribution of different stages of maturity of Dunes: white dunes, dune grasslands, dune heaths, and dune woody; Dune slacks: pioneer dune slacks, dune slack fens, and dune slack woody; Salt marshes: pioneer zone, lower marsh, upper marsh, and brackish marsh.

3.2.2 Species and habitat data

The monitoring data were provided by the Wadden Sea National Park authorities from which we extracted the species recorded in plots, their proportional cover, and the year of measurement as well as the habitat classification of the plots and their total vegetation cover. We kept only data that were sampled after 1990, as the data prior to that year was poorly distributed across the islands and often lacked georeferenced coordinates. We further removed all remaining plots with no geographical coordinates, leaving a total of 427 plots. We then standardized the species names according to the World Flora Online (Kindt, 2020). After standardization, we crossed species names with a local species checklist (Niedringhaus et al., 2008) and with FloraWeb (BfN, 2021). Species that were not found in one of those two sources were classified as misidentified and removed from the data set. Only vascular species were kept, subspecies and variations were treated at the species level, and hybrids were removed from the data set. After removing the species and plots according to the described criteria, we rescaled species coverage percentages so that all the plots would have a maximum sum up of 100%. We applied the Trilateral Monitoring and Assessment Program (TMAP) typology of coastal vegetation (Petersen et al., 2014) classification to our plots, and after excluding habitats classified as urban areas and farming, we retained three different habitats: dunes, dune slacks, and salt marshes. Within each of these habitats, their sub-classifications can be used as a proxy for different maturity stages as shown in Figures 3.1 and 3.2. Dunes were sub-classified into white dune, dune heath, dune grasslands, and dune woodland. Dune slack was divided into pioneer dune slack, dune slack ferns, and dune slack woodland. Salt marshes were further sub-classified as pioneer zone, lower marsh, upper marsh, and brackish marsh.

3.2.3 Functional traits data & Diversity indexes

We obtained most traits from published data that were collected in the East Frisian islands, where trait measurements were done for 6 – 10 individuals of each species, and trait data of individuals were averaged at the species level (Kleyer et al., 2019; Minden et al., 2012; Minden et al., 2015). We further complemented the data set with trait data from the LEDA trait database (Kleyer et al., 2008), as the trait data for species occurring on salt marshes and dunes were collected on the East Frisian islands. Further missing trait information was extracted from the GIFT (Weigelt et al., 2020) and TRY databases (Kattge et al., 2020). We standardized all trait measurements to the same units of measurement and if species had more than one measurement for the same trait, we took the mean, except for maximum plant height where we took the 90th percentile, to preserve the highest values. We had data for 100% of the species for maximum plant height (meters), 99% for seed mass (milligrams), 84% for seed buoyancy (percentage of floating seed after a certain time period), 83% for specific leaf area (millimeter per milligram), 77% for salt tolerance (yes or no) and 73% for leaf dry matter content (milligram per gram). We filled trait information gaps, by imputing the missing values using the "*missForest"* function in the missForest package (Stekhoven et al., 2012). It imputes missing values by repeatedly fitting a random forest (Breiman, 2001) on the observed data and predicting the missing values. To reduce prediction errors, it used phylogenetic eigenvectors (n = 1–30), by selecting the number of phylogenetic eigenvectors that had the minimum imputation error for each trait. For the phylogenetic information, we used the Daphne phylogeny by Durka et al. (2012).

For each trait we calculated community-weighted means per plot and estimated functional and taxonomic diversity using the framework proposed by Chiu & Chao (2014), using the R package 'hillR' (Li, 2018). This framework treats the pairwise trait distance as the functional entity, therefore all entities are functionally different (Chiu et al., 2014). We then calculated the effective number of functional and taxonomical irrespective of species or functional groups coverage (Hill number q= 0, Richness) or weighted by coverage of common (Hill number q= 1, i.e. Shannon diversity) or abundant species or functional groups (Hill number q= 2, i.e. Simpson diversity). Functional and taxonomic diversity using q = 1 and 2, showed similar values and the same patterns of variation over habitat maturation for all habitats, while diversity calculations using q= 0 showed distinct patterns. Thus, here we focus on diversity values using hill numbers zero and two, and results using hill number one can be found in (Appendix Figure S3.16).

3.2.4 Statistical analysis

For plots that were sampled multiple times in different years, we tested if there was a significant variation in functional diversity per plot over time by fitting a linear mixed effect model where functional diversity was the dependent variable, the year of sampling was the fixed effect and the plot a random effect. As no significant variation was found (*p*-value = 0.26) we took the average of the community-weighted means and diversity indexes of the same ID plots and used the averaged result in the subsequent analysis. We tested if community-weighted means (hereafter CWM) per trait and plot varied among the different stages of habitat maturation by performing an analysis of variance, ANOVA, with CWM as a function of maturity stage. We then used Tukey's honest significant differences post hoc tests to assess significant differences among the groups.

We applied ANOVAs variance and Tukey's test for each habitat separately. To assess variations in traits, functional and taxonomic diversity across different habitats, at various stages of maturity, we conducted an ANOVA and Tukey's test, using diversity indexes as a function of maturity stages.

3.3 Results

Functional and taxonomic diversity ($q = 0$) showed similar patterns of variation over habitat maturation gradient (Figure 3.3, A, B). Within dunes, both diversities were higher in dune grasslands and significantly lower in dune heaths. On dune slacks, pioneer dune slacks and dune slack fens showed similar values of both diversities followed by a diversity drop on dune slack woodland. Salt marshes showed a significant increase in functional and taxonomic diversity between pioneer zone and lower marsh, but no significant changes to upper marsh and brackish marsh. Functional diversity ($q=2$) varied significantly along the maturity gradient on dune slacks and salt marshes, but not on dunes (Figure 3.3, C). Within dunes, white dunes and dune woodland had lower functional diversity compared to dune grasslands and dune heaths, however, these differences were not significant. Dune slack maturity showed significantly higher functional diversity on Pioneer dune slacks than the other two maturity gradients. On the other hand, salt marshes increased significantly in functional diversity, with pioneer zone and lower marshes showing lower functional diversity values than upper marshes and brackish marshes. Taxonomic diversity ($q=2$) on dunes, was highest on dune grasslands and lowest in white dunes and dune heaths (Figure 3.3, D).

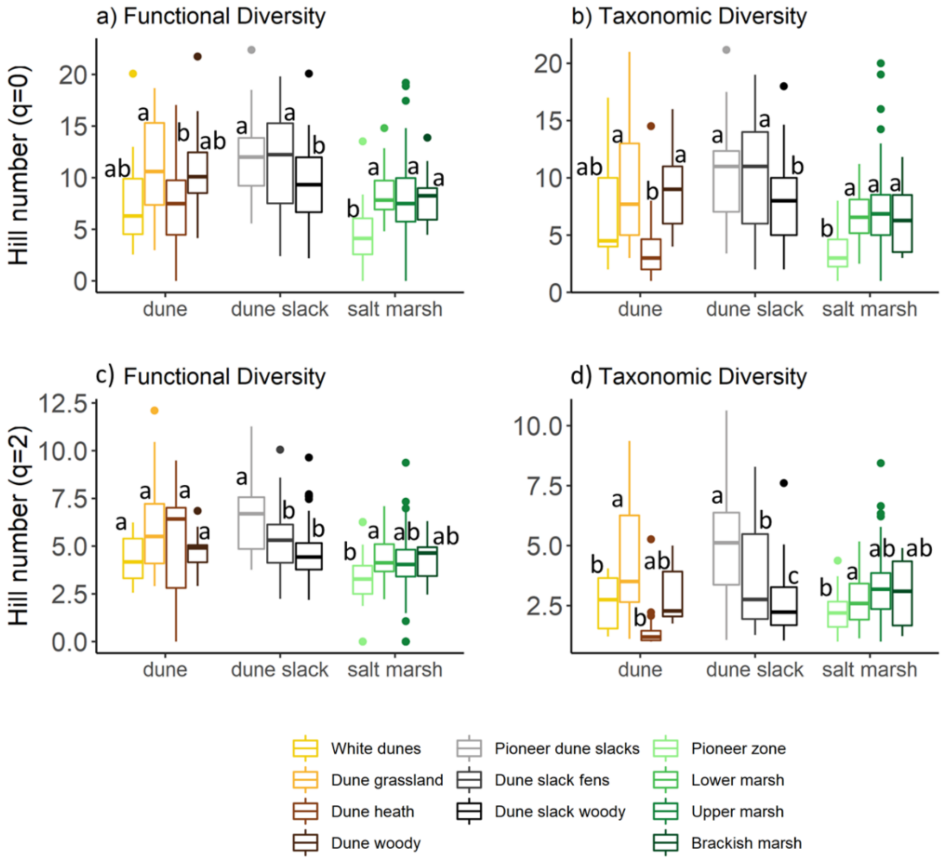

Figure 3.3 Functional and taxonomic diversity variations along habitat maturation gradient within habitat types (n= 427). Letters indicate significant differences (p = 0.05) between maturity stages. Boxes a) and b) show functional and taxonomic diversity where Hill number q= 0, (Richness) and c) and d) show functional and taxonomic diversity where Hill number q =2, (Simpson Index)

Community-weighted means changes along the habitat maturity gradient showed different patterns according to habitat, for most of the traits (Figure 3.4). Specific leaf area in dunes showed a drop on dune heaths while did not show little changes in dune slacks, but did increase in salt marshes between the stages of pioneer zone and lower marsh (Figure 3.4, A). Plant maximum height did show a consistent increase in all habitats being more pronounced in dune slacks (Figure 3.4, B).

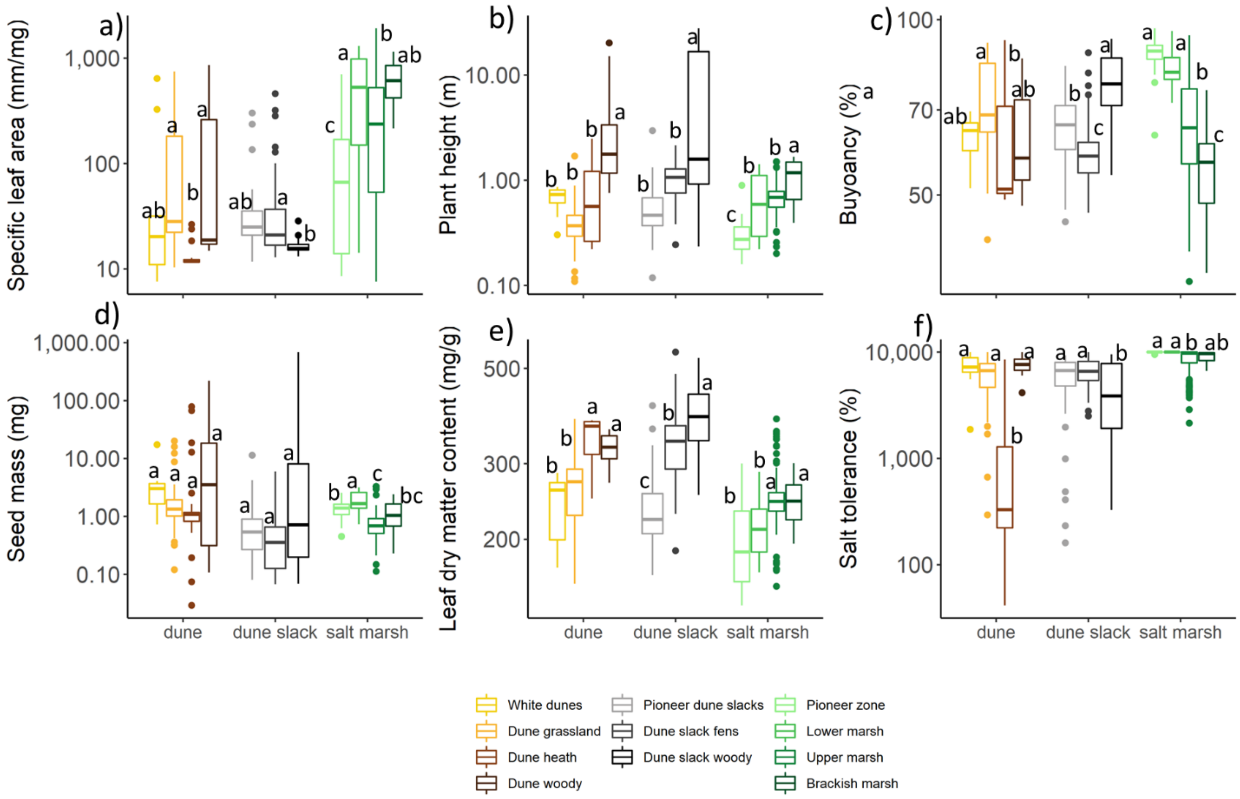

Figure 3.4 Community weighted means for the six plant functional traits along three habitat maturation gradients, for each habitat type: Dune, dune slack, and salt marshes. Letters indicate significant differences (p = 0.05) between maturity stages.

Seed buoyancy only vary significantly in dunes, between dune grasslands and dune heaths, while on dune slack it significantly varied between all maturity stages. On salt marshes, seed buoyancy decreased consistently along the maturity gradient (Figure 3.4, C). Seed mass did not change along maturity stages dune and dune slacks, but on salt marshes showed a significant increase from pioneer zone to lower marsh, and a decreased again on upper marshes (Figure 3.4, D). Leaf dry matter content increased from early stage to mature across all three habitats types (Figure 3.4, E). Lastly, salt tolerance showed a significant decrease in dunes, between dune grasslands and dune heaths, while no significant changes were found for the other habitats (Figure 3.4, F).

3.4 Discussion

Overall, we found little support for a consistent unimodal diversity trend along habitat maturity, either when considering functional or taxonomic diversity. Instead, high habitat-dependent patterns were observed, with these being associated with increases (salt marshes), decreases (dune slacks), or non-changes (dunes) in functional and taxonomic diversity along maturity. While functional and taxonomic patterns within habitat were consistent for diversity - irrespective of functional groups or species dominance (i.e., q=0), there were context-dependent when accounting for functional groups of species dominance (i.e., q=2). Therefore, supporting the idea that multiple facets of diversity can provide different and supplementary information on community composition changes across habitat maturity gradients (Purschke et al., 2013). In addition, shifts along the maturity gradient in community-weighted means showed trait-dependent responses across habitats, likely reflecting trade-offs across species dispersal and establishment capabilities as well as species fitness to highly dynamic environments.

Differences within habitat patterns/trends between functional and taxonomic diversity – when considering dominant functional groups or species – may be associated with few dominant species covering a broad range of functional strategies or with high redundancy (i.e., multiple ecological strategies may be represented by many species, de Bello et al., 2013). Specifically, on dunes, the difference between functional and taxonomic diversity (q=2) is especially noticeable in dune heaths, where functional diversity (q=2) values have a much wider range than taxonomic diversity. In our study area, dune heath is widely dominated by the two ericoid species *Empetrum nigrum* and *Calluna vulgaris*, but those two species present distinct height and leaf trait values, which explains the low taxonomic diversity while maintaining similar levels of functional diversity with the rest of the habitat maturity stages of dunes. On dune slacks, between dune slack fens and dune slack woodland, the decrease of taxonomic diversity (q=2) without significant loss of functional diversity (q=2), could be an indication of functional redundancy, where the loss of species should cause little impact on overall functional diversity since there are many species with similar traits (de Bello, Carmona, et al., 2021). Alternatively, differences might be the outcome of a shift in dominant species, where the new and more dominant tree species, *Betula pubescens*, is functionally different from the, mostly herbaceous species found in the habitat. Thus, preventing a significant drop in functional diversity level while reducing taxonomic diversity.

