Anthropogenic biodiversity changes and altered biogeographic patterns on islands

Dissertation

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Coastline of Madeira. Island biodiversity today is the result of a complex interplay of natural and anthropogenic factors. © Anna Walentowitz

“You cannot get through a single day without having an impact on the world. What you do makes a difference, and you have to decide what kind of difference you want to make.”

- Jane Goodall -

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Graphical Abstract

Guiding theme

Anthropogenic biodiversity changes and altered biogeographic patterns on islands

Background

Extant island biodiversity is the result of a complex interplay between natural and human-mediated factors. As a result, contemporary biodiversity patterns are composed of natural and anthropogenic aspects.

Research questions

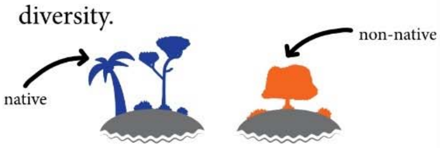
How is island biogeographic theory influenced by anthropogenic biodiversity change?

How do extant insular biodiversity patterns relate to anthropogenic drivers of change?

Multi-island approach (part 1):

Develop, test and challenge theories and notions in island biogeography.

Manuscript 1: Disentangle natural and anthropogenic drivers of native and non-native insular plant diversity.



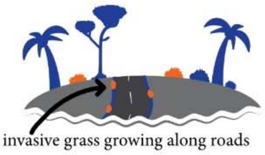
Manuscript 2: Apply functional approaches to island biogeographic theory.

Manuscript 3: Reconstruct past trajectories of non-native vegetation on islands.

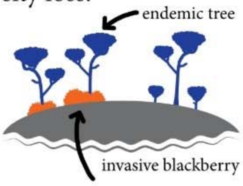
Single island approach (part 2):

Highlight and analyse specific aspects of anthropogenically-altered insular biodiversity patterns.

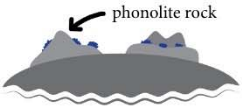
Manuscripts 4 & 6: Investigate invasive plant species as a phenomenon of biodiversity in the Anthropocene.



Manuscript 5: Assess ecosystem restoration as a means to mitigate biodiversity loss.



Manuscripts 7 and 8: Use arks of biodiversity to assess geodiversity-biodiversity relationships.



Manuscript 9: Update a plant species checklist to support open-access policies and biogeographic studies.

Dissertation Summary

German Summary

Aktuelle Biodiversitätsmuster auf Inseln sind das Resultat eines komplexen Zusammenspiels natürlicher und anthropogener biogeografischer Einflussfaktoren. Die Entstehungsgeschichte von Inseln, ihre Größe, Topografie, Isolation und latitudinale Lage, sind nur einige Parameter, die das spezifische Vorkommen von Arten auf Inseln bestimmen. Über Jahrtausende und -millionen haben sich so einzigartige insulare Ökosystemen und Artengemeinschaften entwickelt. Seit der weltweiten menschlichen Besiedlung haben Inseln jedoch eine zusätzliche Dimension des Wandels erfahren. Natürliche Landschaften werden zunehmend in landwirtschaftliche Flächen und Siedlungen umgewandelt. Infrastruktur fragmentiert Ökosysteme, natürliche Ressourcen werden ausgebeutet und das Klima verändert sich mit immenser Geschwindigkeit. Pflanzen- und Tierarten werden weltweit absichtlich oder versehentlich aus ihren natürlichen Verbreitungsgebieten transportiert und gelangen auf diese Weise auch auf Inseln, auf denen sie gebietsfremd sind.

Angesichts der anhaltenden Veränderung natürlicher Ökosysteme im Anthropozän ist es von grundlegender Bedeutung, die Auswirkungen natürlicher Faktoren auf Biodiversitätsmuster von menschlichen Veränderungen zu unterscheiden. Im Zusammenhang mit dem globalen Biodiversitätsverlust ist die Entflechtung von Wirkungsmechanismen und Kausalitäten, welche insulare Biodiversität beeinflussen, für ein besseres Verständnis der natürlichen langfristigen ökologischen und evolutionären Prinzipien in unserer sich schnell wandelnden Welt unerlässlich.

Diese Doktorarbeit widmet sich der Untersuchung vielseitiger inselbiogeographischer Muster und ihrer Entstehung im Anthropozän. Die präsentierten Manuskripte bauen auf dem Vermächtnis vorheriger Forschung im Bereich der Inselbiogeografie auf. Inseln werden dabei als Mikrokosmen oder natürliche Laboratorien genutzt, um biogeografische Theorien zu entwickeln, zu testen, und zu hinterfragen. So erweitert die in dieser Doktorarbeit präsentierte Forschung unser Wissen über spezifische Aspekte der natürlichen sowie der vom Menschen beeinflussten Biodiversität. Diese Arbeit befasst sich somit mit dem sogenannten *Hookerschen* Defizit der Biodiversitätsforschung (engl. *Hookerian* shortfall). Dieses beschreibt die Problematik ob Inselökosysteme trotz anthropogener Überprägung für Biodiversitätsforschung genutzt werden können.

Der erste Teil der zugrunde liegenden Arbeit umfasst biogeografische Studien basierend auf multiplen Inselsysteme. Die hierfür analysierten Referenzsysteme sind küstennahe, kontinentale und ozeanische Inseln weltweit. Hierbei werden anthropogene Aspekte einbezogen, um die klassische Theorie der Inselbiogeografie weiterzuentwickeln. Ein Novum ist die Verknüpfung funktioneller Aspekte, hier speziell Verbreitungsmechanismen von Pflanzen, mit der biogeografischen Inseltheorie, unter Einbezug anthropogener Veränderung der Biodiversität auf Inseln. Eine globale paläoökologische Studie über langfristige Verläufe der zeitlichen Entwicklung gebietsfremder Pflanzen weist auf ein frühes Vorkommen solcher Arten (vor 1000 Jahren) auf Inseln hin, welches von wissenschaftlichen Aufzeichnungen (maximal 500 Jahre) divergiert. Diese Arbeit leistet eine Diskussionsgrundlage für die Existenz von neuartigen Ökosystemen (engl. novel ecosystems) und kann als Referenzstudie für Ökosystemrestauration und Naturschutz auf Inseln dienen.

Im zweiten Teil dieser Arbeit werden Fallstudien mit Fokus auf spezifische Aspekte der kontemporären Inselbiodiversität vorgestellt. Die Untersuchungsgebiete sind hierbei die Kanaren und die Galápagos-Inseln. Diese Archipele wurden von der Autorin für ökologische Feldarbeiten besucht. Dabei den wissenschaftlichen Spuren von Alexander von Humboldt und Charles Darwin zu folgen, deren Entwicklung ökologischer und evolutionärer Theorien von diesen Inselsysteme inspiriert wurde, ist ein enormes Privileg. In den dargelegten Untersuchungen werden biogeographische Muster gebietsfremder Pflanzenarten und deren Auswirkungen auf die heimische Vegetation analysiert. Die Ergebnisse dienen als Grundlage für die Wiederherstellung ursprünglicher Ökosysteme, um nachteilige Auswirkungen eingeführter Neobiota auf endemische Arten zu mindern. Darüber hinaus werden natürliche insulare Biodiversitätsrefugien auf den Kanarischen Inseln hinsichtlich des Geodiversitäts-Biodiversitäts-zusammenhangs untersucht. Diese Refugien sind wichtige Referenzgebiete in einer Welt, die stark durch menschliche Aktivität beeinflusst ist. Ein umfassendes floristisches Gesamtwerk der Kanarenflora als Referenz für biogeografische, ökologische und evolutionäre Studien ergänzt diesen Abschnitt.

Die vorliegende Doktorarbeit leistet einen Beitrag zum verbesserten Verständnis insularer Biodiversitätsmuster im Anthropozän. Die Fortschritte beziehen sich auf die Berücksichtigung anthropogener Einflüsse auf Artverbreitungen, den Einbezug funktionaler Aspekte in die biogeografische Inseltheorie und die Rekonstruktion temporärer Biodiversitätsveränderungen. Generell ist die Berücksichtigung anthropogener Biodiversitätsveränderungen in der Inselbiogeografie eine zukünftige Herausforderung. Meine Arbeit leistet einen Beitrag zu einem verbesserten Verständnis von historischen und aktuellen Biodiversitätsmustern auf Inseln.

English Summary

Current biodiversity patterns on islands are the result of a complex interplay of natural and anthropogenic biogeographic drivers. Island ontogeny, area, topography, isolation, and latitudinal location on the planet, to name just a few, play a central role in determining insular species occurrences. Over millennia and millions of years, islands have assembled unique species communities shaped by their typical environmental characteristics. However, since the emergence and planetary-wide settlement of humans, islands have experienced an additional dimension of change. Natural land was converted into agricultural fields, meadows, and settlements. Infrastructure cuts across ecosystems, natural resources are exploited, and climate is changing at immense speed. Plant and animal species are transported deliberately or accidentally outside their natural ranges and that way also reach islands.

Given the ongoing changes to natural ecosystems in the Anthropocene, it is fundamental to differentiate between impacts of natural and human drivers of changes to biodiversity patterns. In the context of global biodiversity transformation and loss, disentanglement of precise impact mechanisms and causalities affecting insular biodiversity is essential for a better understanding of natural long-term ecological and evolutionary principles in our rapidly changing world.

This thesis is devoted to study biogeographic patterns and their emergence in the Anthropocene in multifaceted ways. The manuscripts presented built upon the legacy of island biogeographic research. Islands with their discrete boundaries are used as microcosms or natural laboratories to develop, test, and challenge biogeographic theory. The presented research thereby extends our knowledge on specific aspects of natural as well as human-mediated biodiversity. This thesis thereby addresses the so-called *Hookerian* shortfall of biodiversity research that focuses on the challenge of using islands as discrete ecosystems to understand biodiversity changes in times of heavy anthropogenic alterations of entire landscapes.

The first part of the underlying work comprises multi-island studies and incorporates anthropogenic aspects to advance classic theory of island biogeography. The analysed reference systems are barrier, continental, and oceanic islands around the globe. A novelty is the linkage of functional aspects, precisely plant dispersal syndromes, to island biogeographic theory while also accounting for human-mediated change of island biodiversity. A global palaeoecological study on long-term trajectories of temporal non-native species development unveils an earlier onset of such species (1000 years ago) than has been deduced from existent censuses and scientific records (500 years ago). This study relates to ongoing discussions about novel ecosystems and provides baseline information for restoration and conservation projects on islands.

The development of specific case studies, presented in the second part of this thesis, enables a detailed view on specific aspects of extant insular biodiversity. The Canary and Galápagos Islands serve as reference systems as these archipelagos were visited by the author of this doctoral thesis for field work. It is a privilege to follow the scientific routes of Alexander von Humboldt and Charles Darwin, whose ground-breaking advances in ecology and evolutionary biology were inspired by these particular island systems. The presented case studies analyse biogeographic patterns of non-native plant species and their impacts on native vegetation. The findings aid understanding of invasions and ecosystem restoration to mitigate adverse impacts of such introduced biota on island endemics. Furthermore, local arks of outstanding insular biodiversity, that constitute important reference sites as opposed to heavily human-impacted areas in the Canary Islands, are studied. A comprehensive floristic baseline established for this archipelago to advance and support biogeographic, ecological, and evolutionary studies complements this section.

This thesis contributes to the general understanding of insular biodiversity patterns in the Anthropocene. Thereby, advancements from the inclusion of the anthropogenic dimensions into assessments of extant species' distributions, incorporation of functional, dispersal-related aspects into island biogeographic theory, and the development of biodiversity timelines are achieved. Contemporizing island biogeography is a future challenge. This doctoral thesis is a contribution to a better understanding of past and current biodiversity on islands.

1. Introduction

1.1. Personal Motivation

Why biogeography? Why islands? These two questions might arise when reading through the pages and manuscripts of this thesis. These topics build the foundation of my work, and I feel privileged to focus on these scientific matters. My motivation to dedicate this thesis to biogeography, mostly on islands, is driven by the following scientific and conservational challenges.

Firstly, the current environmental crises, primarily biodiversity loss and climate change, that we are facing nowadays, can only be tackled on the grounds of sound science. We need data, long-term monitoring, projections, experiments, and reviews that provide the foundation for science-based biodiversity conservation and ecosystem restoration. I am convinced that highly motivated and creative scientists are needed for this task who do not hesitate to work at the interface of science, politics, and hands-on conservation management. I started to write the introduction of my doctoral thesis in the summer of 2022, which brought an exceptional drought to Europe – climate crisis experienced first-hand. During the three years of research and active writing for this doctoral thesis, an estimated total of 900 – 1560 species were driven to extinction globally (considering anthropogenically accelerated extinction rates of the last 500 years, Cowie *et al.* 2022) – the reality of ongoing biodiversity loss. Biogeography has a key role in comprehending human-mediated ecological changes as this discipline aims to detect biodiversity patterns and understand underlying processes. In the first place, this research domain and the related fields of ecology and evolutionary biology have a long tradition of foundational research to understand the emergence and composition of natural systems and species assemblages. These scientific disciplines have shaped our conception of the natural world. Moreover, a recent development in biogeography is the incorporation of the human dimension into foundational research. This diversification is essential to understand and subsequently tackle contemporary challenges, such as ongoing species extinctions and biodiversity degradation. Island biogeography is particularly well suited to investigate such changes, as islands can be seen as miniature ecosystems or natural laboratories where patterns and processes become evident more clearly compared to complex and vast mainland areas. Extended knowledge of biodiversity change and the fundamental underlying drivers will ease the development of effective policy-actions, conservation, and restoration measures to counteract detrimental and worrying biodiversity decline. I hope that my scientific work can contribute to build the foundations for an enhanced understanding and subsequently active protection of the astonishing nature our planet has to offer.

Secondly, I was highly motivated to write this thesis based on my background. I have had outstanding mentors and teachers during my time as a doctoral candidate and Master's student in Biodiversity and Ecology at the University of Bayreuth and Bachelor's student in Landscape Ecology and Nature Conservation International at the University of Greifswald. Moreover, I am convinced that my environmental education began long before. Growing up on the German North Sea coast in a family that taught me to love the outdoors and notice all the astonishing details nature has to offer was the most valuable gift I got. My inherent fascination and curiosity still form the basis and are my motivation to work as a scientist.

1.2. Scientific Background

Obtaining knowledge about a multifaceted and complex concept like biodiversity is challenging. Seven shortfalls hampering the analysis and our understanding of biodiversity patterns were identified. These refer to knowledge gaps concerning undescribed and extinct species (*Linnean* shortfall), unknown species' distributions (*Wallacean* shortfall), abundances (*Prestonian* shortfall), and traits (*Raunkiaeran* shortfall), missing information about the evolutionary history of species (*Darwinian* shortfall), lacking knowledge about species' tolerances of abiotic environmental conditions (*Hutchinsonian* shortfall), and insufficient understanding of interactions among species (*Eltonian* shortfall) (Brown & Lomolino 1998; Bini *et al.* 2006; Cardoso *et al.* 2011; Diniz-Filho *et al.* 2013; Hortal *et al.* 2015). Recently, an additional shortfall of biodiversity research was proposed, namely the *Hookerian* shortfall that describes our limited knowledge about anthropogenic alterations of biodiversity patterns (Carine & Menezes de Sequeira 2020). The British botanist Joseph Dalton Hooker, after whom this knowledge gap is named, already realized back in the 19th century that island floras have been massively influenced by humans. At the example of the Atlantic islands Madeira and St. Helena, Hooker demonstrated that anthropogenic influence on island biodiversity can be difficult to differentiate from natural processes and resulting patterns. Thereby, he pointed out the challenge of utilizing islands as reference systems for investigating the natural world when biodiversity has already been altered by human interventions (Carine & Menezes de Sequeira 2020).