Habitat-dependent maturity trends along maturity suggest that even though those habitats share a similar biogeomorphic succession (Corenblit et al., 2015; Groot et al., 2017), this similarity is not reflected in functional and taxonomic diversity changes. Previous studies have shown that disturbance and competition effects on functional and taxonomic diversity can vary depending on the spatial scale, disturbance regimes, and on which functional traits are being analyzed (de Bello et al., 2013; Mayfield et al., 2010). Moderate levels of disturbance are often linked to higher functional diversity, as the disruptions prevent strong competitors from proliferating and competing out less competitive species (i.e. competitive exclusion, Grime, 2006). Nonetheless, some studies have found that as disturbance decreases, functional diversity increases (de Bello et al., 2013; Mason et al., 2011), thus, no evidence of competitive exclusion taking place. Indeed, increased competition has been demonstrated to lead to an increase or a decrease in functional diversity, depending on the traits being used to quantify functional diversity (Kraft, Godoy, & Levine, 2015; Mayfield et al., 2010). Because here we are not directly measuring competition and disturbances, but instead using the habitat maturity gradient as a proxy for both (Fig. 1 - an adaptation of the model of biogeomorphic succession Corenblit et al., 2015) our results might not capture more locally based of environment differences that can potentially influence the diversity patterns of each habitat.

Trait-dependent responses across habitats influenced by biogeomorphic processes may be associated with the multidimensional nature in which plants have to establish and function (e.g., resource acquisition, resistance to strong winds and sand abrasion, exposition to flood, among others). Specifically, while plant height and LDMC increased with habitat maturity across habitats, specific leaf area, seed mass, and seed buoyancy showed inconsistent trends across habitats, while salt tolerance was relatively stable across habitat maturation gradients for all three habitats. A consistent increase in plant height was expected according to our initial assumption that species in habitats in more mature stages, invest more in resource acquisition and are stronger competitors, as taller species profit from higher light interception. The increase of leaf dry matter content is contrary to our initial hypothesis that it would decrease along the maturation gradient. This increase suggests that in the early stages of maturity, there is a trade-off between mechanical resistance and growth. It also suggests a shift towards a more conservative resource acquisition strategy in late stages of maturity (P. J. Wilson et al., 1999).

These absences of consistent trends (of diversity indexes and CWM), across habitats, could also be interpreted including a neutral ecology perspective (Hubbell, 2000). Due to the highly dynamic nature of barrier islands, stochastic processes may have a stronger influence on community assembly. For instance, a stochastic colonization sequence can generate an unpredictable community composition outcome, as the timing of a species establishment in the community determines the outcome of species interactions (i.e. priority effects, Drake, 1991). Our initial hypothesis already incorporates such an effect to some degree, as it proposes that the early arrival of a species that have spatial engineering traits, will facilitate the establishment of subsequent species. However, the generalization of our hypothesis is limited, as it does not contemplate the effects of the stochastic process on community assembly.

In conclusion, the expectation of generalizable functional and taxonomic diversity trends for habitat maturity did not match with highly dynamic coastal ecosystems of barrier islands. These discrepancies can be related to the natural stochasticity of barrier islands dynamics, where frequent disturbances might lead to a more stochastic community assembly. Furthermore, while by including functional and taxonomic diversity, we provide unique insights in terms of contrasting ecological strategies for dominant species and redundancy, a more mechanistic understanding may require the inclusion of turnover of functional groups and species across maturity stages.

Thesis Discussion

Summary and contributions

Ideally, the development of theoretical frameworks about biodiversity organization starts with the identification of patterns, and once those patterns are identified, researchers investigate how and why they are formed and maintained (Levin, 1992). In my thesis, I used a trait-based perspective to better understand the mechanism underlying frequently observed patterns, such as the scaling of diversity of island floras with island area, island age, and disturbance levels (Borregaard et al., 2017; Scherber et al., 2018; Triantis et al., 2012; Whittaker et al., 2008). I found that the patterns of functional diversity often diverge from those of taxonomic diversity and that external drivers exert different levels of influence on each diversity facet. This incongruence between patterns of functional and taxonomic diversity is consistent across spatial scales and demonstrates that relying exclusively on taxonomic diversity to understand the mechanisms governing biodiversity may not be enough, as it provides only a partial picture. Furthermore, I make valuable contributions to the field of island biogeography. Specifically, I address two main limitations of the equilibrium theory of island biogeography: i) it does not consider the dynamic nature of islands and ii) it neglects species' trait differences, that influence species community assembly and evolution (Lomolino, 2000).

In chapter one, I link oceanic islands' ontogeny with species' functional traits, using the framework of the General Dynamic model. I show that while island ontogeny is a reliable predictor of species richness on oceanic islands, it is an ineffective one for functional diversity aspects. The ontogeny of an island can be measured through its age, which reflects changes in key features such as area, habitat heterogeneity, and resource availability. The hump-shaped relationship frequently found between species richness and island age, where the mature stage of an island's life cycle, marked by its maximum area, heterogeneity, and resources, supports the highest number of species is not found in functional diversity. My results suggest that a large number of island species are functionally similar and exploit similar resources, leading to high functional redundancy. Therefore, the moment at which an island reaches its maximum taxonomic diversity is not the same as when it reaches its maximum functional diversity. Functional redundancy is not uncommon in plant communities but the isolation of islands can add to strong dispersal filtering, further exacerbating the homogenization of species traits. My results also suggest that this homogenization is, to some degree, countered by endemic species, that continue to introduce novel traits to the trait space even in late stage of islands, where islands already lost habitats and might provide fewer resources.

In chapter two, I show the importance of considering more than one diversity facet (i.e. taxonomic, functional, and phylogenetical diversity) when investigating the underlying mechanisms shaping islands' biodiversity. I find that despite area being the best predictor for taxonomic, functional, and phylogenetic diversity, the underlying ecological process of these diversity-area relationships had different degrees of influence across diversity facets. One of the most important factors influencing the diversity-area relationship is habitat heterogeneity (Turner & Tjørve, 2005). Specifically, high habitat heterogeneity in a limited area leads to a decrease in the effective area available per habitat, also known as area-heterogeneity trade-off (Allouche et al., 2012). The results of this chapter show that while larger islands have more unique functional and phylogenetic species, smaller islands that showed high levels of habitat heterogeneity had lower functional diversity. This area-heterogeneity trade-off is likely due to high interspecific competition, favoring stronger competitors which have a specific set of traits.

In chapter three, I investigated changes in taxonomic and functional diversity, and community-weighted mean trait values of plant communities across different stages of habitat maturity in three habitat types in barrier island. I find that taxonomic diversity changed significantly, while functional diversity remained relatively similar within each habitat. However, the maintenance of similar levels of functional diversity was not indication that species' ecological strategies did not change over habitat maturation. Community weighted means varied greatly with habitat type with plant height and leaf dry matter content increasing as habitats became more mature, suggesting a shift towards higher competitive ability and more conservative ecological strategy. The results of this chapter show that the expectation of generalizable diversity trends for habitat maturity did not match with highly dynamic coastal ecosystems of barrier islands, possibly due to the natural stochasticity of their dynamics. My results also highlight the importance of considering individual traits variation and not only multidimensional functional diversity indices.

Finally, this thesis is part of a larger research unity, DynaCom, which aims at better understanding how communities change over time and space, by using trait-based theory and empirical studies. By using this approach DynaCom hopes to disentangling the biodiversity drivers of dynamic environments. My research contributes with the overarching goals of DynaCom by providing a spatial-temporal context to functional trait variation of plant communities and its relation with environmental changes (chapter one and two) and helps extending well known patterns (e.g. species-area relationship; geomorphological succession; environmental selection of traits) to a highly dynamic environment with strong stochastic forces (Chapters two and three).

Challenges and future perspectives

Data

The advances made through trait-based research have expanded our knowledge of several global trends and patterns, such as variations in leaf size (I. J. Wright et al., 2004), seed size and plant height (Moles et al., 2007; Moles et al., 2009), and the global spectrum of plant form and function (Díaz et al., 2016). The majority of these studies used data from databases such as TRY (Kattege et al., 2011) and were focused on mainland systems. However, such studies focusing on island species are significantly more challenging. For instance, the largest trait database for plants, TRY, still lacks substantial trait information regarding island species. Collecting trait information from field measurements is a time-consuming and intensive task, and typically areas with easier access are preferred. As a result, there is a bias in trait data, with species in remote locations, such as oceanic islands, being frequently overlooked due to these islands' isolation and sometimes hard access (Cornwell et al., 2019).

An obvious solution is the larger investment in local field studies where this data can be collected. Such local studies and species trait recordings are the corner-stones of trait-based ecology, and such initiatives are ongoing across different archipelagos (Barajas-Barbosa et al., 2022; Kühn et al., 2021; Schrader, Westoby, et al., 2021; Westerband et al., 2021). However, field-collected data might take many years to be made publicly available. An alternative source for trait data can be found in published literature such as flora descriptions, published papers, and monographs. Trait values from flora books have been successfully used in ecology research (Cutts et al., 2021; Cutts et al., 2023; Hanz et al., 2022; Kissling et al., 2008; Onstein et al., 2019) and are increasingly being integrated into global databases (Weigelt et al., 2020). With the advancement and growing accessibility of artificial intelligence tools like text-mining, the ability to gather trait information from published literature has the potential to be done on a much larger scale and completed much more quickly. These tools may utilize natural language processing to convert unstructured text into structured data, making the process much more efficient and streamlined. This could greatly reduce the gap in trait data, expanding the frontiers of trait-based ecology as the limitation of trait data is hardly exclusive to islands, but rather an overarching limitation of the field of functional ecology (Cornwell et al., 2019).

Another way to mitigate the lack of trait information is the use of imputation methods that rely on trait-trait correlations and phylogenetic relationships to fill the missing values (Penone et al., 2014; Swenson, 2014b). However, these methods were originally developed using mainland plant species, and their effectiveness for island plants remains unclear since islands floras harbor high numbers of endemic species, that often come from *in-situ* speciation and adaptative radiations, and are subjected to high dispersal filtering pressure (Losos et al., 2009). Therefore, there is a pressing need for studies focusing on testing the accuracy of imputation methods when predicting missing traits of island species, particularly when employing phylogenetically close mainland species.

Trait-based approach

Global

To circumvent the lack of trait information, I combined information from databases, published floras, and field-collected data, and I could obtain trait information for a substantial number of oceanic island species (over 3000). However, the traits for which information was obtainable were still limited, especially for endemic species. This limited the options and consequently influenced the functional diversity patterns I found since trait choice has been demonstrated to impact the outcome of functional diversity measurements (Mouillot et al., 2021).

Although the trait combination I used here (i.e. plant height, seed length, leaf width, and leaf length) has been shown to provide a good notion of a species' ecological strategies (Westoby, 1998), some axes of plant form and function are still missing. For instance, while leaf size is informative of leaf energy production and water balance (Ackerly et al., 1998; Farquhar et al., 2002), more detailed leaf traits such as leaf nitrogen content and leaf mass per area, can offer information on leaves tradeoffs between photosynthetic potential and herbivory resistance (Chapin, 1980) and leaves architecture and longevity (Poorter et al., 2009; I. J. Wright et al., 2004) respectively. While woodiness can be used as a proxy for growing strategies, traits such as stem-specific density could offer mode in-depth insights into plants' trade-off between fast growth with high mortality rates and slow growth with high survival (Freschet et al., 2010; S. J. Wright et al., 2010).

Additionally, species dispersal traits are thought to be of central importance to the island's assembly process, since non-endemic species' capacity of colonizing such isolated islands might be dependent on their dispersal abilities (Arjona et al., 2018; Nogales et al., 2012). Dispersal traits that are commonly used, are those related to seeds, specifically seed mass (Moles et al., 2004; Thompson et al., 1993; Wyse et al., 2021). However, not only seed size but how those seeds are spread can further complement our understanding of how islands are colonized. As an example, in a study using the Galapagos islands, Vargas et al. (2014) showed that species with sea-drifting diaspore traits were more widespread than those with other dispersal syndromes, such as wind or animal dispersal.

Thus, further studies that incorporate more detailed traits of island species and link them with the processes of immigration, extinction, and speciation might reveal a clearer picture of the rules governing the assembly of plants in islands. Moreover, the composition of island floras could be better evaluated in the context of a global trait space, where one could contrast mainland and island species distribution within the trait space and potentially find biases, such as the overrepresentation of dispersive species in island floras.

Regional

The research I present in chapter two and other previous studies have shown the potential of using functional diversity-area relationships (FDAR) in revealing the scale-dependent ecological processes involved in the community assembly processes (Schrader, Westoby, et al., 2021; Zhang et al., 2021). However, functional diversity as measured only by richness-based metrics is limited and the consideration of other aspects of functional diversity, weighted by species abundances (i.e. divergence and evenness) might give us a more in-depth understating of the assembly process (Mason et al., 2005). For instance, a decrease in the volume of a functional-trait space occupied by species may suggest greater environmental pressure, while changes in the distribution of abundance may reflect changes in the intensity of competitive interactions (Cornwell et al., 2006; Mason et al., 2007; Mason et al., 2008). Additionally, disentangling abiotic from biotic filtering using functional diversity metrics based on multiple traits (weighted by abundance or not), might lead to an oversimplified interpretation of assembly processes (Mazel et al., 2020) .Certain traits like maximum height and seed size can be related to species fitness, while a combination of traits such as rooting depth and specific leaf area can be related to species competitiveness (Kraft, Adler, et al., 2015). Using both types of traits together restricts the comprehensibility of functional diversity patterns and drivers (Mazel et al., 2020)

A possible approach to mitigate the limitations of functional diversity metrics based on multiple traits is to also investigate the drivers of individual trait variation. The community-weighted mean (CWM) is a simple and effective measure that captures the traits of the most abundant species within a community (de Bello, Carmona, et al., 2021) For instance, in Chapter three, I found that changes in functional diversity did not capture changes in ecological strategies within communities, but those changes were observed when using CWM. As another example, in a study investigating the relationship between island characteristics and traits of plant communities, Schrader, Westoby, et al. (2021) found that area had a positive correlation with seed mass, tree height, and chlorophyll content. However, area had only a strong direct effect on seed mass, while indirectly affecting tree height and chlorophyll content via basal area (the area of tree stems per unit of land area). In this case, the use of CWM helped to shed light on the underlying mechanisms that make up the diversity-area relationship. Adding the use of more than one type of index when assessing patterns of community trait distribution has the potential to provide more nuanced results and aid in their interpretation. Specifically, further studies that focus on linking individual trait variations and island features (e.g. area, habitat heterogeneity, climate) might be successful in disentangling biodiversity drivers.

Local

The results of chapter three highlight the importance of not only using taxonomic and functional diversity but also looking at individual trait variation when investigating diversity changes along maturity gradients in coastal habitats. While functional diversity levels remained relatively stable, community-weighted means showed that ecological strategies were changing along the habitat maturation gradient. Plants in more mature habitats are better competitors as they invest more in resource acquisition than species in early-stage habitats. However, I could not find evidence that in early stages of habitat maturation, plants invest more in tolerance, as proposed by the model of biogeomorphic succession (Corenblit et al., 2009).

In highly dynamic landscapes, often exposed to water, wind, and sediment flows, such as barrier islands, pioneer plant species often have homologous traits that optimize their fitness in response to those disturbances (Bornette et al., 2008; Hesp, 1991). While I targeted some of those traits (i.e. seed buoyance and salt tolerance), other important ones such as specific root length and stem-specific density were left out, due to data constraints. In early stages of habitat maturity, having shallow roots that can quickly anchor is paramount to optimizing species' mechanical resistance, as at this early stage the mechanical forces of water and wind are extreme (Corenblit et al., 2015). Stronger and more flexible stems can also prevent biomass destruction by wave action and are more resilient to strong wind blows, preventing plant uprooting (Corenblit et al., 2015; Vuik et al., 2018). Thus, the addition of traits that better reflect plant biomechanics could improve the assessment of plant ecological strategies and potentially unveil colonization-competition trade-offs.