This doctoral thesis addresses the *Hookerian* shortfall in a wider sense and aims at studying contemporary insular biodiversity by integrating anthropogenic aspects into island biogeography. For the following two main reasons, anthropogenic changes in island biota are of paramount importance for science and society.

1. **Understanding and conserving biodiversity in the Anthropocene**: Human-induced global biodiversity decline is leading to changes in species assemblages around the globe and at immense speed (Pereira *et al.* 2010). Such ecological degradation can be considered one of the most urgent environmental and societal challenges of our times. To understand ongoing changes in biodiversity in particular, and alterations of the natural environment in general, the precise impact mechanisms of anthropogenic encroachment need to be understood. Islands can be seen as miniature replicates of the Earth with individual onsets of the Anthropocene starting with the arrival of humans (Helmus *et al.* 2014; Whittaker *et al.* 2017). This opens unique research opportunities to understand current biodiversity changes caused by humans. Especially biodiversity conservation and ecosystem restoration will benefit from such scientific advances in this field.

2. **Studying natural patterns and processes:** To continue using islands as study areas for developing and testing fundamental theories in biogeography, ecology and evolutionary biology (Warren *et al.* 2015; Whittaker *et al.* 2017), we need to understand how the nature of islands has changed and is changing through human activity. To be able to differentiate between purely natural and anthropogenically-influenced biodiversity patterns and respective drivers, we need to know how humans have been and still are influencing nature, and how resulting impacts affect naturally isolated island systems. The more profoundly island systems are anthropogenically altered, the harder it becomes to detect natural patterns and understand their emergence. Thus, foundational research of natural biodiversity in island biogeography is

dependent on understanding anthropogenic aspects of change to reach the aim of improved understanding of the 'true' nature of island ecology and evolution unaffected by humans (Graham *et al.* 2017).

These two overarching objectives form the foundation of my doctoral thesis. The implied tasks in this vast research field may occupy generations of island biogeographers. Thus, my goal and motivation were to design research projects that cover specific aspects within the large scope of this research field. Within the guiding theme of this thesis, the manuscripts presented comprise a diversity of methodological approaches, temporal and spatial scales, and specific research foci: from field work to modelling, from single island to global analysis, from palaeoecological research covering several millennia to an applied restoration study of five years and snapshot analysis of extant insular biodiversity.

1.3. Structure of this Thesis

In the following, I will describe the background and scientific journey leading from the foundations of island biogeography to current research frontiers (Chapters 2-5). I present how the incorporation of anthropogenic aspects into island biogeography is tackled by the research community (Chapter 4) and how this integration might be reflected in future research (Chapter 5). Thereby, I outline the different scientific trajectories that led to the development of my projects presented in this thesis as Manuscripts 1-9.

An overview of the published and submitted manuscripts forming the core of this thesis, including a declaration of my contributions to single research projects, is presented. Following this overview, I will present the nine scientific manuscripts that form the core of this thesis (Table 1). Preceding each manuscript, a short intermittent introductory text declares the scientific ties of each piece of work to the leading theme. These summaries guide the reader from manuscript to manuscript and highlight the storyline of my doctoral thesis. A list of references for the overall introduction and the summaries preceding each manuscript can be found at the end of the document.

Table 1: Manuscripts presented in this thesis.

Manuscript no.	Title	Publication	Journal
1	Disentangling natural and anthropogenic drivers of native and non-native plant diversity on North Sea islands	Walentowitz *et al.* (accepted)	Journal of Biogeography
2	Plant dispersal characteristics shape the relationship of diversity with area and isolation	Walentowitz *et al.* (2022)	Journal of Biogeography
3	Long-term trajectories of non-native vegetation on islands globally	Walentowitz *et al.* (2023)	Ecology Letters
4	Graminoid Invasion in an Insular Endemism Hotspot and Its Protected Areas	Walentowitz *et al.* (2019)	Diversity

5	Limited natural regeneration of unique Scalesia forest following invasive plant removal in Galapagos	Walentowitz *et al.* (2021b)	PLOS ONE
6	Assessing the Potential Replacement of Laurel Forest by a Novel Ecosystem in the Steep Terrain of an Oceanic Island	Devkota *et al.* (2020)	Remote Sensing
7	Geodiversity and biodiversity on a volcanic island: the role of scattered phonolites for plant diversity and performance	Kienle *et al.* (2022)	Biogeosciences
8	Vegetation plot and trait data from phonolitic and basaltic rocks on La Palma (Canary Islands, Spain)	Walentowitz *et al.* (2021a)	Data in Brief
9	FloCan—A Revised Checklist for the Flora of the Canary Islands	Beierkuhnlein *et al.* (2021)	Diversity

2. The Role of Islands in Biogeography

2.1. The Development of Island Biogeography as a Research Discipline

Islands are ideal study sites for biogeographers and invaluable for biodiversity sciences and conservation (Whittaker & Fernández-Palacios 2007; Santos *et al.* 2016). They pose excellent replicated study areas, and their simplified nature – compared to mainland areas – and discrete boundaries make them excellent model systems (Sax *et al.* 2002; Whittaker & Fernández-Palacios 2007; Helmus *et al.* 2014). Additionally, islands can be outliers of natural phenomena (e.g., insular gigantism and dwarfism, Lomolino 1985; Keogh *et al.* 2005) and are biodiversity hotspots of Earth in general, and endemism hotspots in particular (Myers *et al.* 2000). They contribute roughly 20% to global species richness while covering only 6.7% of the terrestrial landmasses (Whittaker & Fernández-Palacios 2007; Kier *et al.* 2009; Sayre *et al.* 2019). In plants, endemism is 9.5 times higher on islands compared to mainland areas (Kier *et al.* 2009).

These characteristics have made islands predestined to inspire ideas in biogeography, ecology and evolutionary biology and to enable the development and testing of theories within these fields (Whittaker & Fernández-Palacios 2007). Therefore, islands have a long history in sciences like biogeography and evolutionary biology as they ease the understanding of natural processes and pattern formation. Naturalists like Charles R. Darwin, Alfred Russel Wallace, and Alexander von Humboldt were inspired by islands to develop thoughts and theories on evolution and ecology. Von Humboldt was intrigued by the nature of Tenerife (Canary Islands), and in particular, the Teide volcano. He was the first to capture the altitudinal distribution of vegetation of this volcano, reflecting bioclimatic segregation, in a historic illustration (von Humbold & Bonpland 1826). The observations and collections of different subspecies of endemic mockingbirds (*Mimus parvulus*) on the distinct Galápagos Islands were crucial for Darwin to develop his seminal work 'On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life' known under the short title 'On the Origin of Species' (Darwin 1859). This writing built the foundations of evolutionary biology and, by then, was revolutionary at times when the worldview of western societies was very much a biblical one. Simultaneously, Wallace derived similar conclusions about natural selection and the phylogeny of species when meticulously observing the fauna and flora in the Malay Archipelago (Darwin & Wallace 1858; Wallace 1880).

In the aftermath of the seminal works by historic naturalists, islands continued to inspire the natural sciences. Alvar Palmgren (Palmgren 1915, 1921) and Eugene Gordon Monroe (Monroe 1948, 1953; Brown & Lomolino 1989), for example, developed thoughts on the relationship of island characteristics, such as area and geographic isolation, with species richness. However, the formation of 'island biogeography' as a scientific discipline can be pinpointed to the publication of the monography 'The Theory of Island Biogeography' by Robert H. MacArthur and Edward O. Wilson (1967). While island research previously was mostly based on descriptive observations, MacArthur and Wilson were the first to quantify island biogeographic theory. Their theory and work will be thematized in detail in Chapter 2.3 of this thesis. Besides MacArthur and Wilson, the work of Ernst Mayr (1963), Sherwin J. Carlquist (1965, 1974), Daniel Simberloff (1970), and Jared M. Diamond (1975) on island biology, speciation, taxonomy, and community ecology was influential and formative for island biogeography.

The high interest in island systems in scientific research and conservation has led to the development of numerous studies on the topic, with a continuous increase in the annual number of published papers (Figure 1 in Chapter 4.1). Indeed, our evolutionary and ecological understanding of the natural world has been shaped immensely by research conducted on and about insular ecosystems (Santos *et al.* 2016). The manuscripts presented in this doctoral thesis are built upon this legacy in island biogeographical research.

2.2. The Diversity of Islands

The simplest definition of an island is a waterlogged piece of land, also termed a 'true island' (Whittaker & Fernández-Palacios 2007). Marine islands comprise a wide spectrum of different types varying in ontogeny and other characteristics, ranging from island continents (Australia), continental fragments (e.g., Madagascar, Socotra) and continental shelf islands (e.g., Newfoundland, Vancouver Island) to true oceanic islands (e.g., Galápagos Islands, Canary Islands) (Whittaker & Fernández-Palacios 2007). Continental fragments have formerly been part of continental landmasses while shelf islands are located on continental plates. In contrast, oceanic islands have never had a connection to mainland areas and were formed on oceanic plates by volcanic or tectonic activities. Furthermore, coastal islands such as barrier islands (e.g., East Frisian Islands in Germany, Florida Keys in the USA) form in the vicinity of mainland shorelines, generally separated from the mainland (US Department of Commerce 2022). The large spectrum of islands can be perceived to be a gradient rather than fixed categories, and islands can also be of mixed origin belonging to more than one of the mentioned categories (e.g., Kerguelen Islands of the French Southern and Antarctic Lands, Kuril Islands south of Kamchatka). Besides marine islands, islands in riverine systems and lakes also contribute to the immense diversity of islands (Lassen 1975; Ezcurra *et al.* 1988). In a brought sense, islands are not limited to water-logged areas of land, but the concept can be transferred to other isolated systems. These are commonly referred to as habitat islands and can range from fragmented pieces of land to single trees and even rivers being regarded as land-logged isolated system (e.g., Sepkoski & Rex 1974; Matthews *et al.* 2016; Patiño *et al.* 2018).

Islands do not solely differ in ontogeny but also vary at logarithmic scales in area and geographic isolation (Weigelt *et al.* 2013; Sayre *et al.* 2019). They also differ in altitude and age (Weigelt *et al.* 2013). Their arrangement in archipelagos or as single islands varies and their location on a latitudinal gradient, translating mostly into climatic differences, diverges (Weigelt *et al.* 2013). Oceanic currents and winds furthermore distort latitudinal patterns and therefore abiotic island characteristics (Whittaker & Fernández-Palacios 2007).

By nature, islands can be considered rather dynamic than stable systems. Oceanic islands emerge from volcanic hotspots, are shifting on tectonic plates and are subsequently subject to erosion (e.g., Whittaker *et al.* 2008; Borregaard *et al.* 2016). Here, natural disturbances, such as volcanic activity contribute to the dynamic characteristics of islands. All types of islands are furthermore exposed to tides, wind, wave regimes and ongoing fluvial erosion that change their geomorphology (e.g., Rad *et al.* 2007; Ramalho *et al.* 2013). Some islands, such as barrier islands, located near continental shores and consisting of loose sand, can even change visibly over months and decades (Fitzgerald *et al.* 1984).

While on the one hand, the variety of islands, from true oceanic to habitat islands, enables the testing and developing of theories in biogeography and related disciplines, the same characteristics on the other hand also hamper the generalization of patterns (Whittaker & Fernández-Palacios 2007). Nevertheless, the immense natural diversity of islands forms the foundation of island biogeography.

The manuscripts in this doctoral thesis address different island types. The first presented study (Manuscript 1) focuses on barrier islands located along the North Sea coast of the Netherlands, Germany, and Denmark. It thereby follows the steps of seminal island biogeographic work by Alvar Palmgren (1915, 1921) working in the Åland archipelago and MacArthur and Wilson (1967) investigating a subset of the Florida Keys, both also being coastal island systems. Likewise, the second paper (Walentowitz *et al.* 2022, presented here as Manuscript 2) investigates floral distributions on 54 Danish coastal islands located in the North and Baltic Seas. A global island approach encompassing a heterogenous set of island types is taken in the third research item (Walentowitz *et al.* 2023, presented here as Manuscripts 3). Here, 29 different, mostly oceanic, islands serve as study sites. All manuscripts presented in the second part (Devkota *et al.* 2020, Walentowitz *et al.* 2021a, Walentowitz *et al.* 2021b, Beierkuhnlein *et al.* 2021, Kienle *et al.* 2022, presented here as Manuscripts 5-9) focus on particular oceanic islands, namely the Galápagos and Canary Islands.

2.3. Fundamental Theories in Island Biogeography

The most influential work in island biogeography, forming the foundation of this scientific discipline, was introduced by MacArthur and Wilson (1963, 1967). They developed the equilibrium theory of island biogeography (hereafter ETIB) to predict species richness of discrete land units, such as islands, resulting from opposing processes in time expressed as rates of immigration and extinction. The rate of successful establishment of individual species is considered dependent on the actual total species richness, with higher rates of establishment at lower diversity. Establishment of species is furthermore determined by isolation from source populations. This assumption is supported by the availability of unoccupied ecological niches that are likely to correlate with low species diversity. The rate of local extinction of species populations is dependent on the actual species richness and increases with diversity. At the same time, this rate is modified by area as a proxy for resource availability that translates into population sizes, respectively. The strength and charm of the initial theory resulted from its simplicity and strong mathematical foundation that allowed the quantification of rates and species numbers (MacArthur & Wilson 1963, 1967). The ETIB is, in original, refined and complemented versions, applicable to a wide array of geographic units, such as true islands, but also a multitude of island-like systems like edaphic islands or riverine systems (e.g., MacArthur & Wilson 1967; Sepkoski & Rex 1974; Rosenzweig 1995; Itescu 2019; Dengler *et al.* 2020; Mendez-Castro *et al.* 2021). Evidently, the integration of aspects missing from this simplistic model, such as topography, habitat diversity, the direction of dispersal vectors, age, climate, and speciation are necessary to further understand what is naturally driving species diversity in island systems. Even MacArthur and Wilson themselves (1967) acknowledged that the very simplified nature of their theory lacks several of these aspects. To account for the complexity of ecological systems and the emergence of biogeographic patterns, several of these facets were addressed in the legacy of island biogeography, such as habitat heterogeneity (Rosenzweig 1995; Turner & Tjørve 2005; Hortal *et al.* 2009), island ontogeny, and age (Whittaker *et al.* 2008, 2017; Borregaard *et al.* 2016). Depending on how isolated habitats under consideration deviate from the original two-dimensional spatial concept of MacArthur and Wilson (1963, 1967), its applicability was confirmed, refined, and complemented in numerous subsequent island biogeographic studies (e.g., Lomolino 1984, 1990; Kalmar & Currie 2006; Triantis *et al.* 2012; Matthews *et al.* 2016; Valente *et al.* 2020).