Further studies that investigate species strategy changes along habitat maturation gradients would benefit from comparing both taxonomical and functional turnover. Robroek et al. (2017) found that functional and taxonomic diversity were decoupled in their study on European peat bogs. In their study, species turnover across environmental gradients was restricted to functionally similar species. These differences in taxonomic and functional turnover could also occur in highly dynamic landscapes such as barrier islands, where frequent disturbances limit the range of functional trait values necessary for plant survival, ultimately keeping species functionally similar while allowing for taxonomic diversity.

Island dynamics

Oceanic islands

On the chapter one, I also investigate the relationship between functional diversity and dynamic island ontogenies. Yet, geologic island dynamics is made of several processes that go beyond island ontogenies, such as continental drift (plate tectonics) and sea level changes caused by glacial cycles (Pleistocene glaciations, Fernández-Palacios et al., 2016). Both processes influence directly the isolation and connectivity of islands over millions of years. Continental drift acts on the scale of tens to hundreds of million years and causes the relocation of islands and the formation of newly connecting islands, making islands more, or less connected over time, affecting the gene flow and evolution of islands biotas (Fernández-Palacios et al., 2016; Gaina et al., 1998). Sea level changes caused by glacial cycles made islands bigger and smaller and repeatedly joined or disconnected them from the continents, over tens to hundreds of thousands of years. These cycles of less or more isolation and changes in the area have been recognized to have remaining effects on the biodiversity observed on islands today (Weigelt et al., 2016).

However, there is not yet enough understanding of how the historical dynamics of islands affects other facets of island diversity beyond species richness. As I demonstrated in Chapters one and two, functional diversity showed a different response to island ontogeny and historical geomorphology than taxonomic diversity. It is thus possible that these differences are also true to other aspects of island dynamics and diversity facets (i.e. phylogenetic diversity). Building on the functional trait data I mobilized in Chapter one, along with published data on the past spatial arrangement, area, and climate of islands (Weigelt et al., 2016), as well as high-resolution phylogenetic trees (S. A. Smith et al., 2018), one could investigate, the consequences of past and present environmental drivers for taxonomic, functional, and phylogenetic diversity on a global scale. Such an approach could provide a more mechanistic understanding of the underlying factors shaping current islands' flora (Bauer et al., 2021; Latham et al., 1993; Swenson, 2014a)

Barrier islands

Barrier islands are highly dynamic systems and changes in their area and shape can be observed over a span of hundreds of years, but in the last decades, this dynamism is being purposely slowed down by the construction of dykes and dune stabilizations (Reise, 2013). These anthropogenic changes have a direct impact on barrier island floras, as they directly interfere with the natural rejuvenation of barrier island habitats (Groot et al., 2017). Measuring island dynamics using only historical changes in island area, without accounting for how much of each island area was affected by dyke constructions or dune stabilizations, might have masked the effective impact of the geomorphological dynamics on the multiple facets of diversity of islands floras. Further studies including data on when these anthropogenic changes in island landscape were made, and how much area they compromise would show a more accurate relationship between geomorphological dynamics and current island biodiversity.

Furthermore, barrier islands' geomorphology is strongly influenced by climatic events, such as storm frequency (Stutz et al., 2011). Including past and current climatic data when predicting biodiversity patterns are extremely effective and particularly important for island systems (Barajas-Barbosa et al., 2020; Pearman et al., 2008; Weigelt et al., 2016). Specifically, including such data in a regional scale study, as I presented here in chapter two, would likely be ineffective since the islands are too closely located and there is minimal climate variation between islands. However, given that barrier islands are present in numerous continents and climates (Stutz et al., 2011) ,and exhibit similar geomorphological dynamics, a comparative analysis of community assemblies on various barrier islands worldwide could serve as a valuable study model for investigating the relative influence of geomorphological dynamics and climatic features on biodiversity.

In chapter three I address this dynamics of barrier islands by using habitat maturation gradients as a proxy for disturbance intensity, since disturbance levels on barrier islands are higher in the early stages of habitat maturation and subside as habitat matures due to environmental changes promoted by ecosystem engineers (Corenblit et al., 2015). However, using such an approach, I could not investigate potential direct links between trait variation and stochastic disturbances. Future research leveraging local historical data of storm events and precipitation changes could investigate those relationships, helping fill the knowledge gap of functional trait selection in dynamic landscapes. While the influence of environmental variables on functional traits has been established for relatively stable systems (Díaz et al., 2001; McGill et al., 2006), high disturbances levels in community assembly may lead to a neutral relationship between environment and functional traits (Brose et al., 2016).

Conclusion

This thesis highlights the importance of using a trait-based perspective as it provides a more nuanced understanding of the mechanisms that drive insular biodiversity patterns and ecosystem processes. My research findings make a direct contribution to the advancement of the field of functional island biogeography, which is still in its infancy but has great potential to advance our knowledge of plant ecology and evolution in insular systems. Understanding the mechanisms that govern biodiversity is critical for predicting the impact of environmental changes, such as climate change and land use, on biodiversity patterns. This knowledge is fundamental for more effective conservation strategies that seek to preserve the fragile diversity of island floras.

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Finally, my heartfelt thanks go to my family, who supported me unconditionally throughout this journey. I am deeply grateful to my mother, Jeanny da Luz, who set an example of a strong, hardworking woman whom I still aspire to be like. To my father, Wladimir Ferraz, who always gave me honest and wise advice and was my first supporter when I decided to embark on an academic career. I am also thankful to my siblings for their life-long friendship and support. Most of all, I want to thank my husband, Pedro Vinicius, whose partnership was the cornerstone of my ability to complete this PhD. He embarked on this journey with me years ago and have always been there for me, making my days brighter, easier, and better. I could not have asked for a better partner in life.

Author contribution

Chapter 1: Linking plant functional diversity to the general dynamic model of island biogeography

Thalita Ferreira-Arruda: Lead on conceptualization; data curation; formal analysis; methodology; validation; visualization; writing of the original draft. **Patrick Weigelt**: Equal on formal analysis and writing of the original draft. Supporting on conceptualization and methodology. **Nathaly R. Guerrero-ramírez:** Supporting on conceptualization; formal analysis; methodology; writing of the original draft**. Holger Kreft**: Equal on conceptualization; methodology; writing of the original draft. Supporting on data curation.

Chapter 2: Island area and historical geomorphological dynamics shape multifaceted diversity of barrier island floras

Thalita Ferreira-Arruda: Lead on conceptualization; data curation; formal analysis; methodology; validation; visualization; writing of the original draft and reviews. **Nathaly R. Guerrero-Ramírez:** Equal on formal analysis and writing of the original draft and reviews. Supporting on conceptualization and methodology. **Pierre Denelle**: Supporting on formal analysis and writing of the original draft and reviews. **Patrick Weigelt**: Supporting on conceptualization; formal analysis and writing of the original draft and reviews. **Michael Kleyer**: Equal on data curation. Supporting on writing of the original draft and reviews. **Holger Kreft**: Equal on conceptualization; methodology; writing of the original draft. Supporting on data curation.

Chapter 3: Functional diversity and trait changes along maturity gradients in coastal habitats

Thalita Ferreira-Arruda: Lead on conceptualization; data curation; formal analysis; methodology; validation; visualization; writing of the original draft. **Nathaly R. Guerrero-Ramírez**: Equal on formal analysis and writing of the original draft. Supporting on conceptualization and methodology. **Patrick Weigelt:** Supporting on conceptualization; formal analysis; methodology; writing of the original draft**. Pierre Denelle**: Supporting on formal analysis and writing of the original draft. **Holger Kreft**: Equal on conceptualization; methodology; writing of the original draft. Supporting on data curation.

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Holger Kreft

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Center of Biodiversity and Sustainable Land Use, University of Göttingen, Göttingen, Germany.

Michael Kleyer

Institute of Biology and Environmental Sciences, University of Oldenburg, Oldenburg, Germany.

Appendix

Supporting information Chapter 1

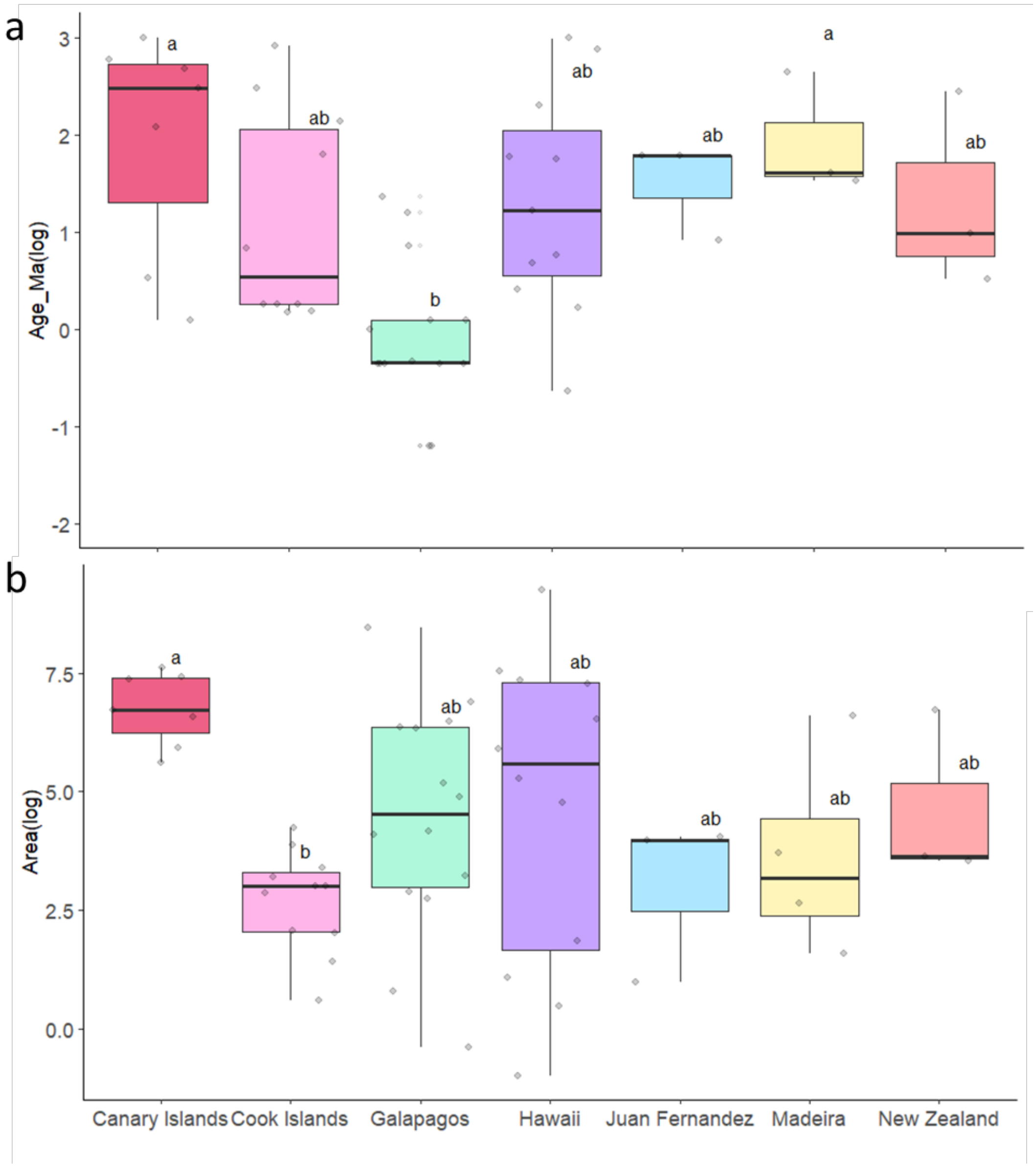


Figure S1.1 Variation in island age (a) and area (b) per archipelago: Compact letter display based Tukey's honest significant differences post hoc test, to assess significant differences among the archipelagos. Only archipelagos used in the GDM analyses are displayed.

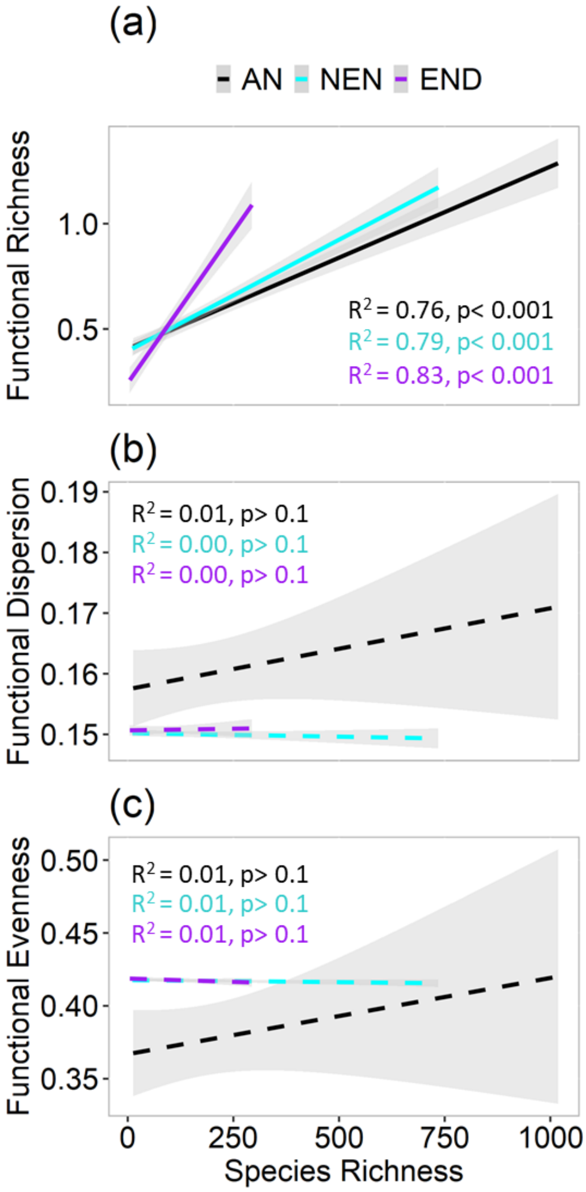


Figure S1.2 Functional diversity metrics correlation with species richness.

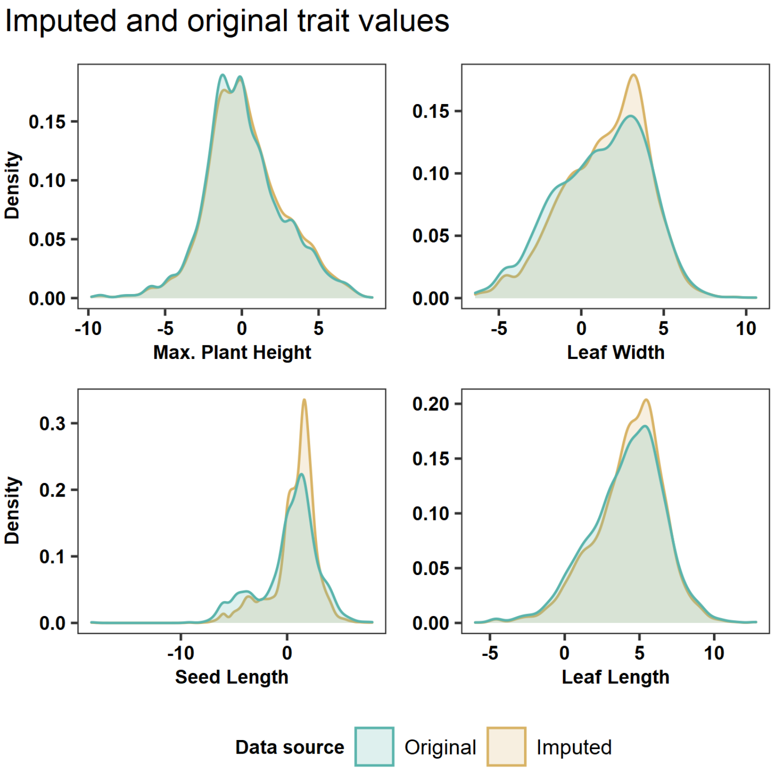
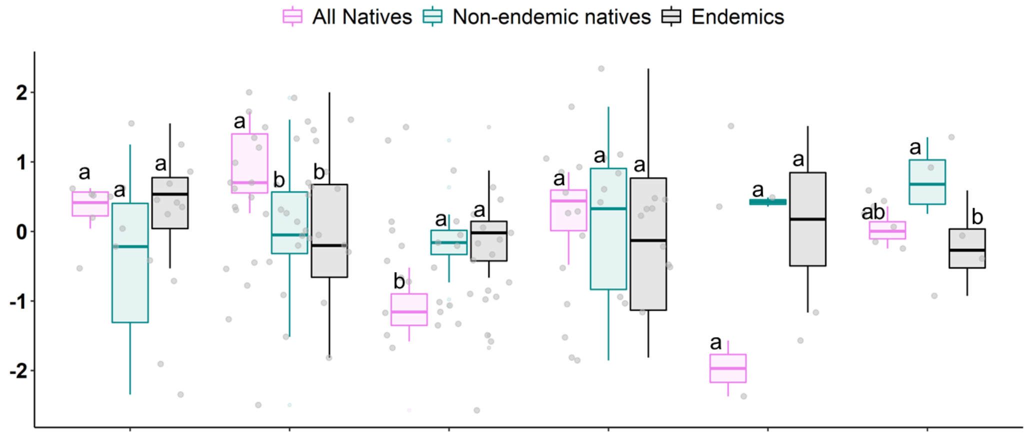


Figure S1.3 Comparison of original and imputed trait values per functional trait.