The most fundamental relationship described in island biogeographic theory is the relation between island area and species richness (MacArthur & Wilson 1963; Lomolino 1982, 1984). Area as a predictor variable for species richness has been part of the core of island biogeography since the development of the seminal ETIB (MacArthur & Wilson 1967). Even today, numerous articles discuss this relationship and additional related investigations are frequently being undertaken. Therein, novel aspects, such as the scale-dependency of species-area relationships (Zhang *et al.* 2021; Ren *et al.* 2022), or the link between plant dispersal syndromes and island area (Walentowitz *et al.* 2022, presented here as Manuscript 2) are introduced.

Besides area, the geographic isolation of islands is a fundamental predictor of species richness (MacArthur & Wilson 1967). Limited connectivity is an influential explanatory variable for species numbers on remote islands and archipelagos (Whittaker *et al.* 2008; Borregaard *et al.* 2016). While there are numerous ways of calculating isolation, the most common and one of the simplest metrics is the Euclidean distance of an island to the nearest mainland (Weigelt & Kreft 2013). However, isolation is not only challenging to determine due to the different methods of calculation but also due to the distorting influences of oceanic currents and prevailing wind patterns (Whittaker & Fernández-Palacios 2007). Additionally, islands can be found alone or in archipelago settings, which also challenges the calculation of isolation (Weigelt & Kreft 2013). Although mainland source pools might be distant, islands close by, belonging to the same archipelago, can serve as source pools. This can be advantageous for the species richness of younger islands that are part of an archipelago. In this context, the 'island progression rule' describes that younger islands in archipelago settings benefit from colonisations from adjacent but older islands (e.g, Whittaker *et al.* 2017).

In island biogeographic theory, habitat heterogeneity (also termed habitat diversity) is considered to beget insular species richness by offering higher numbers of ecological niches (Triantis *et al.* 2003; Hortal *et al.* 2009). A fundamental question is whether area *per se* is the driving force of species numbers on islands or if island area might rather be a proxy for habitat diversity (Triantis *et al.* 2003; Whittaker & Fernández-Palacios 2007). MacArthur and Wilson (1967) used area as a proxy for habitat heterogeneity in the ETIB as quality information on habitat diversity was limited. Other studies differentiate between the effects of area and habitat heterogeneity (Udy *et al.* 2021). The logic behind this is that area increases species richness purely by processes related to space, while habitat heterogeneity functions through the availability of niches (Udy *et al.* 2021). In line with the discussion about effects of habitat heterogeneity versus island area, Manuscript 1 incorporates both area and habitat heterogeneity as potential drivers of insular species richness and also accounts for the interrelatedness of these predictor variables.

In the legacy of the ETIB, the general dynamic model of island biogeography (hereafter GDM) was developed specifically for oceanic islands by Whittaker *et al.* (2008) and refined by Borregaard *et al.* (2016). Besides rates of immigration and extinction introduced in the ETIB (MacArthur & Wilson 1967), the GDM also comprises evolutionary processes and conceives islands as geologically dynamic systems that lead to varying environmental carrying capacities in time. In contrast to the ETIB being mainly developed at the example of barrier islands, the GDM applies to oceanic islands where speciation plays a larger role in shaping island biodiversity. The logic herein is that the highest species richness can be found on an island slightly after full emergence, before erosion becomes the dominant island-shaping force, and when the environmental carrying capacity is the highest. The GDM has been extended by Borregaard *et al.* (2016), among others, to also cover continental fragments in contrast to the initial GDM that focused on oceanic islands.

The use of trait-based approaches in island biogeography is increasing in frequency. They offer new research opportunities and insights into biodiversity patterns (Ottaviani *et al.* 2020). In biogeographic studies, species are commonly the outcome level at which patterns and processes are regarded. The ETIB and GDM treat species to be functionally indifferent. However, considering traits instead can provide new insights into biogeographic processes (Schrader *et al.* 2021, 2022). Especially, the emergence and assemblages of unique endemic species on islands make trait-based approaches appealing. In Manuscript 2 (Walentowitz *et al.* 2022), dispersal syndromes as functional characteristics of vascular plant species were used as research entities in addition to purely considering species numbers. The hypotheses in this study were built on the assumption that species' differences in dispersal syndromes led to distinct species assemblages on individual islands. Thus, this work links island biogeographic theory and functional ecology. Despite an increasing effort to integrate trait-based approaches into island biogeography, the functional characteristics of island-specific biota remain a phenomenon that calls for intensified future investigations. Compared to mainland studies, functional approaches are still underrepresented in biological and ecological research concerning island systems (Schrader *et al.* 2021).

2.4. Transdisciplinary Applicability of Island biogeographic Principles

Theories developed within the field of island biogeography can be applied to a wide array of disciplines. In general, islands are of great importance as testing grounds for ecological and evolutionary processes, conservation biology and ecosystem restoration. Insights derived from island biogeographic theory are used in conservation biology concerning the SLOSS (single large or several small) debate where the optimal design of nature reserves as either a few large or sever small ones is being discussed (Higgs 1981). Considering protected areas to be island-like systems that have a certain size and degree of isolation from other reserves, island biogeographic theory helps to understand potential implications on species numbers. The aim of the SLOSS approach is to maximize the carrying capacity and consequently species richness in a given area (Whittaker & Fernández-Palacios 2007). The SLOSS debate is ongoing with valid arguments for both protected area design types (Deane 2022; Fahrig *et al.* 2022).

Any kind of habitat island (e.g., edaphic islands) can also be the subject of island biogeographic research (Matthews *et al.* 2016; Patiño *et al.* 2018; Mendez-Castro *et al.* 2021). Often, habitat islands are indirectly created by humans through fragmentation. The effect of such anthropogenic barriers on biodiversity can be partly assessed with island biogeographic principles (Dembicz *et al.* 2021).

These selected examples are not exhaustive but serve to illustrate the transdisciplinary applicability of island biogeographic research.

3. Human-induced Biodiversity Changes on Islands

3.1. Brief History and Impacts of human Encroachment on Islands

Since the emergence of the *Homo sapiens* (hereafter humans) on Earth, islands have in addition to natural dynamics experienced another dimension of change (Lekevičius 2022). Humans have become a force of planetary scale, altering the environment tremendously. Islands are no exception to this phenomenon (e.g., Nogué *et al.* 2021), as these pieces of land have been of interest to humans all along. The land-sea interface of islands is ideal for humans to benefit from the amenities of both, the land and the sea (Russell & Kueffer 2019). Still, islands pose an inherent fascination to us humans, which is also reflected by millions of tourists being attracted to islands worldwide each year (Sharpley 2012). However, the interactions of humans with island nature for millennia have had severe implications for insular biodiversity (Russell & Kueffer 2019).

Once settled on an island, humans had the ability to change the nature of islands in manifold ways (Russell & Kueffer 2019). Natural resources were exploited, partly till depletion, (e.g., overexploitation and subsequent extinction of megafauna in New Zealand resulting from hunting, Allentoft *et al.* 2014). Extinction events are subsequently considerably more frequent on islands compared to mainland areas (Nic Lughadha *et al.* 2020; Fernández-Palacios *et al.* 2021). Following the loss of particular species, entire trophic cascades can be outbalanced (Kehoe *et al.* 2021). Such biodiversity changes have far-reaching impacts as they are irreversible. An extinct species is eternally lost (ignoring the intentions of bringing back recently extinct species like the mammoth with modern DNA techniques). The introduction of non-native species to natural island systems poses another dimension of biodiversity change induced by humans. In the early settlement history of humans, the introduction of domesticated plant and animal species as resources for food and other human needs was common (Russell & Kueffer 2019). Additionally, numerous species were introduced accidentally (Hulme 2009; White & Shine 2009). These species used humans as dispersal vectors and were thus able to reach locations far off their natural range. Land use change went along with exploitation and the introduction of non-natives, as space was needed for settlements and agriculture (Russell & Kueffer 2019).

In short, once humans settled on an island, species and explicitly plant biodiversity changed rapidly (Rick *et al.* 2013; Johnson *et al.* 2017; Russell & Kueffer 2019; Nogué *et al.* 2021). Deterministic causes of extinctions (i.e., fragmentation, habitat loss, species introductions as predators, diseases or competitors) were added to the ever-existing stochastic causes of species loss (i.e., demographic collapses, extreme weather events, volcanic activity; Whittaker *et al.* 2007). As a consequence, species turnover on islands is 11-fold higher post- compared to pre-human settlement times (Nogué *et al.* 2021). Even the genetic variability of wild populations of extant species (excluding extinct species) was reduced by humans at an average of 5.4-6.5% globally, but by 27.6% on islands (Leigh *et al.* 2019). The changes in island nature in particular and the Earth's natural systems in general, have led to the introduction of the term 'Anthropocene' to describe an era when humans have become the dominating changing planetary force (see Box 1).

Box 1: Anthropocene

The term Anthropocene was introduced by Paul Crutzen at the beginning of the 21st century (Crutzen 2006; Crutzen & Stoermer 2013). It describes a new era in the history of Earth with humans being a geologic force at planetary scale. The clear onset date is, however, under debate. 1800 AD is proposed as the beginning of the Anthropocene, as by then entire landscapes had been transformed as a consequence of the Industrial Revolution (Steffen *et al.* 2011). Another proposed starting date aligns with the onset of the 'Great Acceleration' in the mid-20th century relating to socio-economic growth trends, i.e., population growth, increases in gross domestic product (GDP), increased energy consumption and water use and the increase of international tourism (Steffen *et al.* 2015). The loss of biodiversity due to human encroachment is also characteristic of the Anthropocene (Johnson *et al.* 2017).

Certain elements of environmental change, such as land conversion for the creation of agricultural areas or the exploitation of natural resources have typically accompanied human presence at any time during their history on islands (indigenous as well as western cultures; Russell & Kueffer 2019). However, a set of novel threats to island biodiversity have become active during the past couple of decades. Worldwide anthropogenic climate change is making islands even more vulnerable to biodiversity change and species loss (Russell & Kueffer 2019; Veron *et al.* 2019; Fernández-Palacios *et al.* 2021). Additionally, urbanization and tourism are closely linked to modern societies and can have negative effects on native species diversity. On tropical atoll islands in the Indo-Pacific, for example, invertebrate richness was reduced significantly by these novel impacts (Steibl & Laforsch 2019; Steibl *et al.* 2021). Specifically, increased fragmentation and reduced vegetation density were the direct causes leading to species richness decline. Tourism and recreational activities are threatening vascular plants in Europe, specifically in the Canary Islands (Ballantyne & Pickering 2013). Manuscript 1 accounts for such novel dimensions of change by incorporating information on tourism to analyse extant plant species distributions on European barrier islands.

Biodiversity change in the era of the Anthropocene has begotten both 'loser' and 'winner' species that either suffer or benefit from the concurrent environmental changes, both as a legacy of long human settlement histories and novel threats (Kress & Krupnick 2022). Species experiencing immense population reductions or even extinctions are disadvantaged while e.g., domesticated species and breeds but also other inadvertently promoted species (e.g., synanthrope or invasive species) are profiting. However, the number of disadvantaged species exceeds the number of benefiting species (Kress & Krupnick 2022). Consequently, the natural global insular biodiversity is currently threatened (e.g., Fernández-Palacios *et al.* 2021). In the same style as referring to islands as biodiversity hotspots, they have therefore been termed so-called 'threatspots' (Whittaker & Fernández-Palacios 2007).

Islands have distinct onset dates of initial human settlement. New Guinea, for example, was settled ca. 45,000 years BP (Before Present), Fiji and Vanuatu about 3,000 years BP, and New Zealand around 1,000 years BP, with ongoing biodiversity changes ever since (McGlone 1989; Ash 1992; O'Connell & Allen 2004; Burley *et al.* 2019). These islands experienced a second wave of settlement with the onset of colonialism after 1492 (year of the discovery of the New World by Christopher Columbus). In contrast, on the Galápagos Islands humans settled first during the late 19th century (Tye 2006). These differences in human settlement history imply that islands were exposed to different periods of human encroachment, leading to diverging anthropogenic impacts on insular biodiversity. The variance in timing and trajectories makes islands predestined to understand changing biodiversity patterns and underlying processes related to human encroachment.

Whilst knowing that humans have significantly altered the nature of islands (Russell & Kueffer 2019; Nogué *et al.* 2021), it remains difficult to track past biodiversity changes. Nowadays, plant species checklists for many islands are available through openly accessible databases and publications (e.g., checklist of vascular plant species in the Canary Islands; Beierkuhnlein *et al.* 2021, presented here as Manuscript 9). However, the picture becomes blurrier when reconstructing the flora over centuries or millennia. In many instances, anthropogenic alterations to natural island environments occurred long before any scientific observations of this process were documented (Connor *et al.* 2012). Palaeoecological data and approaches can be used to reconstruct biodiversity timelines over thousands of years (Willis & Birks 2006; Barak *et al.* 2016; Nogué *et al.* 2017). Such records can open a window into the past, albeit commonly at a coarser taxonomic and temporal resolution compared to extant monitoring or survey data. In Manuscript 3, trajectories of non-native vegetation abundance on islands globally of up to 5,000 years were reconstructed. Such approaches not only contribute to the understanding of past insular biodiversity but also ease the comprehension of extant species communities, which are influenced by the legacy of biodiversity changes over long time-scales (Stuessy 2020; Lenzner *et al.* 2022).

3.2. Impacts of non-native Species on Island Biodiversity

Since the first arrival of humans on islands and ongoing ever since the deliberate and accidental introduction of non-native species has played a significant role in biodiversity transformation. On oceanic islands, the naturalization of non-native (see Box 2 for terminology) plants exceeds the number of extinctions by far, and the number of plant species on islands has thus approximately doubled due to species introductions and naturalisations (Sax *et al.* 2002). Non-native species numbers are on the rise worldwide and show no trend of slowing down (Seebens *et al.* 2017). On ca. ¼ of all islands worldwide, the number of non-native plant species nowadays outnumbers native plants (Essl *et al.* 2019). In the Azores, to pose an extreme example, 69% of the present plant species are non-native (Silva & Smith 2004). This signifies that plant species numbers on islands increase with the introduction of non-native species. The ratio between non-native and native species is continuously changing (Sax & Gaines 2008). Thus, although biodiversity is declining at the planetary scale, areas at sub-global scales commonly exhibit an increase in species richness (Sax *et al.* 2002; Sax & Gaines 2003). The resulting implications for ecological and evolutionary processes, in the long run, are yet mostly unknown.