(a) Functional Dispersion



(b) Functional Evenness

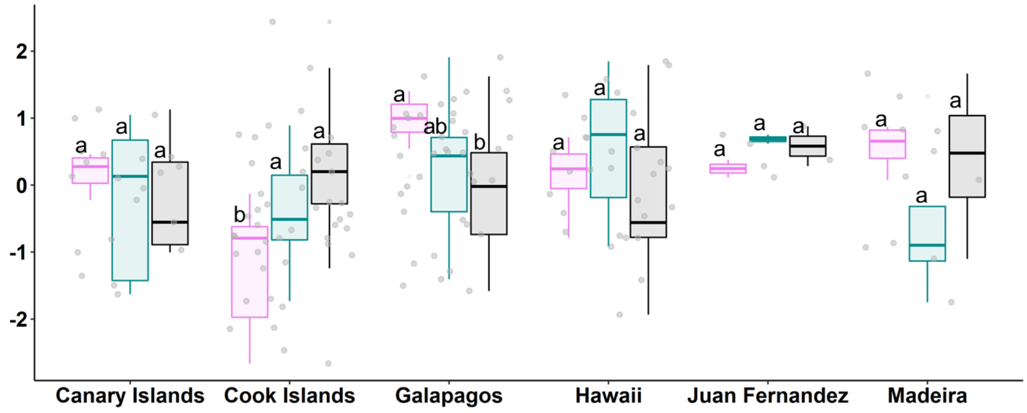


Figure S1.4 . Variation of islands functional dispersion and functional evenness of each species group, per archipelago. Only archipelagos used in the GDM analyses are displayed. Compact letter display is from Tukey's honest significant differences post hoc test, to assess significant differences among the species groups, within archipelago.

Table S1.1. Additional traits used in the imputation and their respective number of observations within our dataset

Trait name	Number of observations
Seed length minimum	610
Seed mass minimum	1004
Seed mass maximum	1398
Seed volume minimum	366
Seed volume maximum	366
Fruit length minimum	992
Fruit width minimum	516
Fruit width maximum	592
Flower length minimum	636
Flower length maximum	737
Flower width minimum	194
Leaf length minimum	1594
Leaf width minimum	1672

Table S1.2 Island age reference per individual island

Island name	Archipelago	Reference
Norfolk Island	New Zealand	Jones, J. G. & Mcdougall, I. (1973). Geological History of Norfolk and Philip Islands, Southwest Pacific Ocean. Journal of The Geological Society of Australia, 20(3), 239–254.
El Hierro	Canary Islands	Cardoso, P., Arnedo, M.A., Triantis, K.A. and Borges, P.A.V. (2010), Drivers of Diversity in Macaronesian Spiders and The Role of Species Extinctions. Journal of Biogeography, 37: 1034-1046.
La Palma	Canary Islands	Cardoso, P., Arnedo, M.A., Triantis, K.A. and Borges, P.A.V. (2010), Drivers of Diversity in Macaronesian Spiders and The Role of Species Extinctions. Journal of Biogeography, 37: 1034-1046.
La Gomera	Canary Islands	Cardoso, P., Arnedo, M.A., Triantis, K.A. and Borges, P.A.V. (2010), Drivers of Diversity in Macaronesian Spiders and The Role of Species Extinctions. Journal of Biogeography, 37: 1034-1046.
Tenerife	Canary Islands	Cardoso, P., Arnedo, M.A., Triantis, K.A. and Borges, P.A.V. (2010), Drivers of Diversity in Macaronesian Spiders and The Role of Species Extinctions. Journal of Biogeography, 37: 1034-1046.
Gran Canaria	Canary Islands	Cardoso, P., Arnedo, M.A., Triantis, K.A. and Borges, P.A.V. (2010), Drivers of Diversity in Macaronesian Spiders and The Role of Species Extinctions. Journal of Biogeography, 37: 1034-1046.
Fuerteventura	Canary Islands	Cardoso, P., Arnedo, M.A., Triantis, K.A. and Borges, P.A.V. (2010), Drivers of Diversity in Macaronesian Spiders and The Role of Species Extinctions. Journal of Biogeography, 37: 1034-1046.
Lanzarote	Canary Islands	Cardoso, P., Arnedo, M.A., Triantis, K.A. and Borges, P.A.V. (2010), Drivers of Diversity in Macaronesian Spiders and The Role of Species Extinctions. Journal of Biogeography, 37: 1034-1046.
Darwin	Galapagos	White, B. & Burdick, B. (2002). Galapagos Geomorphology: A Walk Through the Islands. Available At: Http://Pages.Uoregon.Edu/Drt/Research/Volcanic%20Galapagos/Presentation.View@_Id=9889959127044&.Html (Accessed 10/02/13)
Española	Galapagos	Hall, M. L. (1983). Origin of Espanola Island and The Age of Terrestrial Life on The Galapagos Islands. Science (New York, N.Y.), 221(4610), 545–547.
Fernandina	Galapagos	Simkin, T. (1984). Geology of Galapagos. Biological Journal of The Linnean Society, 21(1-2), 61–75.

Floreana	Galapagos	Bow, C. S. & Geist, D. J. (1992). Geology and Petrology of Floreana Island, Galapagos Archipelago, Ecuador. Journal of Volcanology and Geothermal Research, 52(1-3), 83–105.
Genovesa	Galapagos	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Isabela	Galapagos	Simkin, T. (1984). Geology of Galapagos. Biological Journal of The Linnean Society, 21(1-2), 61–75.
Marchena	Galapagos	Vicenzi, E. P., Mcbirney, A. R., White, W. M. & Hamilton, M. (1990). The Geology and Geochemistry of Isla Marchena, Galapagos Archipelago: An Ocean Island Adjacent To A Mid-Ocean Ridge. Journal of Volcanology and Geothermal Research, 40(4), 291–315. Cox, A. & Dalrymple, G. B. (1966). Palaeomagnetism and Potassium-Argon Ages of Some Volcanic Rocks From The Galapagos Islands. Nature, 209(5025), 776–777.
Pinta	Galapagos	Simkin, T. (1984). Geology of Galapagos. Biological Journal of The Linnean Society, 21(1-2), 61–75.
Pinzon	Galapagos	Simkin, T. (1984). Geology of Galapagos. Biological Journal of The Linnean Society, 21(1-2), 61–75.
San Cristoban	Galapagos	Geist, D. J., Mcbirney, A. R. & Duncan, R. A. (1986). Geology and Petrogenesis of Lavas from San Cristobal Island, Galapagos Archipelago. Geological Society of America Bulletin, 97(5), 555.
Santa Cruz	Galapagos	Simkin, T. (1984). Geology of Galapagos. Biological Journal of The Linnean Society, 21(1-2), 61–75.
Santa Fe	Galapagos	Geist, D. J., Mcbirney, A. R. & Duncan, R. A. (1986). Geology and Petrogenesis of Lavas from San Cristobal Island, Galapagos Archipelago. Geological Society of America Bulletin, 97(5), 555.
Santiago	Galapagos	Simkin, T. (1984). Geology of Galapagos. Biological Journal of The Linnean Society, 21(1-2), 61–75.
Wolf	Galapagos	Bailey, K. (1976). Potassium-Argon Ages from The Galapagos Islands. Science (New York, N.Y.), 192(4238),

		465–467.
Hawai'i Island	Hawaii	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Kaua'i Island	Hawaii	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Kaho'olawe Island	Hawaii	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Ka'ula Island	Hawaii	Garcia, M. O., Frey, F. A. & Grooms, D. G. (1986). Petrology of Volcanic Rocks from Kaula Island, Hawaii. Contributions to Mineralogy and Petrology, 94(4), 461–471.
Lana'i Island	Hawaii	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Lisianski Island	Hawaii	Clague, D.A., Braga, J.C., Bassi, D., Fullagar, P.D., Renema, W. & Webster, J.M. (2010). The Maximum Age of Hawaiian Terrestrial Lineages: Geological Constraints from Kōko Seamount. Journal of Biogeography, 37, 1022-1033.
Maui Island	Hawaii	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Moloka'i Island	Hawaii	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Necker Island	Hawaii	DALRYMPLE, G. B., LANPHERE, M. A. & JACKSON, E. D. (1974). Contributions To The Petrography and Geochronology of Volcanic Rocks From The Leeward Hawaiian Islands. Geological Society of America Bulletin,

		85(5), 727.
Ni'ihau Island	Hawaii	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
O'ahu Island	Hawaii	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Kermadec Islands	New Zealand	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Rarotonga	Cook Islands	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Aitutaki	Cook Islands	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Atiu	Cook Islands	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Mangaia	Cook Islands	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Manihiki	Cook Islands	Wood, B. L. (1967). Geology of The Cook Islands. New Zealand Journal of Geology and Geophysics, 10(6), 1429–1445.
Manuae	Cook Islands	Wood, B. L. (1967). Geology of The Cook Islands. New Zealand Journal of Geology and Geophysics, 10(6), 1429–1445. Lambeck, K. (1981). Lithospheric Response To Volcanic Loading in The Southern Cook Islands. Earth and

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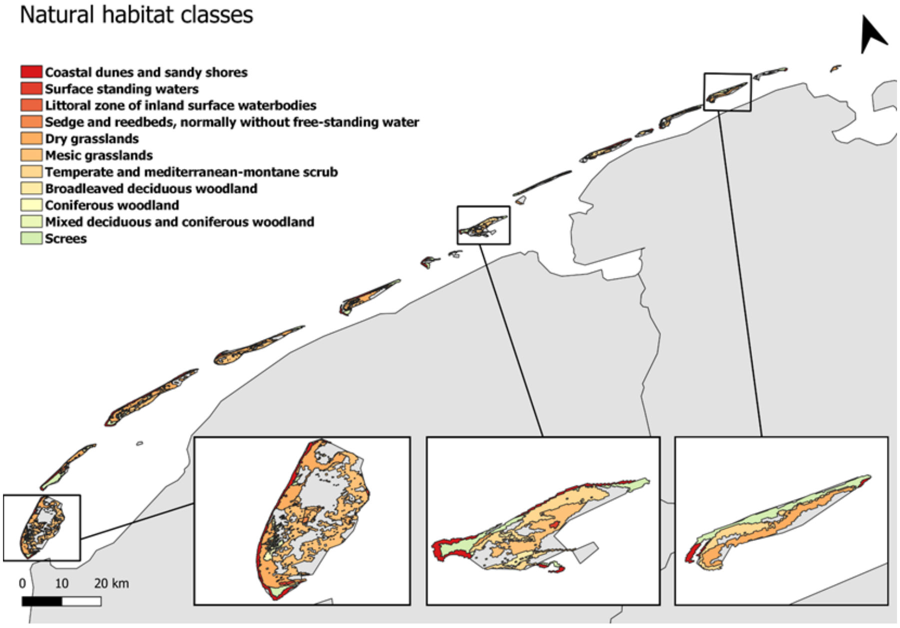
Mauke	Cook Islands	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Mitiaro	Cook Islands	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Pukapuka Cook	Cook Islands	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Suwarrow	Cook Islands	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Penrhyn (Tongareva)	Cook Islands	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Madeira	Madeira	Cardoso, P., Arnedo, M.A., Triantis, K.A. and Borges, P.A.V. (2010), Drivers of Diversity in Macaronesian Spiders and The Role of Species Extinctions. Journal of Biogeography, 37: 1034-1046.
Desertas	Madeira	Cardoso, P., Arnedo, M.A., Triantis, K.A. and Borges, P.A.V. (2010), Drivers of Diversity in Macaronesian Spiders and The Role of Species Extinctions. Journal of Biogeography, 37: 1034-1046.
Porto Santo	Madeira	Cardoso, P., Arnedo, M.A., Triantis, K.A. and Borges, P.A.V. (2010), Drivers of Diversity in Macaronesian Spiders and The Role of Species Extinctions. Journal of Biogeography, 37: 1034-1046.
Savage Islands	Madeira	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Masatierra	Juan	Kueffer, C., Daehler, C.C., Torres-Santana, C.W., Lavergne, C., Meyer, J.-Y., Otto, R. & Silva, L. (2010). A

	Fernandez	Global Comparison of Plant invasions On Oceanic Islands. Perspectives in Plant Ecology Evolution and Systematics, 12, 145-161
Masafuera	Juan Fernandez	Kueffer, C., Daehler, C.C., Torres-Santana, C.W., Lavergne, C., Meyer, J.-Y., Otto, R. & Silva, L. (2010). A Global Comparison of Plant invasions On Oceanic Islands. Perspectives in Plant Ecology Evolution and Systematics, 12, 145-161
Santa Clara	Juan Fernandez	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.
Chatham Islands	New Zealand	Gillespie, R. G. & Clague, D. (Hg.). (2009). Encyclopedias of The Natural World: Bd. 2. Encyclopedia of Islands. University of California Press; Walter De Gruyter Gmbh.

Supporting information Chapter 2



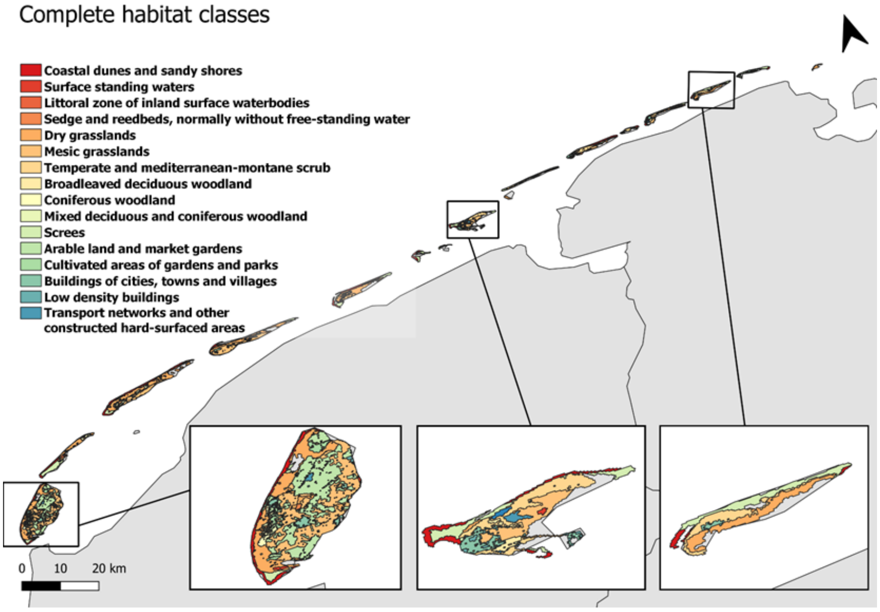


Figure S2.5 Habitat classifications according to the Ecosystem types of Europe from EEA. Figure on the top shows the habitat classes used in the analyses while figure on the bottom show the complete set of habitat classes including the one classified as urban or human-dominated.