Non-native species that spread extensively and cause negative ecological, economic, and societal impacts are known as invasive species (see Box 2 for terminology). Especially this extreme subset of non-native species is responsible for the observed biodiversity changes on islands. In this thesis, three case studies on invasive species and their impact on island biodiversity are provided. In the Canary Islands, the invasive bunch grass *Cenchrus setaceus* (Forssk.) Morrone (known also as *Pennisetum setaceum* (Forssk.) Chiov., Poaceae) is an invasive species of concern for natural biodiversity (Walentowitz *et al.* 2019, presented here as Manuscript 4). On the island of La Palma, the invasive tree species *Castanea sativa* Mill. (Fagaceae), that escaped from abandoned agricultural fields, replaces remnants of the unique laurel forest that hosts numerous endemic species (Devkota *et al.* 2020, presented here as Manuscript 7). In the Galápagos Islands, the invasive blackberry species *Rubus niveus* Thunb. (Rosaceae) inhibits the natural recruitment of endemic *Scalesia pedunculata* Hook.f. (Asteraceae) trees (Walentowitz *et al.* 2021b, presented here as Manuscript 5). Especially with regard to invasive species, the Canary and Galápagos Islands pose interesting opposing examples of island invasibility. On the Canary Islands, for example, natural species communities proved to be quite resistant to invasive plants, despite the archipelago's long history of human encroachment (Fernández-Palacios *et al.* 2022). Hypothesized explanations are that dry lowland areas act as a climatic filter, inhibiting the establishment of newly arrived non-native plant species. Well-preserved natural ecosystems might inhibit plant invasions. Furthermore, the Canary Islands are located close to the African Continent (96 km) and thus the proximity to species source pools might have resulted in permanent colonization events of plant species (Fernández-Palacios *et al.* 2022). Additionally, the legacy of long human presence on the islands might have resulted in plant species adapted to human activities. In contrast to the Canary Islands, the Galápagos Islands suffer massively from introduced species (e.g., Walentowitz *et al.* 2021b, presented here as Manuscript 5). Presenting case studies on invasive plant species from these two archipelagos outlines the scene: Islands have unique invasion histories and their invasibility differs due to abiotic and biotic island characteristics.

Box 2: Terminology of non-native, alien, naturalised, and invasive species

In this thesis, a **non-native** species is defined as a species being absent from a given area (here mostly islands) before human arrival and that has been introduced through means of human transport (sensu Sax & Gaines 2008). These **introductions** usually incorporate human-mediated relocation across major biogeographic barriers like oceans (Richardson *et al.* 2000). Species reaching the focal area by natural means of dispersal after the onset of human settlement cannot be differentiated from non-native species with this approach (Sax & Gaines 2008). This number is, however, expected to be marginal compared to human-mediated introductions. Non-native species are also known as **non-indigenous**, **non-natural**, **alien, exotic, allochthonous** species or **neobiota** in literature (e.g., Occhipinti-Ambrogi & Galil 2004; Hällfors *et al.* 2014; Robinson *et al.* 2016).

Of all non-native species, a subset termed **naturalised** species is often the focus of according ecological and biogeographic literature. This term refers to those non-native species that have established populations and propagate in nature, without any further assistance from humans (Richardson *et al.* 2000).

In the literature, **invasive** species are commonly referred to as non-native species that have negative ecological and economic implications (Simberloff 2013). However, terminology is not unified and can lead to confusion in scientific and conservation debates (Colautti & MacIsaac 2004). An invasive species has also been defined otherwise, for example by Richardson *et al.* (2000), who link this term to non-native species that have dispersed over certain distances. Likewise, Colautti & MacIsaac (2004) advocate a neutral terminology and biogeographic approach to define invasive species. The term 'invasive' has also been proposed to be extended to certain extensively spreading native species, thus using an ecological, not biogeographic definition of this term (Valéry *et al.* 2009). To ease the transferability of insights from this thesis and literature on invasion biology in general, I comply with the definition of an invasive species by Simberloff (2013) to be a non-native species causing adverse ecological, economic, and societal change. It should nevertheless be noted that this terminology is used in many ways in the literature

(Colautti & MacIsaac 2004) and contains a valuation by requiring an assessment of what is considered to be a negative impact on ecological, economic, and societal systems. Manuscripts 4 (Walentowitz *et al.* 2019), 5 (Walentowitz *et al.* 2021b) and 6 (Devkota *et al.* 2020) refer to invasive species using the definition described above.

Furthermore, the term bioinvasion is commonly used to describe entire invasion processes, starting from introductions to naturalisation and extensive spread (Occhipinti-Ambrogi & Galil 2004).

The terms ‘alien species’ and ‘alien invasive species’ are commonly used in legislative frameworks of, e.g., the European Union (Regulation (EU) 1143/2014 on invasive alien species) or by intergovernmental platforms, such as ‘The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services’ (IPBES) when referring to non-native and invasive species, respectively (IPBES secretariat 2019). The International Union for Conservation of Nature (IUCN) also uses the term ‘invasive alien species’ (IUCN 2021). However, critiques of the terminology used in invasion ecology have been raised, as terms such as ‘alien’ might evoke xenophobic associations (Warren 2018). Therefore, the term ‘non-native’ will be used in the introductory text of this thesis. Manuscripts 1, 3 (Walentowitz *et al.* 2023) and 9 (Beierkuhnlein *et al.* 2021) also make use of this rather descriptive and neutral definition. In general, a neutral, unbiased and objective usage of terminology in invasions biology, as also advocated by Brown & Sax (2005), is attempted in this thesis.

Plant species numbers on islands have become larger due to species introduction (Sax *et al.* 2002). However, not all species groups show a net increase in species at the sub-global (also regional) scale due to species introductions. In contrast to plants, the numbers of birds on islands vary marginally over time and introductions and extinctions balance each other (Sax *et al.* 2002). The authors explain this by a higher vagility of birds compared to a lower vagility of plants. The mechanism behind this is that low-vagility species profit stronger from human transport and thus increase in number within a given area while high-vagility species could already disperse easily before anthropogenic forces became dominant. This chain of reasoning is also supported by investigations on fern species. These have very good dispersal abilities and exhibit high vagility (anemochore dispersal of light spores) (Sax *et al.* 2002). On islands, total fern species richness has only increased by 4% since human arrival (Sax *et al.* 2002). In summary, total plant species numbers increase while bird numbers stay constant due to introductions of non-native and the extinction of native species. However, hitherto unknown are the implications of non-native species' introductions to richness at local scales (Sax *et al.* 2002).

Why are islands particularly vulnerable to changes caused by non-native species? Low numbers of native species and imbalanced phylogenetic richness lead to the availability of unsaturated niches, facilitating the establishment and spread of non-natives (Bach *et al.* 2022). Further reasons are the evolution of insular species in isolation and thus the emergence of naïve species (e.g., lacking defence mechanism and competitiveness), the potential absence of pests, predators and competitors from native ranges (enemy release hypothesis, e.g., Funk & Throop 2010), and potential early human colonisation history of humans on islands (e.g., islands in the Caribbean, Indian and Atlantic Ocean, Whittaker *et al.* 2007). Additionally, the small scale of islands leading to a concentration of human impacts within a limited area, and lastly international trade using islands for stopovers to resupply food and fresh water, especially in early colonisation history, add to the vulnerability of islands to non-native plant species occurrences (Whittaker & Fernández-Palacios 2007).

Non-native species occurrence on islands is not only an extant phenomenon, but these species have histories dating back thousands of years (Rick *et al.* 2013). Thereby, trajectories of non-natives are majorly intertwined with human histories and cultures. The legacy of European colonial history has, for example, left an imprint on the extant distribution of non-native species (Lenzner *et al.* 2022). Additionally, the establishment of botanical gardens has eased the spread of numerous invaders globally (Hulme 2011). Ornamental species, selected and transported by humans because of their physiognomy have a special role in invasion biology (Li *et al.* 2004; Niemiera & Holle 2009; van Kleunen *et al.* 2018). The aforementioned invasive grass species *Cenchrus setaceus* (Walentowitz *et al.* 2019, presented here as Manuscript 4) is an example of a species whose introduction to many areas worldwide can be attributed to its pleasing appearance (to the human eye) and its use for ornamental purposes. The long-term parallel histories of non-native species and humans illustrate that an understanding of the past is necessary to comprehend the current distributions and impacts of non-native species, and therefore reconstruct biodiversity changes on islands. Paleoecologic data and approaches can help to reconstruct past species compositions (Willis & Birks 2006; Barak *et al.* 2016; Nogué *et al.* 2017, see also Walentowitz *et al.* 2023, presented here as Manuscript 3).

3.3. Novel Ecosystems

In the context of anthropogenic alterations of ecosystems and high abundances of non-native species, the terms ‘novel ecosystem’ and ‘emerging ecosystem’ have been developed (Hobbs *et al.* 2006, 2013). The term ‘novel ecosystem’ was first introduced by Chapin III and Starfield (1997). As such, ecosystems or biotic assemblages are described that do not exist naturally and emerged as a consequence of (direct and indirect) human activities (Hallett *et al.* 2013; Collier & Devitt 2016). Restoration to ‘natural’ states of these ecosystems is highly unlikely (Hallett *et al.* 2013; Collier & Devitt 2016). An estimate of 50% of the land’s terrestrial surface across all biomes has shifted from predominantly wild to anthropogenic landscapes (Ellis *et al.* 2010), thus calling for the need of the term ‘novel ecosystem’ to adequately describe current environmental stages on Earth. Arguments are that restoring ecosystems to natural or close to natural states is elusive due to the multifaceted anthropogenic changes of many landscapes. In Manuscript 6, the emergence of *Castanea sativa* forests as a novel ecosystem in La Palma, Canary Islands, is outlined (Devkota *et al.* 2020). This broadleaf tree species was planted for agricultural purposes and ever since thrives on the islands, extending its range into natural habitats. *Castanea sativa* shows tendencies of replacing unique laurel forests. This tree species has introduced an entirely new phenologic forest feature to the island as it is deciduous in contrast to the evergreen native island flora.

With the emergence of novel ecosystems at large scales, implications for nature conservation and ecological restoration have to be considered (Lemoine & Svenning 2022). The incorporation of novel ecosystems into conservation biology is both advocated and extensively discussed in the literature (Seastedt *et al.* 2008; Perring *et al.* 2013). In ecosystems under restoration the problem often arises that potentially natural baselines are unreachable, e.g., the removal of all invasive species from a certain area is not feasible. However, treating the ecosystem under restoration as a novel ecosystem, reducing the amount of non-native species to reach biodiversity goals, but still accepting their presence within the system (albeit at lower abundances) could be a new approach and practice in conservation and restoration, adapted to the new reality of anthropogenically changed landscapes (Hobbs *et al.* 2009). A related approach is to view the terms 'native' and 'non-native' as a continuum rather than binary categories, which might also help to set realistic conservation and restoration goals (Lemoine & Svenning 2022). However, critiques of the term 'novel ecosystem' have been raised (Aronson *et al.* 2014; Murcia *et al.* 2014) and the concept is subject-matter of discussions among scientists and conservationists (Miller & Bestelmeyer 2016). The ambiguous definition of the term has strengthened criticising voices (Murcia *et al.* 2014; Truitt *et al.* 2015). A major concern is that the basis for restoration and conservation efforts is weakened: if an increasing number of ecosystems is novel, why engage in and finance conservation and restoration? Arguing against this logic, Goldman *et al.* (2008) and Mendenhall (2020) state that also human-altered areas have conservation value by providing habitat for diverse communities of species and stipulating ecosystem services (Hallett *et al.* 2013; Evers *et al.* 2018).

3.4. Arks of Island Biodiversity

Although changes to the natural environment on islands occur globally, there are so-called 'arks of insular biodiversity' that remain negligibly changed. These are commonly extreme environments close to the physiological limits of many plant species. As an example, high-elevation islands exhibit high topographic complexity and high-altitudinal zones can function as a refuge for native (especially endemic) diversity (Irl *et al.* 2015). Mountaintops in the Canary Islands still host numerous endemic and no invasive species (Irl *et al.* 2015). Another example of arks of native biodiversity are phonolite rocks, which are small rocky outcrops located for example amid basaltic lava fields on La Palma (Canary Islands). These rocks host numerous native and Macaronesian endemic plant species and comprise close to no non-native species (Walentowitz *et al.* 2021a; Kienle *et al.* 2022, presented here as Manuscripts 8 and 7, respectively). Furthermore, steep and inaccessible cliffs, ridges, and valleys can host mostly native plant communities until today. In the Canary Islands or the Juan Fernández archipelago, such areas have retained high natural biodiversity (Stuessy *et al.* 2017; Beierkuhnlein *et al.* 2021). Such arks of native insular biodiversity are valuable reference sites to gain insights into the appearance and functioning of native biodiversity that have experienced negligible anthropogenic change.

3.5. Conservation and Restoration

To mitigate and counteract global biodiversity loss, the development of holistic and ambitious conservation goals is key (Díaz *et al.* 2020). For the development and implementation of successful restoration and conservation projects, a scientific foundation and knowledge of the socioeconomic contexts is essential (Temperton 2007). This thesis contributes to conservation and restoration ecology with an applied scientific project on long-term monitoring alongside an experimental approach to restoring parts of a unique forest ecosystem in the Galápagos Islands (Walentowitz *et al.* 2021b, presented here as Manuscript 5). The biodiversity in the Galápagos Islands, comprising a multitude of endemic species, has been transformed by invasive plant species (e.g., Jäger *et al.* 2009; Rentería *et al.* 2012). The endemic tree species *Scalesia pedunculata*, for example, naturally dominating the so-called Scalesia forest on several islands within the archipelago, has suffered from the invasion of the blackberry species *Rubus niveus* that inhibits forest regeneration (Rentería *et al.* 2012; Jäger *et al.* 2015). The shrubby invader forms dense and impenetrable thickets in the understory of the Scalesia forest, thereby inhibiting the natural recruitment of *Scalesia pedunculata*. In a team of scientists and conservationists, I monitored and investigated the natural recruitment of the endemic tree species after the removal of invasive plant species, particularly *Rubus niveus*, over the course of five years (Walentowitz *et al.* 2021b).

4. Island Biogeography of the Anthropocene

4.1. Incorporating anthropogenic Factors to predict insular Species Richness

Considering the manifold anthropogenic changes of island biodiversity across spatial scales (Vellend *et al.* 2017), the question arises whether contemporizing island biogeography by embracing the anthropogenic dimension of biodiversity change is necessary and timely. In this thesis, I argue that a considerable number of discrete communities (e.g., true islands, habitat fragments) on Earth are experiencing anthropogenically-induced change (Chapter 3). To adequately reflect this reality, the human factor needs to be considered in a modern and contemporary framework of island biogeography. In recent publications the need for biogeography and ecology to incorporate anthropogenic and societal processes to understand how biodiversity is being shaped today has also been emphasized (e.g., Ellis *et al.* 2010; Santos *et al.* 2016; Delgado *et al.* 2017; Wood *et al.* 2017; Gleditsch *et al.* 2023). This chapter outlines how a framework on 'island biogeography of the Anthropocene' could address these needs.

Naturally, species assemblages form at slow rates, but island biodiversity nowadays is changing rapidly due to human activity. Although the time span of the natural history of islands is usually considerably longer compared to human settlement histories, the magnitude of change caused by humans can be high. Turnover of plant species increases 11-fold due to human activities (Nogué *et al.* 2021), numerous native species are imperilled or have been driven to extinction (Fernández-Palacios *et al.* 2021), and non-native species have been introduced in high numbers (Essl *et al.* 2019). This change has impacted our ability to understand the patterns and functioning of island ecology and biodiversity. Recorded and unrecorded historic extinctions of island biota have, for example, distorted current biodiversity patterns (Whittaker & Fernández-Palacios 2007). Additionally, we might be observing a transient diversity of plants on islands exhibiting extinction debts (Jackson & Sax 2010; Triantis *et al.* 2010). Extant native species that have been severely diminished in population size and might be functionally extinct (Anderson *et al.* 2011; Sekercioglu 2011). In short, human-induced biodiversity changes on islands are manifold, complex, and intertwined, and drivers of change and exact cause-effect chains are not easy to detect. Island biogeography is a core scientific discipline to contribute to the disentanglement and comprehension of these changes. This is also reflected in an increasing number of publications that integrate anthropogenic aspects into island biogeographic research (Figure 1).

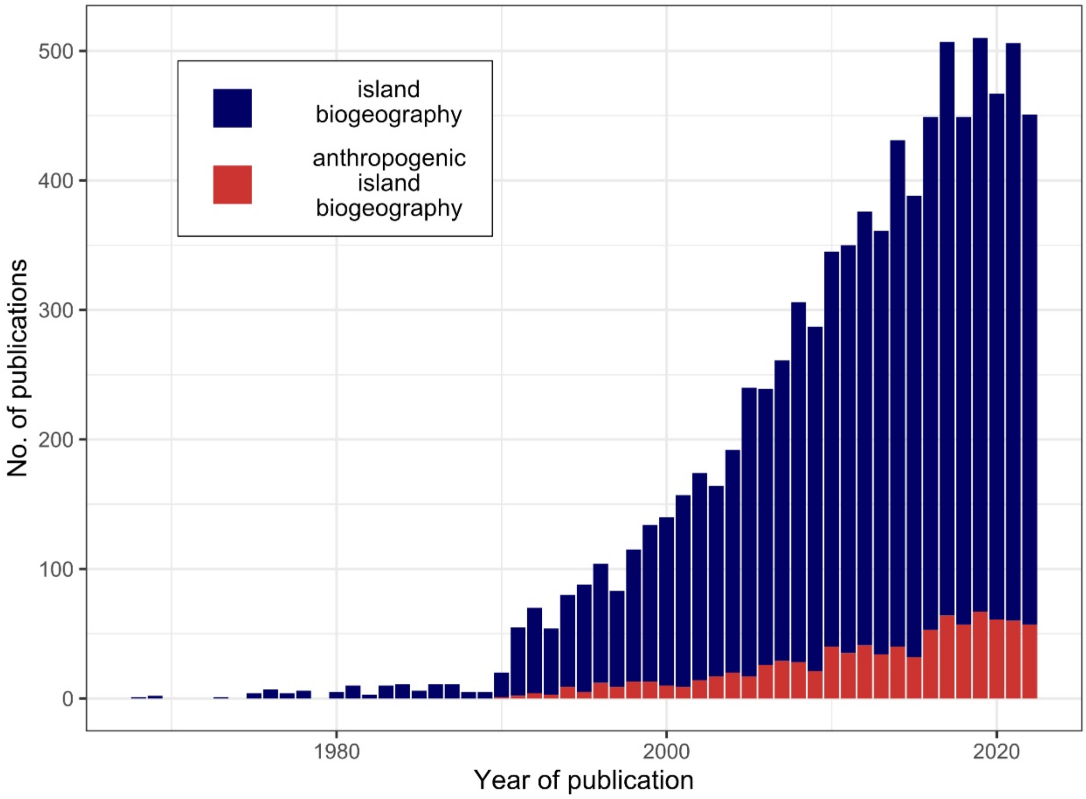


Figure 1: Number of publications thematising island biogeography (blue) and jointly containing the terms island biogeography and Anthropocene (red) listed in the Web of Science. Data accessed on 18.10.2023. Search string: island biogeography AND (anthropo* OR human OR Anthropocene), applied to paper titles, keywords, and abstracts.

Although anthropogenic encroachment has partly been perceived as a disturbance that impedes to test biogeographic theories (e.g., Borregaard *et al.* 2017), I argue that the incorporation of anthropogenic drivers into the analysis of biodiversity formations has the advantage of understanding extant species assemblages and can help to dissect the effect of natural and anthropogenic drivers. In the following, I demonstrate how current human-mediated changes to biogeographic patterns and processes can impact well-established theories in island biogeography (i.e., ETIB and GDM). At the example of the most frequently used drivers of insular biodiversity (i.e., area, habitat heterogeneity and isolation) I show how human encroachment might even alter hitherto conceived 'natural' drives of species richness.

Revisiting two seminal theories in island biogeography, the ETIB and GDM, it is evident that the core of both concepts are opposing immigration and extinction rates (plus speciation in the case of the GDM) (MacArthur & Wilson 1967; Whittaker *et al.* 2008). However, especially plant species numbers have increased on islands due to introductions of species by humans (Essl *et al.* 2019). These human-mediated introductions artificially increase immigration rates and human encroachment has led to altered, mostly elevated, carrying capacities (by forming new habitats) (Sax *et al.* 2002; Whittaker & Fernández-Palacios 2007). Integrating the known fact of increased immigration rates due to introductions of non-native plant species on islands worldwide (Sax *et al.* 2002) automatically raises the question if a shift in the hypothesized equilibrium of insular species numbers is to be expected. Additionally to be considered is that extinction rates of plants are lower than immigration rates (Sax *et al.* 2002), which could partly be attributed to unknown extinction debts (Jackson & Sax 2010; Triantis *et al.* 2010). How are current extinction rates, potential extinction debts, and anthropogenically-raised immigration rates influencing hypothesized equilibria of species numbers on islands? Such questions illustrate how basic theories in island biogeography need to be extended in future research to incorporate the human dimension.

After first hypothetical reflections on human impacts on seminal theories in island biogeography, a closer look at 1) area, 2) habitat heterogeneity, and 3) isolation as the most prominent drivers of species richness furthermore stresses the point that human-altered species assemblages need new scientific approaches and thinking that incorporate the anthropogenic dimension. The effects of natural drivers on species richness are thereby certainly not completely levered out by human activity but remain a steady, slow underlying force shaping species assemblages.

1) Area: The species-area relationship is one of the most prominent relationships in island biogeography (see chapter 2.2). However, on islands that have undergone extreme land use changes and where parts of the island might be sealed by concrete and asphalt (e.g., Steibl *et al.* 2021), lots of potential habitat is lost for native species. Is total island area really the area that native species have access to, or has this area been reduced by anthropogenic activities, thus calling for new area metrics? Is the function and interpretation of area thus changing in island biogeographic theory? In current times, the total island area might not adequately represent the habitat available for plants anymore. Additionally, the correlation of area with other anthropogenic variables can be problematic. In Manuscript 1, for example, a strong correlation between island area and the number of island inhabitants was found. Thus, using area as an explanatory variable might mask relationships between anthropogenic variables and richness. This problem has also been identified by Blackburn *et al.* (2016), who found that the effect of human population size might be vailed by island area when aiming to explain plant and bird species richness on islands globally.

2) Habitat heterogeneity: An aspect hinting at increased species numbers on islands in the Anthropocene is that habitat heterogeneity is commonly increased by human activity via the creation of new man-made habitats (e.g., agricultural fields and pastures; Whittaker *et al.* 2007). The overall carrying capacity of islands for species might change by opening vacant niches through the addition of habitats associated with human encroachment. We have to ask the question if human-altered islands, thus possessing increased habitat heterogeneity, change the interpretation of this factor. Another critical point is that area is commonly used as a proxy for habitat heterogeneity. However, with island area remaining the same, but habitat heterogeneity being raised by human interventions, the relationship between those variables needs to be reconsidered.

3) Isolation: Accordingly, the role of isolation has to be rethought. While isolation from the continent usually remains the same for a given island, we have to incorporate human-mediated transport via marine and air traffic that can reduce the functional isolation of islands. Globalised trade has changed the isolation of islands and has led to the introduction of numerous non-native species (Hulme 2009). Economic factors are used as proxies to account for changed isolation metrics (Denslow *et al.* 2009; Essl *et al.* 2019; Rojas-Sandoval *et al.* 2020; Tordoni *et al.* 2021) as geographic isolation from continents becomes neglectable, albite still being an underlying driver of biodiversity. This can be explained by geographic isolation functioning at longer timescales while human-mediated transport affects biodiversity quickly.

The use of 'natural' biogeographic drivers of species richness adapted to the anthropogenically-changed reality is one way of accounting for changed biodiversity in modern times. Additionally, a set of anthropogenic biodiversity drivers has been developed in the scientific literature of which an overview is presented in the following Chapter 4.2.

4.2. Anthropogenic Drivers of Biodiversity

Human activity adds another layer of complexity to the emergence of biodiversity patterns in the Anthropocene. For advanced understanding, the inclusion of anthropogenic impacts into established island biogeography theory is key (Gleditsch *et al.* 2023). Indeed, it is paramount to understand precisely which anthropogenic disturbance is responsible for what kind of change (Steibl & Laforsch 2019).

One way of accounting for anthropogenic alterations of biodiversity patterns is the adjustment of 'classic' natural factors, such as island area, or habitat heterogeneity. Rojas-Sandoval *et al.* (2020), for example, take the amount of natural land area as opposed to the total island area as a metric to explain insular species richness. Similarly, area calculations of anthropogenic land use categories can be applied. The proportion of land used for agricultural purposes has been utilised as an explanatory variable to explain plant species richness on islands (Essl *et al.* 2019; Rojas-Sandoval *et al.* 2020). Habitat heterogeneity, if not reduced to natural categories, but extended to human land use categories, is another example of how anthropogenic factors can be incorporated in explanatory variables to current biodiversity patterns (e.g., Manuscript 1).

Besides the adjustment of originally natural biogeographic factors, a diverse set of anthropogenic factors has been applied in scientific literature to explain aspects of extant biodiversity on islands (Table 2). Frequently applied as a proxy for human encroachment to explain richness of a variety of groups (plants, arthropods, fish, etc.) is the number of people living on an island (e.g., Chown *et al.* 1998; Denslow *et al.* 2009; Blackburn *et al.* 2016; Furness *et al.* 2016), also expressed as human population density (e.g., McMaster 2005; Denslow *et al.* 2009; Essl *et al.* 2019). In Manuscripts 1 and 2 (the latter published as Walentowitz *et al.* 2022) this metric is used to explain contemporary plant distributions on European Islands. To demonstrate the diversity of anthropogenic biodiversity drivers published in literature, I conducted a literature review and present the obtained results in Table 2.

Another proxy for human interventions is the number of visiting tourists (e.g., Chown *et al.* 2005; Hall 2010; Rojas-Sandoval *et al.* 2020). Considering tourists as temporal inhabitants, similar effects as those from permanent inhabitants can be expected. Thereby the length of stay and the activities undertaken by the tourists can be taken into account. Taking the number of visiting tourists into consideration can be especially important on islands, where mass tourism takes place. Tourism can also be related to reduced effects of isolation, as the transportation of people and goods increases the likelihood of increased propagule pressure, thereby raising the immigration rate and ultimately species numbers on islands.

To explain insular patterns of species diversity, the presence of non-native or introduced species has been used in the literature. For example, the vascular plant species diversity in the Aleutian Islands was explained by Garroutte *et al.* (2018) with past introductions of foxes (for fur farming) and large mammals, such as caribou, cattle or reindeer as proxies for human encroachment, next to using natural biogeographic explanatory variables. Luna-Jorquera *et al.* (2012) used the presence of non-native animals and plants as a predictor for the diversity of plant, mammal, and bird species on coastal Chilean islands. They binarily characterized islands based on the collection of bird eggs, the existence of unregulated tourism, and the undertaking of fishing activities in coastal waters. Another example is that arthropod diversity on small sandy islands along the east coast of Australia was significantly driven by the occurrence of non-native species (Nakamura *et al.* 2015).

The economic capacity of an island, commonly expressed as Grosse Domestic Product (GDP) per capita (e.g., Denslow *et al.* 2009; Essl *et al.* 2019), has been used as a proxy for human interventions. GDP is assumed to be correlated with economic development and therefore trade and travel can be used as surrogates to explain the diversity of non-native species (Denslow *et al.* 2009). As a measure of economic connectedness, the number of ships docking within an island was also used as an anthropogenic variable to explain fish species (precisely poecilid) richness on Caribbean islands (Furness *et al.* 2016). Similarly, the number of boat docks is a predictor of the richness of invasive wasps on islands off the coast of New Zealand (Schmack *et al.* 2020). Ship docks are part of infrastructure, like roads and settlements. Road length or density (Rojas-Sandoval *et al.* 2020; Irl *et al.* 2021) and distance to cities (Tordoni *et al.* 2021) were also used as determinants of non-native plant species distribution.

The colonial history of New World islands can be considered a historic anthropogenic variable (Lenzner *et al.* 2022). In this manner, Rojas-Sandoval *et al.* (2020) incorporated the relatedness of Caribbean Islands to different historic European colonial empires (e.g., United Kingdom, France, Netherlands) to predict extant plant species richness.

Table 2: Anthropogenic factors used in scientific publications to explain biodiversity and species richness (response variable) on islands. These were usually used in combination with other factors to explain different aspects of biodiversity or richness response variable (see individual publications). The geographic scope of each study is provided.