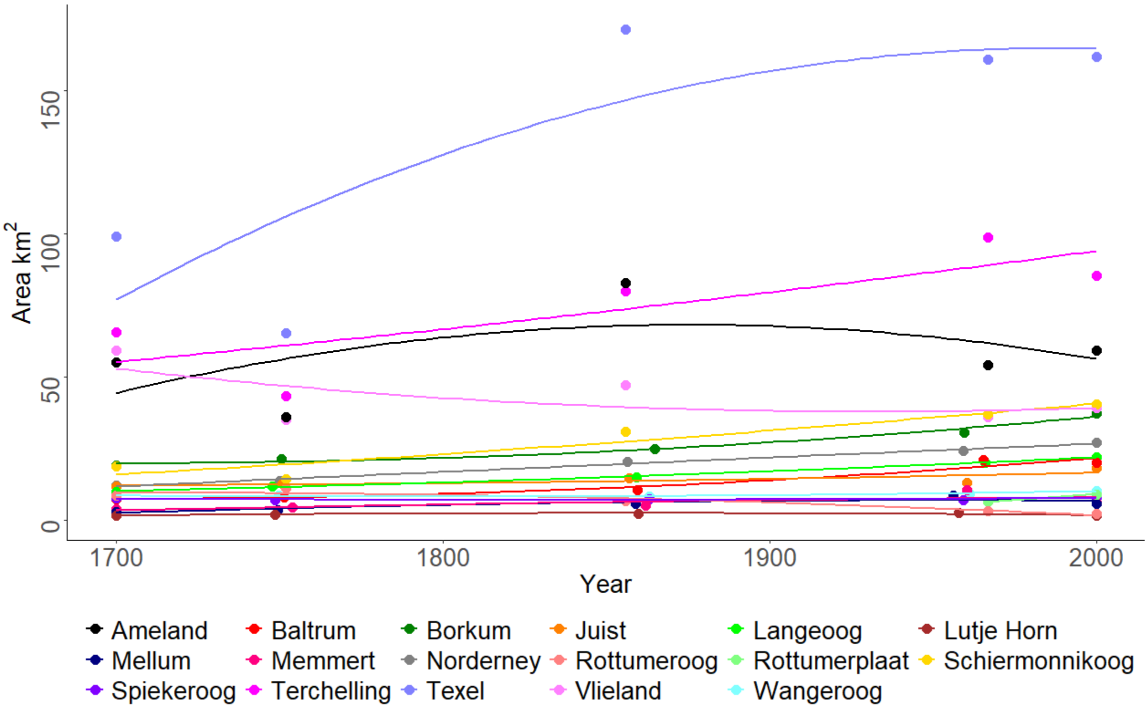


Figure S2.6 Island area temporal changes from the year 1700 to 2008.

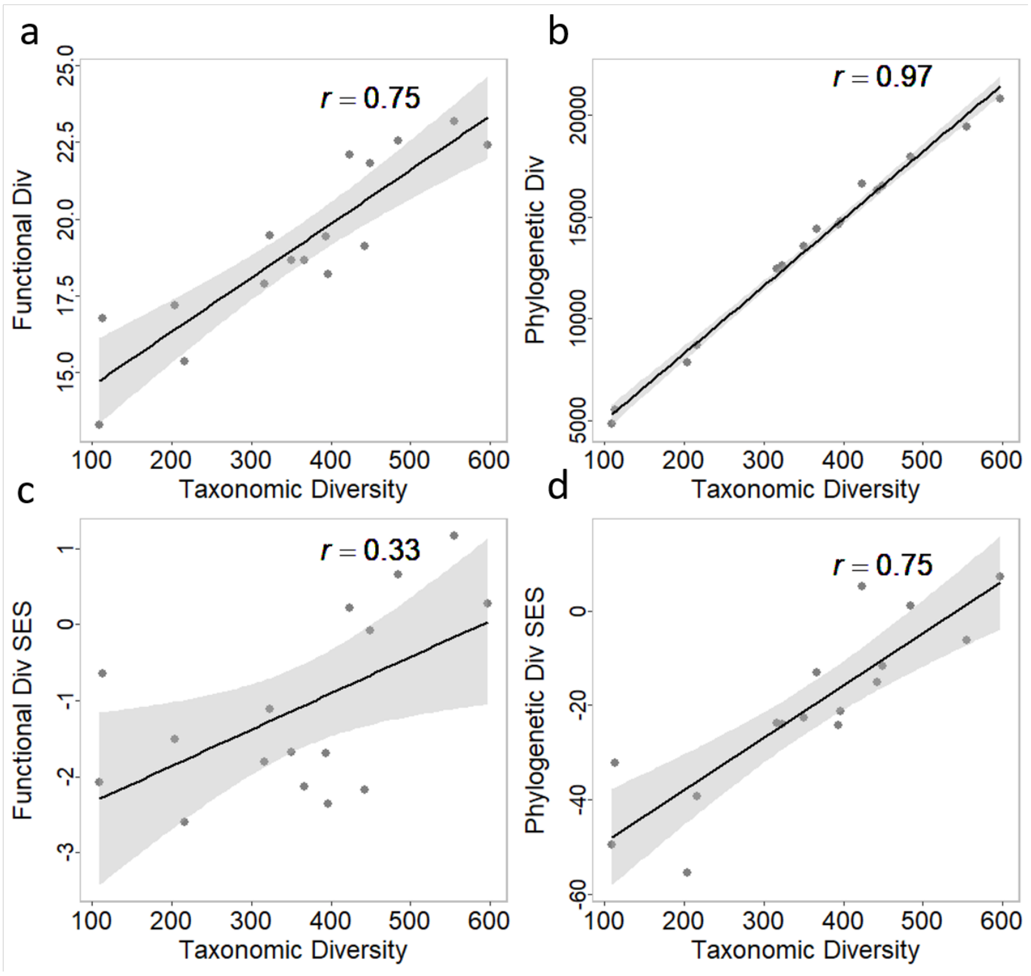


Figure S2.7 Correlations (Kendall rank) between functional and taxonomic diversities and phylogenetic and taxonomic diversities. Observed functional (a) and phylogenetic (b) diversity are correlated with taxonomic diversity (r=0.75, r=0.97, respectively). When using standardized effect size functional (c) and phylogenetic (d) diversities, their correlations with taxonomic diversity weaken (r = 0.33 and r = 0.75, respectively).

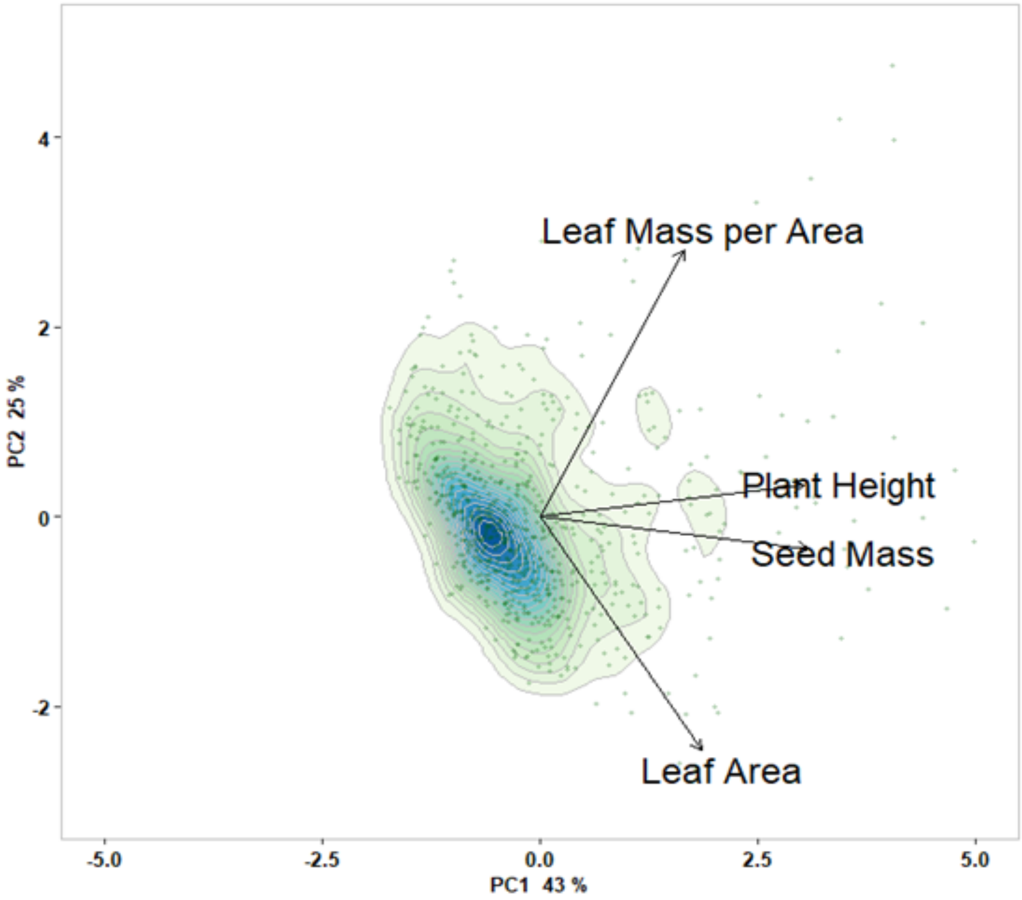


Figure S2.8 Principal component analyses used to estimate the hypervolumes of functional diversity measured by functional richness used in the main analyses. The species (n=712) are shown as the green dots with shading indicating species density. Solid arrows indicate direction of vectors representing the four traits considered.

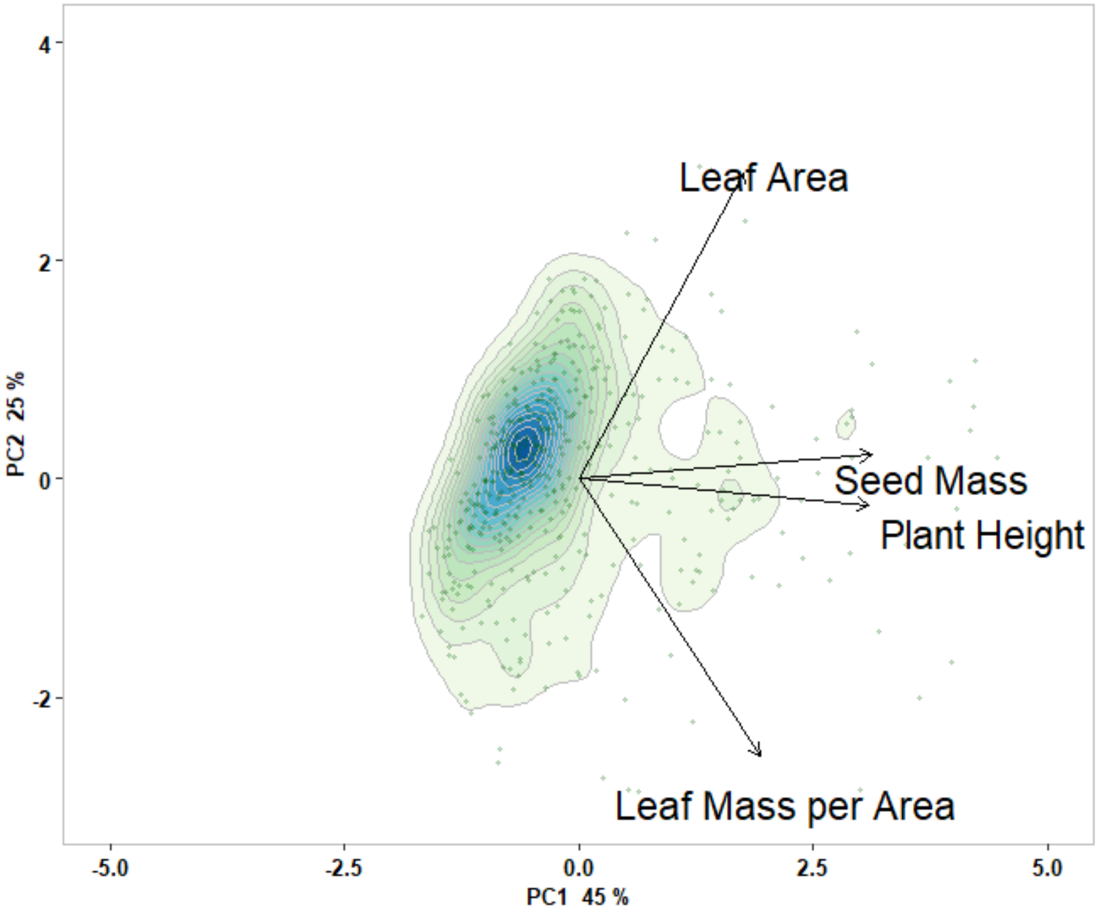


Figure S2.9 Principal component analyses used to estimate the hypervolumes of functional diversity measured by functional richness four traits. The species (n=461) are shown as the green dots with shading indicating species density. Solid arrows indicate direction of vectors representing the four traits considered.

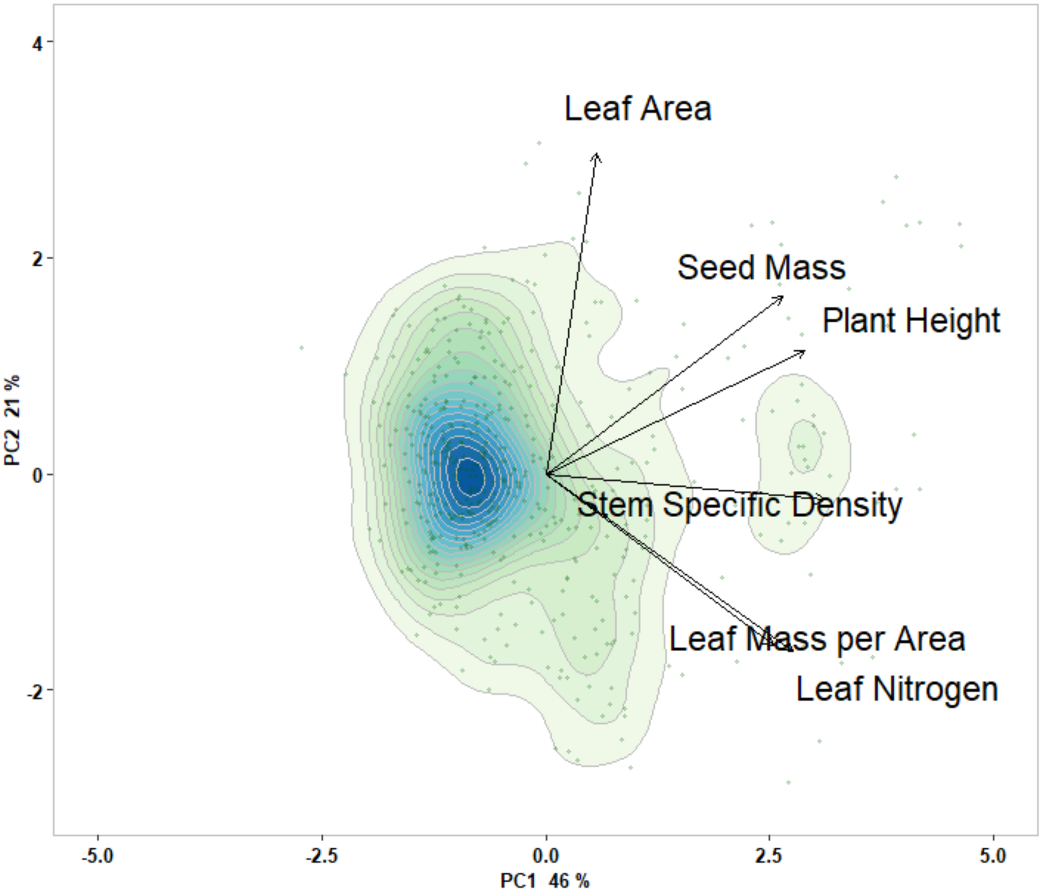


Figure S2.10 Principal component analyses used to estimate the hypervolumes of functional diversity measured by functional richness using six traits. The species (n=461) are show as the green dots with shading indicating species density. Solid arrows indicate direction of vectors representing the four traits considered.