Anthropogenic factor	Publication	Response variable	Geographic scope
Human population			
Number of inhabitants, human population density	Chown *et al.* (1998)	Indigenous and introduced vascular plants, insects, land and seabirds, mammals	Islands in the Southern Ocean
	Bailey *et al.* (2017)	Native and alien vascular plant species	Great Britain
	Guo *et al.* (2017)	Invasive plants	Global
	Rojas-Sandoval *et al.* (2020)	Alien and native plant species	Lesser Antilles, Caribbean
	Tordoni *et al.* (2021)	Native and alien vegetation on coastal sand dune	Global
	Blackburn *et al.* (2016)	Plant and bird species	Global
	Denslow *et al.* (2009)	Invasive plant species	Tropical Pacific Islands
	Furness *et al.* (2016)	Poecilid species	Caribbean Islands
	Essl *et al.* (2019)	Naturalized and invasive plant species	Global
	McMaster (2005)	Native and non-native vascular plant species	North American coastal islands
	Luck (2007), review	Biodiversity	Global
	Walentowitz *et al.* (2022), presented here as manuscript 2	Vascular plant species	Danish islands
	Manuscript 1	Native and non-native vascular plant species	European barrier islands
Presence of human settlement	Schmack *et al.* (2020)	Invasive wasps	Islands offshore New Zealand
Infrastructure and traffic			
Number of boat docks	Schmack *et al.* (2020)	Invasive wasps	Islands offshore New Zealand
	Furness *et al.* (2016)	Poecilid species	Caribbean Islands
Number of docking boats	Furness *et al.* (2016)	Poecilid species	Caribbean Islands
Distance to nearest port	Tordoni *et al.* (2021)	Native and alien vegetation on coastal sand dunes	Global
Road density	Irl *et al.* (2021)	Non-native plant species	Tenerife, La Palma, Island of Hawai'I, Maui, La Réunion, Socotra
Length of paved roads	Rojas-Sandoval *et al.* (2020)	Alien and native plant species	Lesser Antilles, Caribbean
Distance to nearest city with more than 50,000 inhabitants	Tordoni *et al.* (2021)	Native and alien vegetation on coastal sand dunes	Global

Distance to nearest airport	Tordoni *et al.* (2021)	Native and alien vegetation on coastal sand dunes	Global
Tourism			
Tourism (theoretical approach)	Hall (2010)	Biodiversity	Caribbean and Pacific Islands
Presence of unregulated tourism (binary)	Luna-Jorquera *et al.* (2012)	Diversity of plant, mammal, and bird species	Coastal Chilean islands
Number of visiting tourists	Chown *et al.* (2005)	Introduced plant and insect species	Islands in the Southern Ocean
	Rojas-Sandoval *et al.* (2020)	Alien and native plant species	Lesser Antilles, Caribbean
	Manuscript 1	Native and non-native vascular plant species	European barrier islands
Per capita gross domestic product (GDP)	Rojas-Sandoval *et al.* (2020)	Alien and native plant species	Lesser Antilles, Caribbean
	Tordoni *et al.* (2021)	Native and alien vegetation on coastal sand dunes	Global
	Denslow *et al.* (2009)	Invasive plant species	Tropical Pacific Islands
	Essl *et al.* (2019)	Naturalized and invasive plant species	Global
Agricultural land cover (%)	Rojas-Sandoval *et al.* (2020)	Alien and native plant species	Lesser Antilles, Caribbean
	Essl *et al.* (2019)	Naturalized and invasive plant species	Global
Cover of human land-use categories	Manuscript 1	Native and non-native vascular plant species	European barrier islands
Exploitation			
Fishing activities	Luna-Jorquera *et al.* (2012)	Diversity of plant, mammal, and bird species	Coastal Chilean islands
Collection of bird eggs	Luna-Jorquera *et al.* (2012)	Diversity of plant, mammal, and bird species	Coastal Chilean islands
Presence of non-native species			
Introductions of foxes (for fur farming) and large mammals, such as caribou, cattle, or reindeer	Garroutte *et al.* (2018)	Vascular plant species diversity	Aleutian Islands
Presence of non-native animals and plants	Luna-Jorquera *et al.* (2012)	Diversity of plant, mammal, and bird species	Coastal Chilean islands
Presence of non-native species	Nakamura *et al.* (2015)	Arthropod diversity	Islands (here cays) along the east coast of Australia
Colonial history	Rojas-Sandoval *et al.* (2020)	Alien and native plant species	Lesser Antilles, Caribbean

4.3. Island Biogeography of non-native Species

In this thesis, I demonstrate how islands can be considered natural laboratories and thus contribute to an improved understanding of the natural world. In the same manner, non-native species can be regarded as ‘model organisms’ that help to understand extinction events, species responses to climate change or the functioning of ecosystems (Sax *et al.* 2007). The introduction of species hitherto unknown to a certain area can be seen as an experimental approach and as an opportunity to test theories in island biogeography and beyond. Stating this, the often detrimental effects of non-native species on native insular biodiversity should not be underestimated or trivialised. Nevertheless, having a scientific view on non-native species introductions and naturalizations, these can be conceived as a mass experiment at the planetary scale with yet unknown outcomes and yet much to explore. Single studies demonstrate how we can learn from bioinvasions. For example, Helmus *et al.* (2014) used the intentional introduction of lizards to Caribbean island banks to experimentally test classic theories in island biogeography. They showed that lizard introductions strengthen the species-area relationship while the species isolation relationship is weakened (considering total native and non-native lizard richness). Here, instead of geographic isolation, the economic isolation of islands has been identified to better explain contemporary lizard species patterns on these islands (Helmus *et al.* 2014).

The reversed species-isolation relationship identified for non-native plants, ants, reptiles, and mammals on tropical and subtropical islands underlines how non-native species can challenge established theories in island biogeography (Moser *et al.* 2018). Unfilled ecological niches on more isolated islands are supposed to enable the inversion of the species-isolation relationship for non-native species. Considering total species richness, the species-isolation relationship is commonly weakened (e.g., Economo *et al.* 2017).

In contrast to diverging directions of the species-isolation relationship for native and non-native species, the species-area relationship for native and non-native species often seems similar (e.g., Sax *et al.* 2002; Whittaker & Matthews 2014). The species-area relationship for total species richness changes due to introduction (Guo *et al.* 2021) and is strengthened (e.g., Economo *et al.* 2017). However, complicating the interpretation of species-area relationships for non-native species is that area can correlate with other drivers of richness. In Manuscript 1, the number of human island inhabitants explained the number of non-native plant species present on barrier islands along the European North Sea Coast.

Usually, a combination of anthropogenic and underlying environmental drivers determine the distribution of naturalised plant (Wohlwend *et al.* 2021, Pacific Islands) and bird species (Blackburn *et al.* 2016, islands globally) on islands best. However, several publications identified a stronger influence of anthropogenic than natural environmental variables. In the first presented study (Manuscript 1), island inhabitants as an anthropogenic variable were most influential to explain non-native plant species occurrences on islands. Similarly, Roura-Pascual *et al.* (2016) also found a higher influence of human-related variables on non-native ant species based on a global island assessment. Additionally, drivers of richness cannot only differ between native and non-native species (Manuscript 1) but also vary between naturalised and invasive species (Essl *et al.* 2019).

Due to the special role of non-native species in island biogeographic theory, alterations and extensions of this theoretical framework to non-native species have been attempted (Burns 2015; Cassey *et al.* 2015). This not only increases our theoretical understanding of biodiversity patterns of non-natives but subsequently also increases the usefulness of such theories for conservation (Burns 2015). Further theoretical and data-driven approaches are needed to firstly, fathom basic understanding of biodiversity patterns of non-native species, and secondly, support conservation and restoration of native biodiversity that is threatened by invasive species introductions.

5. Emerging Research Challenges and Frontiers

Based on Chapters 1 to 4, I identified research challenges, frontiers, and perspectives related to island biogeography that are presented in the following sections. The overarching theme is to distinguish between natural and anthropogenic patterns and underlying processes in time and space. This will be crucial to 1) understand (negative) impacts of human activities on biodiversity to overcome or at least mitigate the current biodiversity crisis we are facing and 2) continue to develop and test natural theories on biogeographical processes and patterns.

Thereby the usage of islands as testing grounds and natural laboratories to understand current anthropogenic biodiversity changes will be of paramount importance. Upcoming challenges and prospects regarding the integration of island biogeography and anthropogenic aspects are listed in the following, divided into thematic (Chapter 5.1) and methodological aspects (Chapter 5.2).

5.1. Thematic Challenges and Perspectives

The thematic challenges and perspectives identified range from advances in island biogeographic theory to applied conservation topics and encompass temporal as well as spatial dimensions.

- **Biodiversity timelines:** The consideration of biodiversity timelines is pivotal to understand extant diversity patterns. Past changes and legacies need to be considered in order to advance ecological sciences (Estes & Vermeij 2022). The development of the GDM (Whittaker *et al.* 2008; Borregaard *et al.* 2016) is an example, of how the incorporation of long-term temporal aspects improves our biogeographic understanding of ecological and evolutionary processes and patterns on islands. Historic written records (Seebens *et al.* 2017), herbaria (James *et al.* 2018; Carine & Menezes de Sequeira 2020), and palaeoecological data (Willis & Birks 2006; Nogué *et al.* 2017) are sources to gain information about the past. Novel approaches, like the combination of data on fossil pollen from sedimentary sequences and information from extant plant species lists, are developed to understand long-term biodiversity patterns (Walentowitz et al. 2023, presented here as Manuscript 3).

- **Holistic biodiversity assessments:** Science devoted to biogeography and conservation mostly focuses on species richness (e.g., MacArthur & Wilson 1967; Borregaard *et al.* 2016; Walentowitz *et al.* 2022, and many more), thereby often ignoring that habitat and genetic richness are also aspects of biodiversity. For a true understanding of insular biodiversity patterns, all aspects of biodiversity would need to be holistically integrated. Rare exceptions are studies by Vellend (2003), McGlaughlin *et al.* (2014), and Leigh *et al.* (2019), which also consider genetic diversity in island biogeographic research. Among the 50 fundamental questions identified for island biology by an expert panel, the question of how to better integrate population genetics into the island biogeographic theory was raised (Patiño *et al.* 2017). This question ultimately aims at promoting a more holistic view on biodiversity and underlines the existing research gap concerning this topic.

- **Arks of biodiversity:** The detection, documentation, monitoring, and protection of arks of natural insular biodiversity, retaining a nature almost unimpacted by humans, has two aims. Firstly, these function as reference sites exhibiting the 'true' nature of islands that has been hardly changed by humans. Secondly, by protecting such sites, unique island biodiversity including numerous endemic species is preserved, thereby contributing to global biodiversity conservation.

- **Functional biogeography:** In island biogeographic theory, species are typically treated to be functionally indifferent (Violle *et al.* 2014; Burns 2015). However, considering species' traits can offer insights into species interactions and assemblages (Schrader *et al.* 2021). Walentowitz *et al.* (2022, presented here as Manuscript 2) complement data on insular plant species' distributions with information on dispersal characteristics to improve the understanding of basic relationships in island biogeography. Furthermore, the inclusion of functional traits in island biogeography will help to identify and understand 'losers' and 'winners' of current developments in the Anthropocene (i.e., species experiencing population reductions or expansions, respectively). The underrepresentation of functional approaches in island biogeography can be attributed to the recent emergence of this young research field (Violle *et al.* 2014) and the limited availability of trait data. Despite the increasing availability of data on plant traits in the TRY (Kattge *et al.* 2020) or GIFT (Weigelt *et al.* 2020) database (see sources listed in Schrader *et al.* 2021), trait information for insular floras is often incomplete (Beierkuhnlein *et al.* 2021, presented here as Manuscript 9, TRY data coverage of Canary Island plant species).

- **From numbers to abundances:** In island biogeography theory, species number-games are the norm and insular biotic communities are mostly investigated by how many species they consist of. The consideration of species abundances in island biogeographic theory is appealing as species-abundance distributions are the basis to explain numerous principles in ecology (Whittaker & Fernández-Palacios 2007). Especially with regard to rising numbers of non-native species on islands research potential arises: Some islands may exhibit equal numbers of non-native species, but does the abundance of these species differ? How much area do invasive species cover? In addition and related to 'functional biogeography', the integration of functional approaches in explaining species abundance distributions seems promising but is mathematically and methodologically challenging (Koffel *et al.* 2022).

- **Non-natives in island biogeography:** A stronger integration of non-native species into island biogeographic theory and respective model development is currently ongoing (Burns 2015; Cassey *et al.* 2015), but yet an underrepresented approach. Perceiving non-native and invasive species as a global experiment can support to develop and challenge established theories (see Chapter 4.3.).

- **Anthropogenic impact on evolution:** How do humans interfere with future evolutionary dynamics of insular species? What consequences do bioinvasions have for evolutionary dynamics on islands? Introductions of non-native species have the potential to alter evolutionary trajectories in different ways. Vellend *et al.* (2007) propose that 1) non-native species represent allopatric populations with opportunities to evolve into distinct subgroups with differing characteristics from native populations, 2) non-natives change the environment in which native species are evolving, and 3) hybridization between native and non-native taxonomic lineages offer further opportunities of changes in evolutionary trajectories in island biota. These proposed three modalities of altering future evolutionary developments are convincing in the sense that future evolutionary trajectories are likely to be impacted by human actions via the introduction of non-native species. However, precise evolutionary trajectories remain unknown and could be the subject of numerous investigations to come. Regarding changed evolutionary trajectories of species on islands, our understanding of what is native and non-native might additionally be challenged. Non-native species can evolve into genetically unique varieties when isolated from native populations through e.g., genetic bottlenecks, hybridisation or polyploidy (Prentis *et al.* 2008). Are such insular varieties that descend from non-native species to be regarded as endemic, non-native or another novel entity?

- **Scale:** The effect of scale on biodiversity is known and subject of numerous studies (e.g., Vellend *et al.* 2017; Chase *et al.* 2018; Zhang *et al.* 2021). However, how scale relates to anthropogenic impacts on biodiversity is largely unknown. Complicating the assessment of scale-dependent anthropogenic aspects of biodiversity changes is that human activities can be strongly impacted by individual cultures and societies. Nevertheless, the investigation of scale-dependent anthropogenic biodiversity alterations will likely be an interesting extension to contemporary island biogeography.

- **Speed of impacts:** Do effects of humans on biodiversity lag in time, e.g., by provoking extinction debts? Impacts of anthropogenically increased species' immigration and extinction rates are unclear and might be strongly timescale-dependent (Sax *et al.* 2002). Causal relations might not be immediate but the effects of human interventions on biodiversity can lag in time.

- **Stagnant islands:** Species are generally termed and treated as non-native when emerging on an island after human arrival (e.g., Sax *et al.* 2002). Thus, no distinction is made between species introduced by humans and species that arrived by natural means. Thus, we assume natural biodiversity to be stagnant. This issue is difficult to tackle and remains a so-far unresolved challenge in island biogeography.

- **Invasion arenas:** Endemic species evolve within a context of concomitant species, also called evolutionary arenas (Nürk *et al.* 2020). Likewise, non-native species can naturalise and spread within specific island species communities. Can we thus refer to 'invasion arenas'? The species' context into which non-native species are introduced is rarely considered in research but opens opportunities to understand invasion processes.

- **Biodiversity conservation:** A priority of natural scientists nowadays should be to document and study anthropogenic changes in the natural environment as biodiversity loss concerns everyone, across cultures and societies (Whittaker & Fernández-Palacios 2007). Therefore, there is a need to compile information on imperilled species and ecosystems and their anthropogenic threats while also protecting and restoring species and ecosystems (Fernández-Palacios *et al.* 2021). Thereby, the importance of including anthropogenic factors in biogeographical studies of islands and island-like systems, and nature conservation becomes more evident. Joint efforts of scientists, policymakers and conservationists are needed, therefore (Hochkirch *et al.* 2021).

5.2. Methodological Challenges and Perspectives

Methodological challenges and perspectives relate to the development of new technologies and methods in island biogeography and thereby touch upon advances in species' taxonomy, databases, and modelling.

- **Dynamic taxonomy:** Species' taxonomy is dynamic, of ever-changing nature, and constantly being improved based on new studies and technologies. This can challenge the attribution of species to conservation listing, distribution data and other types of species' information from databases (Domínguez Lozano *et al.* 2007; Taylor 2010). In Manuscript 4 (Walentowitz *et al.* 2019), the mentioned invasive grass species *Pennisetum setaceum* (Forssk.) Chiov. has recently undergone taxonomic revisions and is now known as *Cenchrus setaceus* (Forssk.) Morrone (POWO 2022). However, according to the EU Regulation 1143/2014 it is still to be found under its synonym *Pennisetum setaceum* in the list of Invasive Alien Species of Union concern (European Commission 2022). Thus, an ongoing challenge is building well-connected databases so that changing taxonomy does not hamper the attribution of information.

- **Tapping novel data:** The creation of novel databases and incorporation of new types of information will be key for advances in island biogeography. I expect citizen science data to gain importance due to the immense quantities of data being produced and due to advances in the processing and interpreting such data, also in island biogeographic research (e.g., La Sorte & Somveille, 2021, using eBird). Furthermore, the creation of topically new databases is going to inspire future research undertakings and projects. Regarding the incorporation of anthropogenic aspects into island biogeography, the emergence of databases compiling human-related information is going to foster research. For example, the BioTIME database was established to track changes in the Anthropocene, although so far only dating back to 1874 (Dornelas *et al.* 2018). Furthermore, increased open-access to databases will support future research projects (e.g., Maitner *et al.* 2018; Jarić *et al.* 2020).

- **Species distribution modelling:** Species distribution models (SDMs) have increased our understanding of past, extant, and projected future biodiversity distributions. However, an aspect commonly missing from simple correlative SDMs (Wisz *et al.* 2013), and also mostly ignored in island biogeographic theory (Burns 2015), is the incorporation of biotic interactions. The integration of species interactions into species distribution modelling opens immense opportunities (e.g., Trøjelsgaard & Olesen 2013). Joined species distribution models (JSDMs) were designed to address this need (Ovaskainen *et al.* 2010; Kissling *et al.* 2012; Clark *et al.* 2014), with however challenges like scale-dependency yet to be resolved (König *et al.* 2021). Additionally, overcoming limitations of model predictions caused by species' niche shifts related to climate change and invasions (Early & Sax 2014) will furthermore challenge research utilizing SDMs.

- **Double analysis:** The application of double analysis approaches is rarely applied but has the potential to increase the understanding of complex ecological data. Analysing the same dataset with different statistical approaches opens the opportunity to get a multi-dimensional view on a given dataset. In Manuscript 3 (Walentowitz *et al.* 2023), generalized linear models (GLMs) and structural equation models (SEMs) were built for the analysis of the same data and together increased the insights into the underlying data.

Manuscripts presented in this Thesis

On the following pages, I present the manuscripts that form the scientific backbone of this thesis (Table 1). The nine manuscripts are categorized depending on the geographic scale (Figure 2) and thematic scope. Part 1 comprises manuscripts developing and challenging theories in island biogeography at the example of multiple islands at a spatial meso- or macroscale. Part 2 contains case studies from single islands or archipelagos focusing on specific aspects of human-induced biodiversity changes on islands.

In part 1, three manuscripts at the meso- and macro scale are presented (Manuscripts 1-3). Manuscripts 1 and 2 test theories related to insular species richness at the example of European islands located in the North Sea and Baltic Sea. Both manuscripts combine natural and anthropogenic drivers to explain contemporary biogeographic patterns. Manuscript 3 takes a global and palaeoecological approach to obtain long-term trajectories of non-native vegetation of up to 5,000 years.

In part 2, six manuscripts are presented that focus on specific aspects of anthropogenically driven change and resulting biodiversity patterns at the example of the Canary and Galápagos Islands. Non-native and invasive plant species are the thematic focus of Manuscripts 4-6. In Manuscript 4, a modelling approach is applied to project the distribution of one the most widely spread invasive grass species on La Palma (Canary Islands). A five-year-long study alongside a forest restoration trial in the Galápagos Islands focuses on restoration success and limitations after invasive plant species removal in a native forest dominated by an island-endemic tree species in Manuscript 5. In Manuscript 6, the replacement of the native laurel forest on La Palma by an invasive tree species is thematised. Thereafter, I present a study that focuses on the interplay of geodiversity and biodiversity at the example of phonolite rocks (Manuscript 7). These rocks can be considered arks of biodiversity and are used as reference sites as opposed to mostly human-influenced landscapes. The last two manuscripts focus on methodological aspects in support of this doctoral thesis. Manuscript 8 can be considered to form one research entity together with Manuscript 7 and describes the data on which the preceding manuscript is based. In Manuscript 9, an updated checklist of the flora in the Canary Islands is provided that underlines the importance of sound taxonomic and openly accessible databases on plant diversity in insular settings for contemporary biogeographic research.

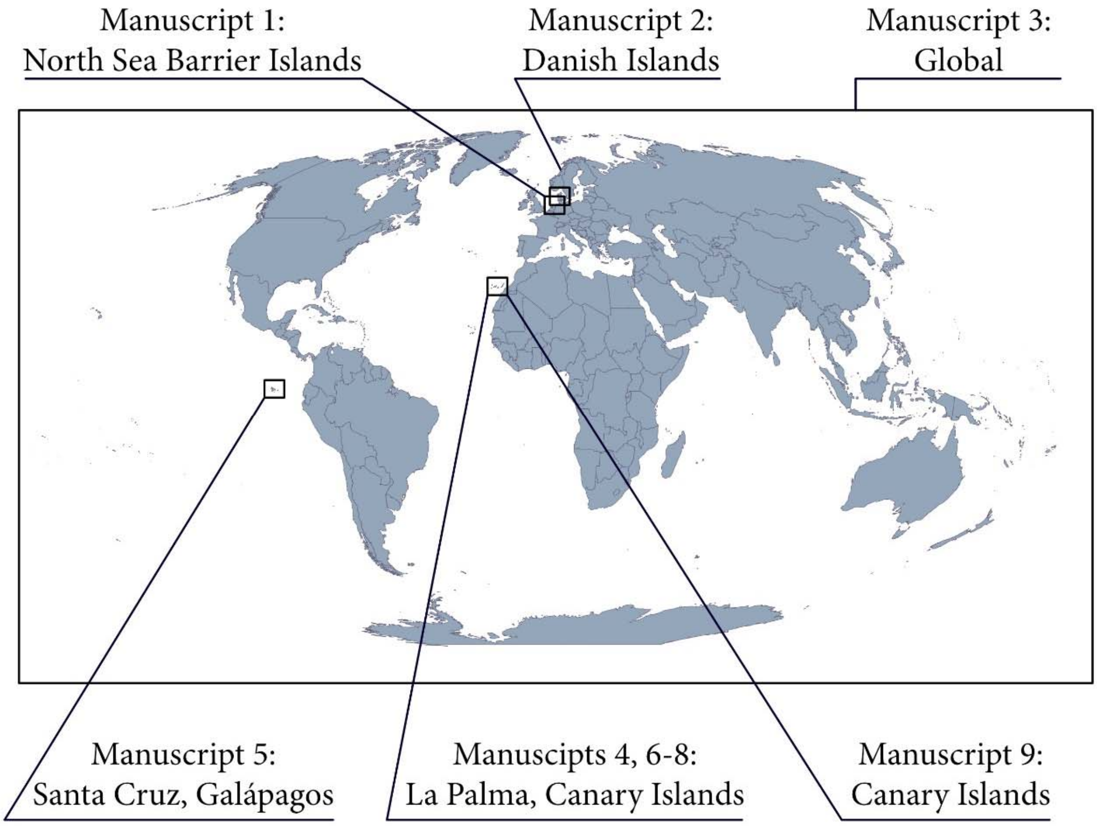


Figure 2: Geographic scope of all manuscripts included in this thesis.

Author's contributions

The overall theme of this PhD thesis was developed by myself in exchange with my supervisor Prof. Dr Carl Beierkuhnlein (University of Bayreuth). Furthermore, Prof. Dr Manuel Steinbauer (University of Bayreuth), Dr Sandra Nogué (CREAF and Universitat Autònoma de Barcelona) and my mentoring team consisting of Prof. Dr Andreas Schweiger (University of Hohenheim), and Dr Dov Sax (Brown University) supported this thesis and inspired the research topics compiled therein. I conducted fieldwork in the Galápagos Islands from 2015 to 2021 which led to the development of Manuscript 5. The respective funding was organised by myself and came from the German Academic Exchange Service (DAAD), the Manfred Hermsen Stiftung, the Greenpeace Umweltstiftung and the Barthel Stiftung. My fieldwork in Ecuador was organised in close collaboration with the Galápagos National Park Directorate and the Charles Darwin Foundation. The data forming the basis of Manuscripts 7 and 8 were collected by myself together with David Kienle and Leyla Sungur under the supervision of Prof. Dr Carl Beierkuhnlein, Prof. Dr Anke Jentsch, Dr Richard Field, Dr Ole Reidar Vetaas, Prof. Dr Alessandro Chiarucci and Prof. Dr Severin Irl on La Palma (Canary Islands) in 2018. For the development of Manuscript 3, I organised a research stay at the Ecological and Forestry Applications Research Centre (Centro de Investigación Ecológica y Aplicaciones Forestales, CREAF) and the Universitat Autònoma de Barcelona, to initiate a collaboration with Dr Sandra Nogué and therefore obtained funding from the Bayreuth Graduate School. In the following, a detailed description of my contributions to each manuscript is provided.

Part 1: Island biogeographic Studies

Manuscript 1:

Title: Disentangling natural and anthropogenic drivers of native and non-native plant diversity on North Sea islands

Authors: Anna Walentowitz, Thalita Ferreira-Arruda, Severin D. H. Irl, Holger Kreft, Carl Beierkuhnlein

Journal: *Journal of Biogeography* (accepted)

Personal contributions: data acquisition 80%, data analysis 90%, visualization 90%, writing 70%, idea and concept 70%; corresponding author

Manuscript 2:

Title: Plant dispersal characteristics shape the relationship of diversity with area and isolation

Authors: Anna Walentowitz, Claudia Troiano, Julie B. Christiansen, Manuel J. Steinbauer, Anders S. Barfod

Journal: *Journal of Biogeography* (2022) 49, 1599–1608 [Editor's choice]

Personal contributions: data acquisition 10%, data analysis 50%, visualization 70%, writing 50%, idea and concept 40%; corresponding author

Manuscript 3:

Title: Long-term trajectories of non-native vegetation on islands globally

Authors: Anna Walentowitz, Bernd Lenzner, Franz Essl, Nichola Strandberg, Carl Beierkuhnlein, Álvaro Castilla Beltrán, José Maria Fernández-Palacios, Svante Björck, Simon Connor, Simon G. Haberle, Karl Ljung, Matthew Prebble, Janet M. Wilmshurst, Cynthia A. Froyd, Erik J. de Boer, Lea de Nascimento, Mary E. Edwards, Janelle Stevenson, Manuel J. Steinbauer, Sandra Nogué

Journal: *Ecology Letters* (2023) 26, 729–741

Personal contributions: data acquisition 30%, data analysis 80%, visualization 90%, writing 50%, idea and concept 60%; corresponding author

Part 2: Case studies

Manuscript 4:

Title: Graminoid Invasion in an insular Endemism Hotspot and its Protected Areas

Authors: **Anna J. Walentowitz**, Severin D. H. Irl, Aurelio Jesús Acevedo Rodríguez, Ángel Palomares-Martínez, Vanessa Vetter, Barbara Zennaro, Félix M. Medina, Carl Beierkuhnlein

Journal: *Diversity* (2019) 11, 192

Personal contributions: data acquisition 70%, data analysis 90%, visualization, 90%, writing 60%, idea and concept 60%

[Work on the manuscript was initiated before the official start of this doctoral thesis. The data and topic of this work was not used for a thesis or any other kind of work to obtain an academic degree.]

Manuscript 5:

Title: Limited natural regeneration of unique Scalesia forest following invasive plant removal in Galapagos

Authors: **Anna Walentowitz**, Michael Manthey, María Belén Bentet Preciado, Rafael Chango, Christian Sevilla, Heinke Jäger

Journal: *PLOS ONE* (2021) 16(10), e0258467

Personal contributions: data acquisition 90%, field work 90%, data analysis 90%, visualization 90%, writing 60%, idea and concept 60%; corresponding author

Manuscript 6:

Title: Assessing the Potential Replacement of Laurel Forest by a Novel Ecosystem in the Steep Terrain of an Oceanic Island

Authors: Ram Sharan Devkota, Richard Field, Samuel Hoffmann, **Anna Walentowitz**, Félix Manuel Medina, Ole Reidar Vetaas, Alessandro Chiarucci, Frank Weiser, Anke Jentsch, Carl Beierkuhnlein

Journal: *Remote Sensing* (2020) 12, 4013

Personal contributions: data acquisition 10%, data analysis 10%, visualization, 20%, writing 20%, idea and concept 0%

Manuscript 7‡:

Title: Geodiversity and biodiversity on a volcanic island: the role of scattered phonolites for plant diversity and performance

Authors: David Kienle*, **Anna Walentowitz***, Leyla Sungur*, Alessandro Chiarucci, Severin D. H. Irl, Anke Jentsch, Ole R. Vetaas, Richard Field, Carl Beierkuhnlein [* equal contributions]

Journal: *Biogeosciences* (2022) 19, 1691–1703

Personal contributions: data acquisition 30%, field work 30%, data analysis 30%, visualization 40%, writing 40%, idea and concept 30%; corresponding author

Manuscript 8‡:

Title: Vegetation plot and trait data from phonolitic and basaltic rocks on La Palma (Canary Islands, Spain)

Authors: Anna Walentowitz*, David Kienle*, Leyla Sungur*, Carl Beierkuhnlein [*equal contributions]

Journal: *Data in Brief* (2021) 37, 107229

Personal contributions: data acquisition 30%, field work 30%, visualization 30%, writing 30%, idea and concept 20%

‡Note that Manuscripts 7 and 8 form one research entity, as in Manuscript 8 the data is presented on which manuscript 7 is based.

Manuscript 9:

Title: FloCan—A Revised Checklist for the Flora of the Canary Islands

Authors: Carl Beierkuhnlein, **Anna Walentowitz**, Walter Welss

Journal: *Diversity* (2021) 13, 480

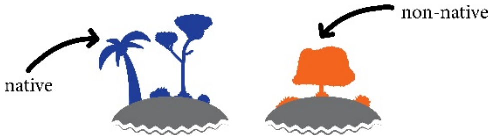
Personal contributions: data acquisition 30%, data analysis 70%, visualization, 90%, writing 20%, idea and concept 20%

Manuscript 1

European coastal islands and their vegetation are constantly being shaped by wind, waves, and tides, but also by humans. This picture shows the coastline of the German island Hiddensee. © Anna Walentowitz

Summary

In accordance with MacArthur & Wilson (1963, 1967) we advance island biogeographical theory at the example of barrier islands. These have the advantage of not showing any evolutionary processes and possess similar settings, varying only slightly. Here, we examine what drives extant native and non-native plant species diversity on 31 European barrier islands. A focus is set on disentangling the effects of natural and anthropogenic drivers of native and non-native plant species diversity. Models need to be balanced between simplicity and accurately depicting reality. While MacArthur & Wilsons (1967) seminal ETIB is elegant yet simple, this manuscript includes complex interrelations between response and natural and anthropogenic explanatory variables.