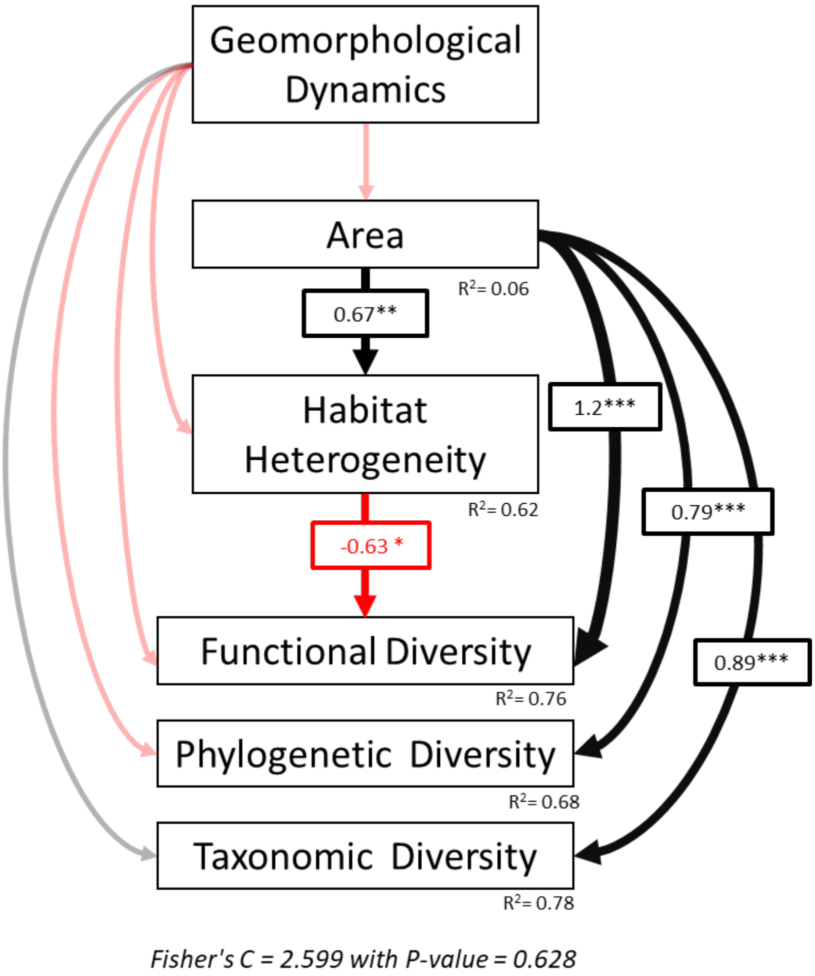


Figure S2.11 Piecewise structure equation models using the subset data with four traits. Black arrows denote positive relationships, and red arrows negative ones. Arrows for non-significant paths ($P \geq 0.05$) are semi-transparent. The thickness of the significant paths has been scaled based on the magnitude of the standardized regression coefficient

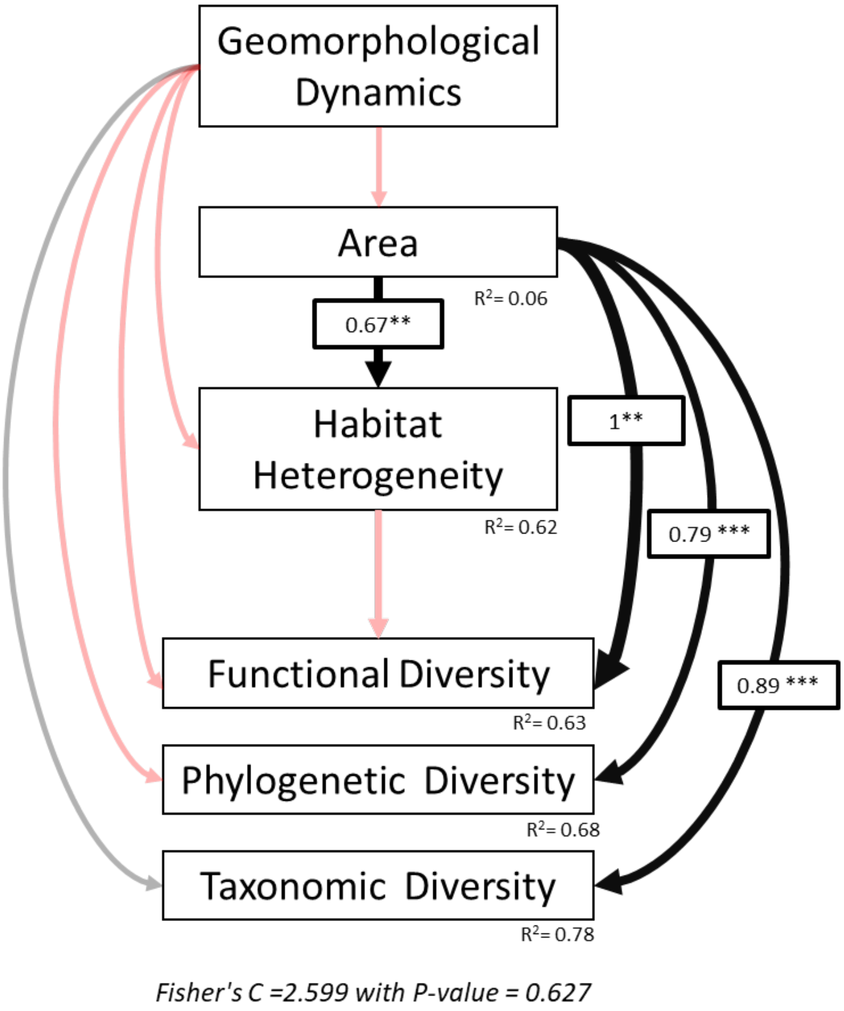


Figure S2.12 Piecewise structure equation models using the subset data with six traits. Black arrows denote positive relationships, and red arrows negative ones. Arrows for non-significant paths ($P \geq 0.05$) are semi-transparent. The thickness of the significant paths has been scaled based on the magnitude of the standardized regression coefficient.

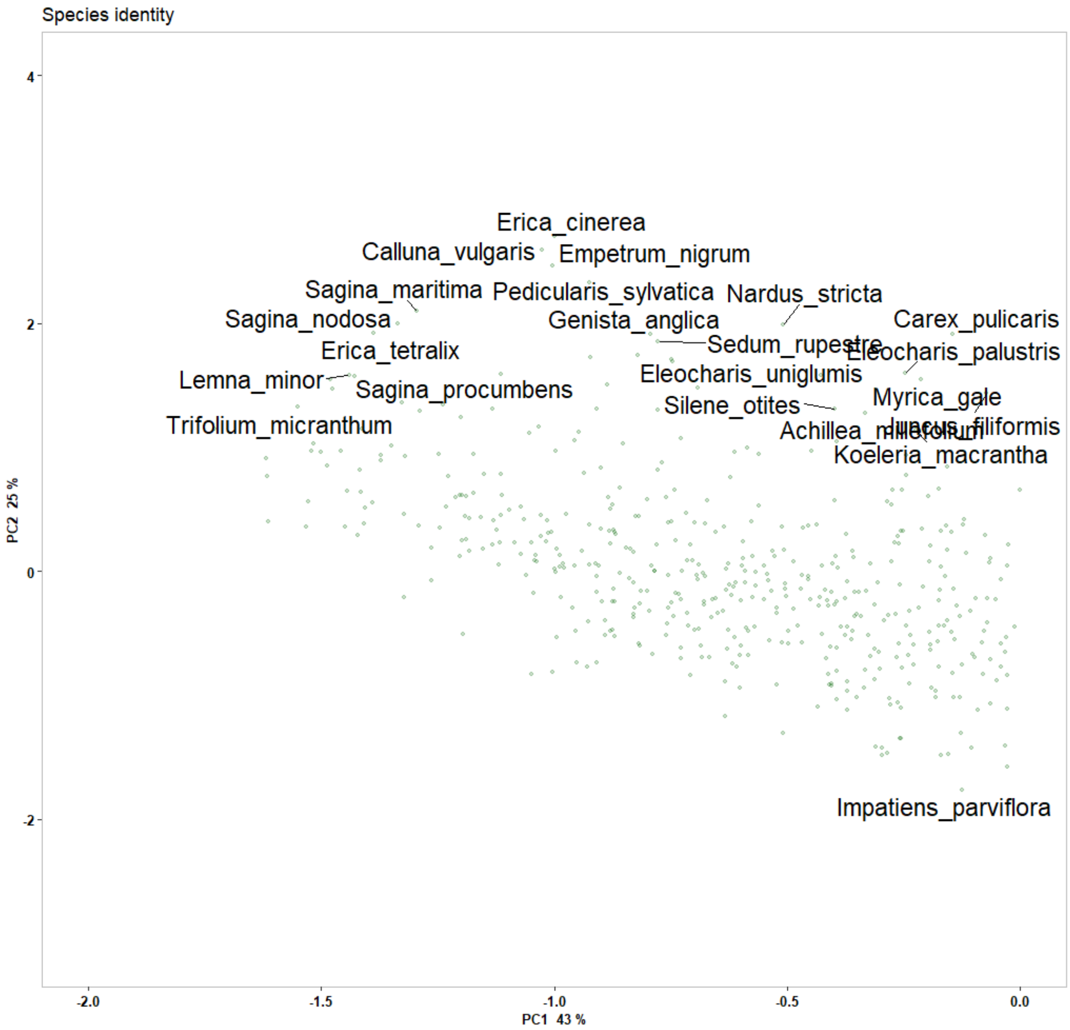


Figure S2.13 Species identity and their position on the lower half of the PC1 (from -2 to 0). PCA used in the main analyses (n=712).

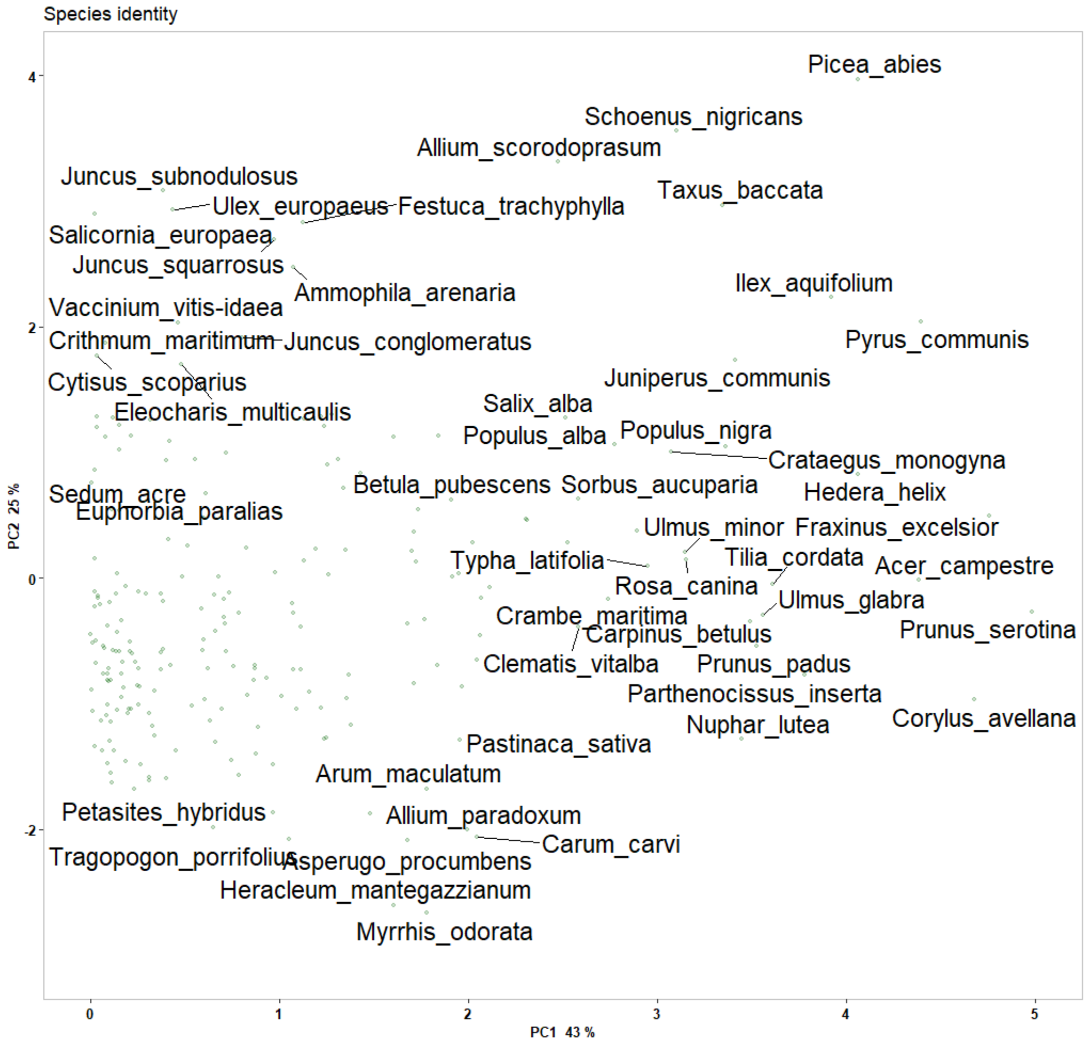


Figure S2.14 Species identity and their position on the upper half of the PC1 (from 0 to 5). PCA used in the main analyses (n=712).

Table 0.3 Principal component analysis (PCA) of West and East Frisian islands plants. Eigenvalues and trait loadings of principal components (PC1 and PC2) in two different PCAs. Main analysis corresponds to the PCA performed on 712 species for which values of four traits were available, and which is reported in the main text. The rest of the columns correspond to PCAs carried out on a subset of the main analysis data with only 461 species using the same four traits as main analyses and with two additional traits (stem specific density and leaf nitrogen content).

	Main analysis (712 species, 4 traits)		**Subset data** (461 species, 4 traits)		**Subset data** (461 species, 6 traits)	
	PC1	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**
Variation explained (%)	**42.6**	**24.8**	45.3	24.99	46	20.9
Eigenvalue	**1.71**	**0.98**	1.81	0.99	2.74	1.25
Variable Loadings						
Seed Mass	**0.81**	**-0.08**	0.80	-0.05	0.69	0.43
Plant Height	**0.79**	**0.08**	0.81	-0.06	0.76	0.29
Leaf Area	**0.48**	**-0.64**	0.46	0.73	0.15	0.78
Leaf Mass per Area	**0.43**	**0.73**	0.50-	-0.06	0.66	-0.42
Leaf Nitrogen	-	-	-	-	0.72	-0.43
Stem Specific Density	-	-	-	-	0.82	-0.06
Contributions (%)						
Seed Mass	**38.19**	**0.81**	37.2	0.33	17.71	14.99
Plant Height	**37.04**	**0.74**	36.5	0.38	21.15	7.14
Leaf Area	**13.8**	**42.85**	11.8	54.6	0.82	48.62
Leaf Mass per Area	**10.94**	**55.58**	14.2	44.6	16.34	14.05
Leaf Nitrogen	-	-	-	-	19.33	14.86
Stem Specific Density	-	-	-	-	24.65	0.31

Table S2.4 Traits used on the quantification of FD as functional richness, on the subset data analysis and their respective measured units. Observed values referred to trait values that derived from field observations.

Functional Trait	**Functional Relevance**	**Unit**	**Observed values %**
Maximum plant height	Light interception and seed dispersal facilitation (Westoby *et al.*, 2002; Moles *et al.*, 2009; Garnier *et al.*, 2016).	m	100
Seed mass	Colonization capacity and seedling survival (Thompson, K. *et al.*, 1993; Moles *et al.*, 2004; Wyse & Hulme, 2021).	mg	94.6
Leaf mass per area	Carbon gain and leaf life span (Wright *et al.*, 2004; Poorter *et al.*, 2009).	mm^2/g	99.7
Leaf area	Leaf energy production and water balance (Ackerly & Donoghue, 1998; Farquhar *et al.*, 2002).	mm^2	91.9
Stem specific density	Growing strategy and mechanical resistance (Freschet *et al.*, 2010; Wright *et al.*, 2010).	g/cm^3	65.4
Nitrogen per leaf area	Photosynthetic potential and herbivory resistance (Chapin, 1980; Diaz *et al.*, 2004).	mg/mm^2	98.2

Table S2.5 Non-standardized estimates of structural equation models exploring the influence of spatial features on island's multifaceted diversity. Geomorphological dynamics may influence diversity facets through area and habitat heterogeneity or through unmeasured mechanisms (direct path between geomorphological dynamics and diversity facets). Values on this table refer to the analyses done on a subset of the species data (n=461) and using **four** traits on the calculation of functional diversity.

Response	**Predictor**	**estimate**	**standard error**	**p-value**
Functional diversity (SES) R^2: 0.72	Geomorphological dynamics	-1.32	1.91	0.50
	Area	3.13	0.64	0.0004
	Habitat heterogeneity	-9.2	4.17	0.04
Phylogenetic diversity (SES) R^2: 0.68	Geomorphological dynamics	-12.7	19.2	0.51
	Area	21.7	4.46	0.0003
Taxonomic diversity R^2: 0.78	Geomorphological dynamics	58.3	92.2	0.53
	Area	141.3	21.3	0.0000
Area R^2: 0.06	Geomorphological dynamics	-1.02	1.12	0.37
Habitat heterogeneity R^2: 0.69	Geomorphological dynamics	-0.19	0.11	0.12
	Area	0.12	0.02	0.0006
Partial correlations				
Functional (SES) ~ phylogenetic (SES) diversities		0.09		0.36
Functional (SES) ~ taxonomic diversities		-0.03		0.44
Phylogenetic (SES) ~ taxonomic diversities		0.55		0.01

Fisher's C = 2.354, df = 4, p-value = 0.671, n = 16

Table S2.6 Non-standardized estimates of structural equation models exploring the influence of spatial features on island's multifaceted diversity. Geomorphological dynamics may influence diversity facets through area and habitat heterogeneity or through unmeasured mechanisms (direct path between geomorphological dynamics and diversity facets). Values on this table refer to the analyses done on a subset of the species data (n=461) and using **six** traits on the calculation of functional diversity.

Response	**Predictor**	**estimate**	**standard error**	**p-value**
Functional diversity (SES) R^2: 0.61	Geomorphological dynamics	-1.06	2.22	0.64
	Area	2.55	0.75	0.0054
	Habitat heterogeneity	-5.37	4.85	0.35
Phylogenetic diversity (SES) R^2: 0.68	Geomorphological dynamics	-12.7	19.2	0.51
	Area	21.7	4.46	0.0003
Taxonomic diversity R^2: 0.78	Geomorphological dynamics	58.3	92.2	0.53
	Area	141.3	21.3	0.0000
Area R^2: 0.06	Geomorphological dynamics	-1.02	1.12	0.37
Habitat heterogeneity R^2: 0.69	Geomorphological dynamics	-0.19	0.11	0.12
	Area	0.12	0.02	0.0006
Partial correlations				
Functional (SES) ~ phylogenetic (SES) diversities		0.1		0.35
Functional (SES) ~ taxonomic diversities		-0.02		0.46
Phylogenetic (SES) ~ taxonomic diversities		0.55		0.01

Fisher's C = 2.354, df = 4, p-value = 0.671, n = 16

Table S2.7 Non-standardized estimates of structural equation models exploring the influence of spatial features on island's multifaceted diversity, **using historic area** (from the year 1700, with the exception of Rottumerplaat island which is from 1900)**.** Geomorphological dynamics may influence diversity facets through area and habitat heterogeneity or through unmeasured mechanisms (direct path between geomorphological dynamics and diversity facets).

Response	**Predictor**	**estimate**	**standard error**	**p-value**
Functional diversity (SES) R^2: 0.67	Historic area	0.86	0.19	0.0005
Phylogenetic diversity (SES) R^2: 0.85	Habitat Heterogeneity	31.33	9	0.0041
	Historic area	12.06	1.75	0.0000
Taxonomic diversity R^2: 0.72	Habitat Heterogeneity	245.1	99.8	0.
	Historic area	87.25	19.4	0.0006
Geomorphological dynamics R^2: 0.03	Historic area	-0.02	0.03	0.53
Habitat heterogeneity R^2: 0.45	Geomorphological dynamics	-0.65	0.3	0.04
	Historic area	0.08	0.04	0.06
Partial correlations				
Functional (SES) ~ phylogenetic (SES) diversities		0.02		0.47
Functional (SES) ~ taxonomic diversities		-0.07		0.39
Phylogenetic (SES) ~ taxonomic diversities		0.43		0.05

Fisher's C = 6.242, df = 4, p-value = 0.62, n = 16

Supporting information Chapter 3

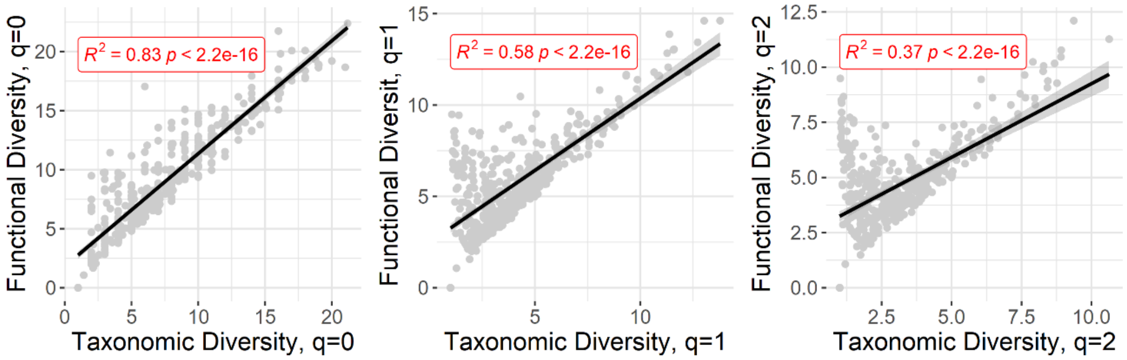


Figure S3.15 Correlation between functional and functional diversity of the three different orders of hill numbers (q = 0,1 and 2)

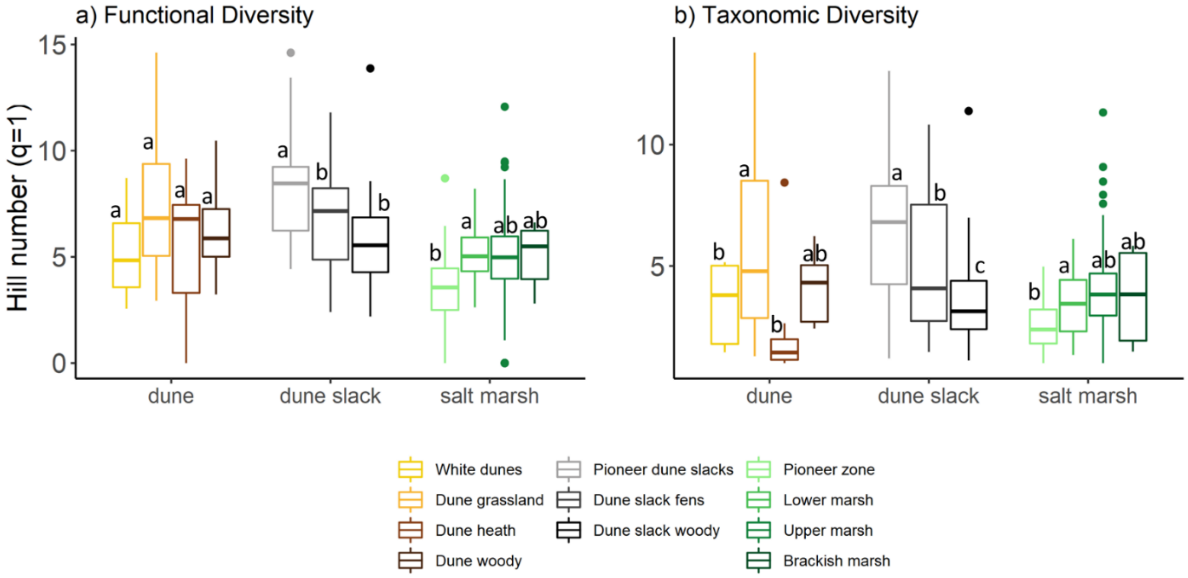


Figure S3.16 Functional (a) and taxonomic (b) diversity (Hill number q =1, Shannon Index) variations along habitat maturation gradient within habitat types (n= 427). Letters indicate significant differences (p = 0.05) between maturity stages.

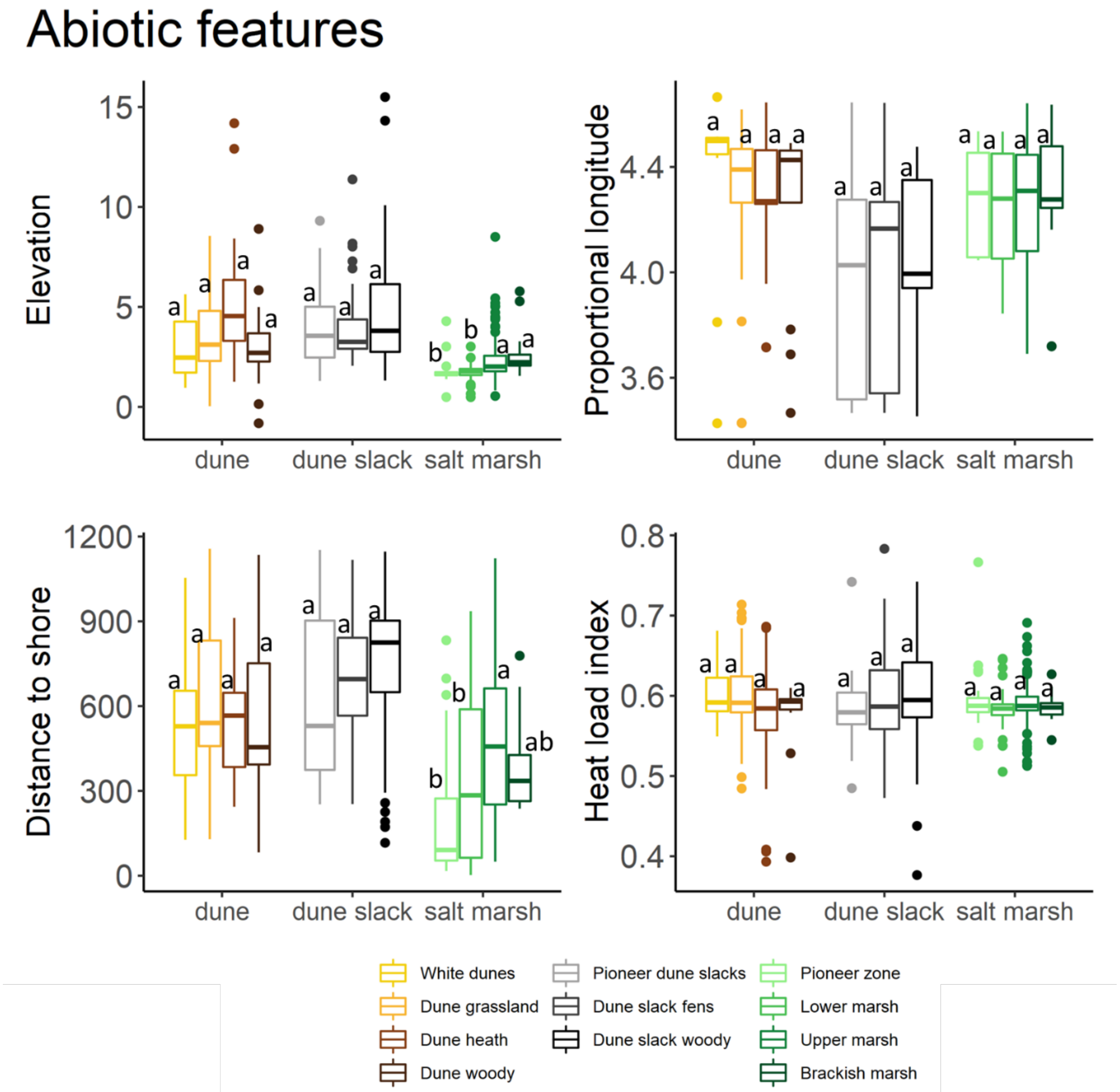


Figure S3.17 Abiotic features variations over habitat maturation gradient for each habitat type. Elevation and heat load index from digital elevation models of 1 m^2 resolution, provided by the State Office for Geoinformation and State Surveying of Lower Saxony. Proportional longitude is a proxy for sediment age, since eastern parts of islands are made by more recently deposited sediment than western parts. Thus, proportional longitude was calculated as the distance of each plot from the furthest west point of each island and divided it by the maximum eastern distance. Distance of each plot to the shore, as a proxy of susceptibility to wave action and salt spray was calculated using CORINE Land Cover 2018. Heat load index was calculated from digital elevation models of 1 m^2 resolution, provided by the State Office for Geoinformation and State Surveying of Lower Saxony.

Table S3.8 List of species occurring in the four maturity stages of dune habitats, ranked by species commonness

White dunes	Dune grassland	Dune heath	Dune woodland
Ammophila arenaria	Corynephorus canescens	Empetrum nigrum	Agrostis gigantea
Festuca rubra	Agrostis capillaris	Salix repens	Holcus lanatus
Elymus farctus	Lotus corniculatus	Calluna vulgaris	Festuca rubra
Sonchus arvensis	Jasione montana	Festuca ovina	Polypodium vulgare
Galium mollugo	Ammophila arenaria	Polypodium vulgare	Salix repens
Linaria vulgaris	Rumex acetosella	Anthoxanthum odoratum	Ammophila arenaria
Oenothera parviflora	Viola canina	Luzula campestris	Galium mollugo
Elymus athericus	Luzula campestris	Agrostis capillaris	Lonicera periclymenum
Eryngium maritimum	Festuca rubra	Ammophila arenaria	Populus tremula
Poa pratensis	Aira praecox	Nardus stricta	Agrostis capillaris
Rumex acetosella	Hypochaeris radicata	Hieracium umbellatum	Elaeagnus rhamnoides
Agrostis gigantea	Hieracium umbellatum	Lonicera periclymenum	Prunus virginiana
Galium verum	Galium mollugo	Rumex acetosella	Quercus robur
Holcus lanatus	Holcus lanatus	Danthonia decumbens	Rubus pseudojaponicus
Honckenya peploides	Koeleria macrantha	Festuca rubra	Sorbus aucuparia
Koeleria macrantha	Linaria vulgaris	Holcus lanatus	Anthoxanthum odoratum
Plantago lanceolata	Anthoxanthum odoratum	Quercus robur	Calamagrostis epigejos
Sedum acre	Plantago lanceolata	Rubus pseudojaponicus	Crataegus monogyna
Anthoxanthum odoratum	Poa pratensis	Agrostis gigantea	Luzula campestris
Armeria ruscinonensis	Sedum acre	Pinus sylvestris	Poa pratensis
Artemisia maritima	Polypodium vulgare	Rosa rugosa	Potentilla anserina
Atriplex portulacoides	Veronica officinalis	Centaurium littorale	Rosa canina
Bromus secalinus	Cerastium fontanum	Cirsium palustre	Veronica officinalis
Cakile maritima	Claytonia exigua	Erica tetralix	Dactylis glomerata
Calystegia soldanella	Eryngium	Festuca filiformis	Dryopteris

	maritimum		carthusiana
Cerastium semidecandrum	Salix repens	Hydrocotyle vulgaris	Dryopteris filix-mas
Cirsium arvense	Senecio vulgaris	Juncus articulatus	Empetrum nigrum
Corynephorus canescens	Stellaria graminea	Juncus conglomeratus	Festuca filiformis
Elymus repens	Botrychium lunaria	Linnaea borealis	Hieracium umbellatum
Hieracium umbellatum	Calystegia soldanella	Lotus corniculatus	Hypochaeris radicata
Jacobaea vulgaris	Cerastium semidecandrum	Phragmites australis	Jacobaea vulgaris
Lathyrus linifolius	Dactylis glomerata	Pinus mugo	Lathyrus pratensis
Leymus arenarius	Danthonia decumbens	Ranunculus pulchellus	Rosa rugosa
Limonium vulgare	Deschampsia flexuosa	Sorbus aucuparia	Rumex acetosa
Lotus corniculatus	Deschampsia media	Viola canina	Rumex acetosella
Lysimachia maritima	Elymus repens	Aira praecox	Sambucus nigra
Plantago maritima	Honckenya peploides	Betula pubescens	Stellaria graminea
Poa infirma	Polygala vulgaris	Calamagrostis epigejos	Urtica dioica
Potentilla anserina	Trifolium pratense	Dryopteris carthusiana	Vicia cracca
Rumex crispus	Achillea millefolium	Galium mollugo	Achillea millefolium
Sagina nodosa	Agrostis gigantea	Kobresia esenbeckii	Aira praecox
Senecio viscosus	Anthyllis vulneraria	Leymus arenarius	Apium graveolens
Solanum dulcamara	Armeria ruscinonensis	Ranunculus repens	Betula pendula
Stellaria graminea	Calamagrostis epigejos	Rumex acetosa	Carex binervis
Stellaria media	Centaurium littorale	Senecio vulgaris	Cirsium arvense
Tripleurospermum maritimum	Cynosurus cristatus		Corynephorus canescens
Viola tricolor	Empetrum nigrum		Elymus athericus
	Jacobaea vulgaris		Elymus farctus
	Leucanthemum vulgare		Elymus repens
	Linum catharticum		Festuca ovina

	Lonicera periclymenum		Galium aparine
	Pilosella officinarum		Galium verum
	Potentilla anserina		Juncus effusus
	Ranunculus acris		Leymus arenarius
	Rhinanthus minor		Linaria vulgaris
	Rhinanthus serotinus		Lotus corniculatus
	Rubus pseudojaponicus		Phragmites australis
	Scleranthus perennis		Plantago lanceolata
	Silene otites		Polygala vulgaris
	Sonchus arvensis		Rumex crispus
	Trifolium repens		Solanum dulcamara
	Tuberaria guttata		Sonchus arvensis
	Asparagus officinalis		Tripleurospermum maritimum
	Bromus secalinus		Viola canina
	Calluna vulgaris		Viola tricolor
	Carex flacca		
	Cirsium arvense		
	Cuscuta europaea		
	Elymus athericus		
	Elymus farctus		
	Erophila verna		
	Festuca arundinacea		
	Festuca filiformis		
	Galium verum		
	Hypericum perforatum		
	Lathyrus pratensis		
	Leymus arenarius		
	Lysimachia maritima		
	Nardus stricta		
	Oenothera parviflora		
	Phragmites australis		
	Plantago coronopus		
	Plantago maritima		
	Rosa canina		

	Sagina nodosa		
	Senecio sylvaticus		
	Stachys annua		
	Taraxacum campylodes		
	Trifolium campestre		
	Vicia lathyroides		
	Viola tricolor		

Table S3.9 List of species occurring in the three maturity stages of dune slack habitats, ranked by species commonness

Pioneer dune slacks	Dune slack fens	Dune slack woodland
Juncus articulatus	Salix repens	Betula pubescens
Hydrocotyle vulgaris	Agrostis gigantea	Salix repens
Salix repens	Potentilla anserina	Phragmites australis
Agrostis gigantea	Festuca rubra	Calamagrostis canescens
Ranunculus pulchellus	Hydrocotyle vulgaris	Rubus pseudojaponicus
Eleocharis palustris	Juncus articulatus	Erica tetralix
Mentha aquatica	Calamagrostis epigejos	Sorbus aucuparia
Phragmites australis	Mentha aquatica	Empetrum nigrum
Samolus valerandi	Phragmites australis	Agrostis gigantea
Potentilla anserina	Holcus lanatus	Calamagrostis epigejos
Equisetum palustre	Carex flacca	Juncus conglomeratus
Equisetum arvense	Epipactis palustris	Anthoxanthum odoratum
Baldellia ranunculoides	Galium palustre	Holcus lanatus
Galium palustre	Linum catharticum	Poa pratensis
Centaurium littorale	Parnassia palustris	Urtica dioica
Holcus lanatus	Schoenus nigricans	Agrostis capillaris
Littorella uniflora	Elaeagnus rhamnoides	Quercus robur
Utricularia australis	Liparis loeselii	Dryopteris dilatata
Kobresia esenbeckii	Juncus conglomeratus	Festuca rubra
Sagina nodosa	Kobresia esenbeckii	Galium palustre
Eleocharis uniglumis	Betula pubescens	Mentha aquatica

Radiola linoides	Eupatorium cannabinum	Calluna vulgaris
Lotus corniculatus	Anagallis minima	Carex riparia
Festuca rubra	Elymus repens	Galium aparine
Armeria ruscinonensis	Juncus gerardii	Lonicera periclymenum
Anagallis minima	Lysimachia maritima	Alnus glutinosa
Plantago coronopus	Pyrola rotundifolia	Poa trivialis
Rumex acetosella	Sonchus arvensis	Bromus secalinus
Trifolium repens	Eleocharis uniglumis	Cirsium palustre
Juncus bufonius	Rubus pseudojaponicus	Hydrocotyle vulgaris
Calamagrostis canescens	Carex binervis	Juncus effusus
Potamogeton gramineus	Dactylorhiza incarnata	Kobresia esenbeckii
Cerastium fontanum	Calamagrostis canescens	Luzula campestris
Agrostis capillaris	Cirsium palustre	Festuca ovina
Cardamine pratensis	Lycopus europaeus	Lycopus europaeus
Juncus conglomeratus	Ranunculus pulchellus	Populus tremula
Poa infirma	Eleocharis palustris	Vaccinium uliginosum
Calamagrostis epigejos	Lotus corniculatus	Vicia cracca
Carex flacca	Sagina nodosa	Deschampsia flexuosa
Cirsium palustre	Comarum palustre	Viburnum opulus
Myosotis scorpioides	Lythrum salicaria	Cladium chinense
Sagina procumbens	Oenanthe lachenalii	Crataegus monogyna
Calluna vulgaris	Prunella vulgaris	Dactylis glomerata
Lycopodiella inundata	Samolus valerandi	Danthonia decumbens
Anthoxanthum odoratum	Anthoxanthum odoratum	Lathyrus pratensis
Drosera rotundifolia	Carex notha	Lythrum salicaria
Juncus gerardii	Centaurium littorale	Nardus stricta
Odontites verna	Eleocharis quinqueflora	Potentilla recta
Danthonia decumbens	Empetrum nigrum	Solanum dulcamara
Epipactis palustris	Eriophorum angustifolium	Comarum palustre
Lysimachia maritima	Hypochaeris radicata	Polypodium vulgare
Stellaria media	Plantago coronopus	Ranunculus repens
Centaurium pulchellum	Cirsium arvense	Scutellaria galericulata
Corynephorus canescens	Festuca arundinacea	Acer pseudoplatanus

Eleocharis quinqueflora	Lathyrus pratensis	Aira praecox
Erica tetralix	Plantago lanceolata	Cardamine pratensis
Gnaphalium uliginosum	Rumex acetosa	Eriophorum angustifolium
Liparis loeselii	Armeria ruscinonensis	Galium mollugo
Lycopus europaeus	Calluna vulgaris	Luzula multiflora
Empetrum nigrum	Cardamine pratensis	Potentilla anserina
Juncus bulbosus	Carex pseudocyperus	Ribes nigrum
Linum catharticum	Centaurium pulchellum	Rosa canina
Nardus stricta	Cerastium fontanum	Rubus gratus
Rubus pseudojaponicus	Danthonia decumbens	Utricularia australis
Betula pubescens	Erica tetralix	Betula pendula
Eriophorum angustifolium	Odontites verna	Cirsium vulgare
Limosella aquatica	Radiola linoides	Drosera rotundifolia
Elaeagnus rhamnoides	Trifolium repens	Dryopteris carthusiana
Elymus athericus	Agrostis capillaris	Eleocharis palustris
Juncus acutiflorus	Dactylis glomerata	Epilobium hirsutum
Lythrum portula	Juncus bufonius	Equisetum arvense
Myosotis laxa	Linaria vulgaris	Equisetum palustre
Poa pratensis	Luzula campestris	Hypericum tetrapterum
Ranunculus baudotii	Ophioglossum vulgatum	Iris pseudacorus
Ranunculus repens	Pedicularis palustris	Jacobaea vulgaris
Senecio vulgaris	Plantago maritima	Juncus maritimus
Sonchus arvensis	Polygala vulgaris	Lotus corniculatus
Aira praecox	Triglochin maritima	Molinia caerulea
Ammophila arenaria	Utricularia australis	Myosotis scorpioides
Artemisia maritima	Vaccinium uliginosum	Myrica gale
Carex binervis	Vicia cracca	Prunella vulgaris
Cerastium semidecandrum	Viola palustris	Prunus cornuta
Equisetum variegatum	Apium graveolens	Radiola linoides
Linaria vulgaris	Baldellia ranunculoides	Rosa rubiginosa
Lythrum salicaria	Blysmus rufus	Sambucus nigra
Plantago major	Bromus secalinus	Stellaria graminea
Potamogeton polygonus	Carex sartwellii	Stellaria holostea
Sagina maritima	Cirsium vulgare	Stellaria media
Scorzoneroides autumnalis	Drosera rotundifolia	Vaccinium macrocarpon

Atriplex portulacoides	Galium mollugo	Viola palustris
Bolboschoenus maritimus	Jacobaea vulgaris	
Bromus secalinus	Lysimachia thyrsiflora	
Carex sartwellii	Myosotis scorpioides	
Cirsium arvense	Nardus stricta	
Dactylorhiza incarnata	Pinguicula vulgaris	
Elymus repens	Potentilla recta	
Eupatorium cannabinum	Ranunculus acris	
Festuca ovina	Rumex acetosella	
Jacobaea vulgaris	Scorzoneroides autumnalis	
Lysimachia thyrsiflora	Silene flos-cuculi	
Myriophyllum spicatum	Trifolium dubium	
Parnassia palustris	Urtica dioica	
Persicaria amphibia	Viola canina	
Plantago lanceolata		
Plantago maritima		
Potentilla recta		
Rorippa palustris		
Rosa canina		
Rosa rugosa		
Rumex crispus		
Senecio inaequidens		
Senecio sylvaticus		
Trifolium campestre		
Trifolium dubium		
Trifolium fragiferum		
Typha latifolia		
Vaccinium uliginosum		
Vicia cracca		
Viola palustris		
Zanthoxylum leprieurii		

Table S3.10 List of species occurring in the four maturity stages of salt marshes, ranked by species commonness

Pioneer zone	Lower marsh	Upper marsh	Brackish marsh
Suaeda maritima	Puccinellia maritima	Festuca rubra	Bolboschoenus maritimus
Salicornia procumbens	Suaeda maritima	Juncus gerardii	Agrostis gigantea
Puccinellia maritima	Atriplex portulacoides	Agrostis gigantea	Potentilla anserina
Atriplex portulacoides	Salicornia europaea	Artemisia maritima	Eleocharis uniglumis
Limonium vulgare	Artemisia maritima	Elymus athericus	Juncus gerardii
Salicornia europaea	Triglochin maritima	Lysimachia maritima	Lysimachia maritima
Spergularia marina	Limonium vulgare	Atriplex portulacoides	Phragmites australis
Triglochin maritima	Spergularia media	Potentilla anserina	Plantago maritima
Spergularia media	Festuca rubra	Limonium vulgare	Puccinellia distans
Agrostis gigantea	Lysimachia maritima	Armeria ruscinonensis	Atriplex portulacoides
Artemisia maritima	Elymus athericus	Plantago maritima	Chenopodium rubrum
Elymus farctus	Plantago maritima	Suaeda maritima	Cotula coronopifolia
Lysimachia maritima	Salicornia procumbens	Elymus repens	Salicornia europaea
Plantago maritima	Spergularia marina	Trifolium repens	Spergularia marina
Poa pratensis	Juncus gerardii	Poa pratensis	Blysmus rufus
Spartina maritima	Armeria ruscinonensis	Juncus maritimus	Festuca rubra
	Atriplex cristata	Triglochin maritima	Juncus articulatus
	Agrostis gigantea	Carex binervis	Odontites verna
	Carex diluta	Puccinellia maritima	Ranunculus baudotii
		Salicornia europaea	Scorzoneroides autumnalis
		Lolium perenne	Triglochin maritima
		Odontites verna	Armeria ruscinonensis
		Plantago coronopus	Bromus secalinus
		Scorzoneroides autumnalis	Eleocharis palustris

		Trifolium pratense	Elymus athericus
		Atriplex cristata	Galium palustre
		Holcus lanatus	Glyceria fluitans
		Lotus corniculatus	Hydrocotyle vulgaris
		Cirsium arvense	Juncus maritimus
		Cochlearia danica	Lemna minor
		Cerastium fontanum	Lotus corniculatus
		Phragmites australis	Mentha aquatica
		Plantago lanceolata	Myosotis scorpioides
		Plantago major	Oenanthe lachenalii
		Salix repens	Plantago coronopus
		Sonchus arvensis	Ranunculus pulchellus
		Trifolium fragiferum	Ranunculus sceleratus
		Spergularia media	Rumex acetosa
		Carex diluta	Rumex crispus
		Carex flacca	Schoenoplectus tabernaemontani
		Eleocharis uniglumis	Senecio viscosus
		Rumex crispus	Spergularia media
		Spergularia marina	Suaeda maritima
		Anthoxanthum odoratum	Taraxacum campylodes
		Centaurium littorale	Trifolium fragiferum
		Poa infirma	Triglochin palustris
		Sagina maritima	Typha latifolia
		Agrostis capillaris	
		Bolboschoenus maritimus	
		Linum catharticum	
		Rumex acetosa	
		Salicornia procumbens	
		Taraxacum campylodes	
		Cirsium palustre	
		Festuca arundinacea	
		Linaria vulgaris	

		Oenanthe lachenalii	
		Silene flos-cuculi	
		Stellaria graminea	
		Apium graveolens	
		Calamagrostis epigejos	
		Cirsium vulgare	
		Dactylis glomerata	
		Galium palustre	
		Lathyrus pratensis	
		Ranunculus repens	
		Sagina nodosa	
		Sagina procumbens	
		Schoenus nigricans	
		Angelica sylvestris	
		Bromus secalinus	
		Cynosurus cristatus	
		Elaeagnus rhamnoides	
		Elymus farctus	
		Empetrum nigrum	
		Hypericum tetrapterum	
		Hypochaeris radicata	
		Lotus pedunculatus	
		Lythrum salicaria	
		Mentha aquatica	
		Myosotis scorpioides	
		Nardus stricta	
		Vicia cracca	