Disentangling natural and anthropogenic drivers of native and non-native plant diversity on North Sea islands

Journal of Biogeography (accepted)

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Abstract

Aim: Biodiversity on islands is commonly explained by a set of natural drivers such as area, isolation, and habitat heterogeneity. However, constant human impact has led to considerable changes in island floras worldwide. This is reflected, among others, in increased numbers of non-native species. Barrier islands are discrete land units, strongly influenced by humans and not displaying significant evolutionary dynamics. This makes them highly suitable for studying contemporary patterns of species richness and underlying processes. We aim to disentangle the effects of established natural and anthropogenic drivers on native and non-native plant species richness at the example of 31 European barrier islands.

Location: 31 North Sea barrier islands located off the Dutch, German and Danish coast

Taxon: Native and non-native plant species (spermatophytes and ferns)

Methods: Individual relationships of natural and anthropogenic drivers with native and non-native plant species richness are analysed with generalised linear models (GLMs). We use structural equation models (SEMs) to additionally account for interrelations between drivers.

Results: Island area was the strongest predictor of native and non-native plant species richness but affected richness mostly indirectly through habitat heterogeneity (non-native species) and island inhabitants (native species). Isolation had a slightly negative effect on native and non-native plant species numbers on islands.

Main conclusions: The richness of native and non-native plant species on islands is associated with different drivers, i.e., habitat heterogeneity and island inhabitants, respectively. This might be caused by distinct underlying processes forming native and non-native richness patterns. Area was confirmed to be the most important driver of species richness but acting primarily through other natural and anthropogenic drivers of plant species richness. We encourage considering both natural and anthropogenic drivers and their interrelatedness to explain contemporary biogeographic patterns of species richness.

Keywords: Wadden Sea, SAR, isolation, habitat heterogeneity, biodiversity, island biogeography, barrier islands, alien species, structural-equation model, nature conservation

1 | Introduction

Extensive human impact on islands worldwide challenges the equilibrium theory of island biogeography (MacArthur and Wilson, 1967) - an elegant yet simple model that predicts species richness of discrete land units (e.g., islands). Humans have intentionally and unintentionally altered large parts of biotic as well as abiotic aspects of islands in all oceans (e.g., Rojas-Sandoval et al., 2020; Fernández-Palacios et al., 2021; Nogué et al., 2021; Tordoni et al., 2021). Thus, in times when humans considerably influence islands worldwide (e.g., Steinbauer and Beierkuhnlein, 2010; Helmus et al., 2014; Graham et al., 2017; Irl et al., 2021; Nogué et al., 2021; Gleditsch et al., 2023, Walentowitz et al. 2022), and natural systems are severely under pressure, it is paramount to consider anthropogenic in addition to natural drivers of insular biodiversity to advance our basic understanding of processes generating biodiversity on islands (Gleditsch et al. 2023).

Species numbers on islands have been increasing and are predicted to continue to rise in the future, mainly due to the accidental and deliberate introduction of non-native species (also referred to as alien species) by humans (Sax et al., 2002; Seebens et al., 2017, Walentowitz et al. 2023). In consequence, total plant species richness on some islands has more than doubled, and the number of non-native species exceeds the number of native species (Essl et al. 2019). Additionally, turnover rates increased 9.5-fold with the onset of human settlement on islands, as palaeoecological research, data dating back up to 5000 years, revealed (Nogué et al., 2021). The introduction of non-native species even changes fundamental biogeographical relationships such as the species-isolation relationship (Moser et al., 2018). In natural island systems, species numbers predictably decrease with increasing spatial isolation. However, the number of successfully established non-native species increases with spatial isolation. As already predicted from the equilibrium theory (MacArthur and Wilson, 1967), isolation is linked with low species richness of native species and, consequently, increased invasibility (Moser et al., 2018). Human influence supports this process mainly by functioning as vectors of transportation, reducing functional isolation, and changing the available area of suitable habitat conditions on islands through land use change.

Hence, it is evident that studies profit from complementing natural biogeographic drivers with anthropogenic drivers when aiming to unveil drivers of contemporary biodiversity. To explain the number of insular non-native species, anthropogenic predictor variables such as the number or density of human inhabitants and tourists (e.g., MacMaster, 2005; Essl et al., 2019; Rojas-Sandoval et al., 2020; Walentowitz et al., 2022), human infrastructure such as roads (e.g., Rojas-Sandoval et al., 2020; Irl er al., 2021) or per capita gross domestic product (GDP; e.g., Tordoni et al, 2021; Denslow et al., 2009) have been proven influential. Additionally, the number of native species has been shown to be directly influenced by anthropogenic drivers, such as human population or roads (e.g., Bailey et al., 2017; Rojas-Sandoval et al., 2020). Native plant diversity can additionally be influenced indirectly by human activity through introduced animal and plant species (Luna-Jorquera et al., 2012). The number of native and introduced species (termed naturalized species by the respective study) seem to be directly related as native richness is an excellent predictor of naturalized plant species (Sax & Gaines 2008). In most studies, natural biogeographic drivers of species richness, primarily island area and isolation, were shown to have stronger influences on insular species numbers compared to the effects of human activities (e.g., Moody, 2000, Rojas-Sandoval et al., 2020; Tordoni et al., 2021; Walentowitz et al., 2022). Nevertheless, anthropogenic drivers increase the explanatory power of models explaining insular species numbers and with continuing and increasing anthropogenic pressure on islands the importance of these variables can be expected to increase.

A little-acknowledged fact is that island biogeographic theory is rooted in barrier islands (Palmgren, 1915-1917 on Åland archipelago; MacArthur Wilson, 1967 on the Florida Keys). Barrier islands are highly suitable to exclusively account for species assemblages and underlying processes as these systems are commonly dynamic and short-lived (compared to oceanic islands) and usually do not exhibit evolutionary processes (e.g., speciation) (Niedrighaus et al., 2008). Thus, barrier islands fall perfectly into the domain of the equilibrium theory of island biogeography as missing speciation dynamics of barrier islands and their proximity to the mainland enable unhindered colonisation-extinction dynamics. Since the seminal work on island biogeography theory by MacArthur and Wilson (1967), the valuable contributions of such coastal islands and the characteristics of coastal islands lying in-between oceanic and continental islands have been corroborated by several studies aiming at understanding patterns and processes of species occurrences on islands (Kohn and Walsh, 1994; Scherber et al., 2018). On a gradient between oceanic islands (e.g., Hawaii, Canary Islands, Galapagos) and habitat islands or fragmented pieces of land (e.g., hedges between agricultural fields; a lake amidst terrestrial land), barrier islands, as a particular case of coastal islands, can be regarded as an intermediate system.

The focus of studies in island biogeography on oceanic islands contrasts the global importance of barrier islands. Worldwide, there are more than 2,000 barrier islands along the world's coasts, covering more than 20,000 km^2 of coastline (based on remote sensing images at 30 m resolution; Stutz et al., 2011). These islands commonly show very dynamic morphologies over time as they are commonly agglomerations of loose sediments and are constantly shaped by tides, waves, wind, and extreme events such as storms or storm surges (Zhang, 2016). Compared to oceanic island ontogeny, which operates on geological timeframes of hundreds of thousands or millions of years (Whittaker et al., 2008; Boregaard et al., 2016), barrier islands can change within decades. The proximity to continental areas makes barrier islands more susceptible to anthropogenic disturbances as the vicinity to permanently settled continental areas increases the likelihood of settling on barrier islands nearby. Additionally, barrier islands are attractive for tourism and recreational sports activities. The strong anthropogenic imprint on barrier islands calls for a socio-ecological perspective on insular floristic assemblage.

Along the Dutch, German, and Danish coast, a chain of barrier islands is arrayed. Scherber et al. (2018) identified habitat heterogeneity to best explain multidiversity (cross-taxa) on the East Frisian Islands (German coastal islands), and Ferreira-Arruda et al. (2022) describe island area and geomorphological changes to best explain plant diversity on these islands. However, the magnitude of influence by anthropogenic drivers and the interrelation of natural and anthropogenic biogeographic drivers of species richness remain unclear. In this study, we aim to disentangle anthropogenic and natural biogeographic drivers of native and non-native plant species richness at the example of barrier islands located along the Dutch, German, and Danish North Sea coasts. Our approach considers natural and anthropogenic drivers and their interrelatedness to challenge a set of hypotheses (figure 1) presented in detail in the following.

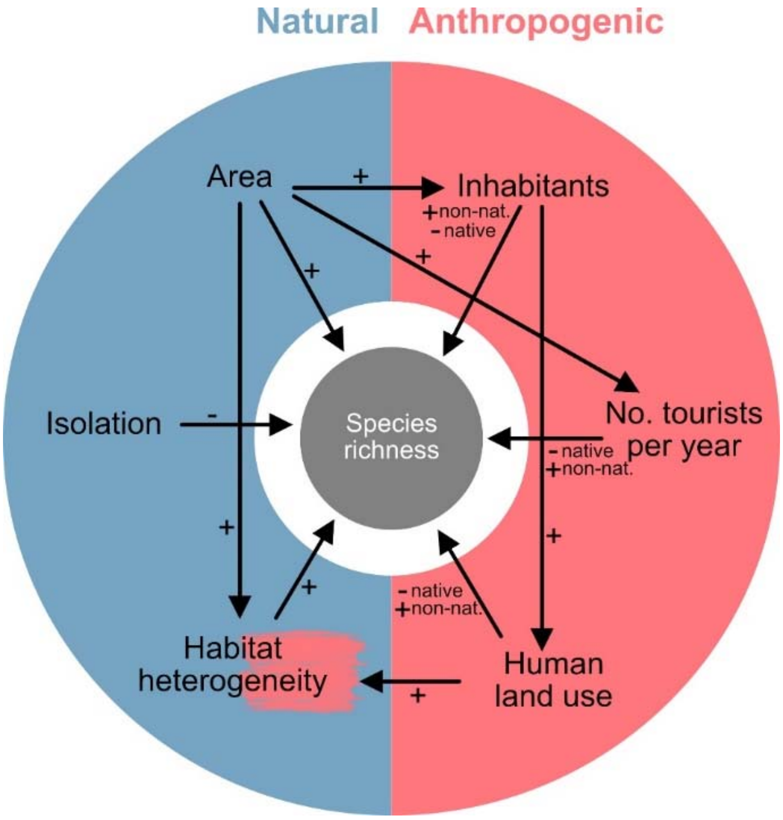

Figure 1: Schematic representation of hypothesized relationships between natural biogeographic (blue) and anthropogenic (light red) drivers of native and non-native plant species richness. Richness can be influenced directly (e.g., by area) or indirectly (e.g., larger island area leading to increased habitat heterogeneity that positively influences species richness). Positive relationships are indicated by a plus (+) and negative relationships with a minus (-) and are hypothesized to differ between non-native and native species in the number of inhabitants, tourists, and the impact of human land use. Habitat heterogeneity is mainly considered to be a natural driver but can be anthropogenically influenced, hence the colouring in blue and light red.

Natural drivers

(a) Area: Area generally emerges as the strongest predictor of species numbers on islands (e.g., MacArthur and Wilson, 1967; Lomolino, 2000; Kreft and Jetz, 2007). Thus, we expect area to drive both native and non-native plant species richness. As habitat heterogeneity is often highly correlated with area, we subsequently expect area to contribute directly and indirectly (through habitat heterogeneity) to insular species richness (Kohn and Walsh, 1994). We also expect area to influence species richness via the number of inhabitants and tourists, as larger islands will have a higher influx of people which can potentially negatively impact native species richness and lead to increased non-native plant species richness (Denslow et al., 2009; Spear et al., 2013).

(b) Habitat heterogeneity: The higher the diversity of habitats, the more species (native and non-native) can establish due to vacant niches (Hortal et al., 2009). The inclusion of area and habitat heterogeneity, being interrelated, allows testing for the relative roles of spatial processes (area) and niche-related processes (habitat heterogeneity) (Udy et al., 2021). This parameter represents not purely a natural biogeographic driver but can be influenced by human activities.

(c) Isolation, often measured as Euclidean distance from an island to the next mainland, is considered the second most relevant driver of species richness for insular species after area and is expected to be negatively related to species richness (MacArthur and Wilson, 1963; 1967). For barrier islands, Diver (2008) used the area of the landmasses surrounding an island to explain species numbers. We therefore expect isolation according to Diver (2008) to be negatively correlated with native species richness on North Sea Islands. We also expect non-native species numbers to decrease with increasing isolation as these plants can not only reach the islands via human transport but can also self-disperse from the near mainland, which is highly populated and hosts numerous non-native species.

Anthropogenic drivers

(d) Human land use: We expect native species to be negatively influenced by human land use due to reductions in natural habitat (e.g., Sánchez-Ortiz et al., 2020) and non-native species to be positively affected by this anthropogenic driver as it leads to the creation of novel human-dominated and disturbed habitats for non-native species (e.g., Pretto et al., 2010). Furthermore, habitat heterogeneity is impacted by human land use (Geri et al., 2010).

(e) Inhabitants: We hypothesise that a larger number of inhabitants affects the number of non-native species by increasing propagule pressure, as has been previously shown for other systems (Denslow et al., 2009; Spear et al., 2013). Meanwhile, more inhabitants increase the pressure on native habitats and are expected to reduce native species richness. Additionally, the number of inhabitants present on an island is predicted to influence the amount of anthropogenically used land.

(f) Touristic pressure: Tourism might affect propagule pressure; thus, we expect the number of non-natives to be positively associated with the number of tourists (Dimitrakopoulos et al., 2022). Negative impacts of tourism on native species richness are expected for the same reasons as those expected for inhabitants.

2 | Material and methods

2.1 | Study area

For this study, 31 islands located along the coast of the Netherlands, Germany (Lower Saxony, Schleswig-Holstein), and Denmark were considered (figure 2). Of these, 20 are true barrier islands, eight islands have formed around mainland cores ("Geestkerninseln"), and three islands are Halligen (very small marsh islands that are frequently impacted by storm surges). The island Nigehörn is exceptional as it was created artificially through hydraulic filling in 1989. The prevailing wind conditions come from a west-south-westerly direction (Siegismund and Schrum, 2001). The North Sea exhibits areas with microtidal (up to 1.35 m), mesotidal, and macrotidal (more than 2.90 m) ranges (Hayes, 1975; Böse et al., 2018).

The Frisian Islands resulted from the dynamic interactions between sea and land and commonly consist of unconsolidated sandy material (Davis, 1994; Wang and Briggs, 2015). Periodic and aperiodic disturbances lead to a constant relocation of material from west to east (e.g., inlet sedimentation bypassing; Fitzgerald et al., 1984). At the same time, these natural processes are being counteracted by human activities, slowing down or preventing these dynamics by building dikes, relocating tons of sand, or greening dunes (de Groot et al., 2017). The Frisian saying "Gott schuf das Meer aber der Friese die Küste" (*God created the sea but Frisians created the coast*) illustrates how natural forces predominantly determine local environmental conditions and that coastal environments result from the interplay of natural forces and centuries of anthropogenic management. The islands are popular for real estate with touristic attractions and numerous recreational activities. Land is partly used for agriculture, however, shifting towards increased touristic use in recent decades.

The native habitats are mainly composed of salt marshes and dunes (TMAP, 2017). Plant species occurring in salt marshes are predominantly herbs and are well adapted to a high salt content in the soil (e.g., *Salicornia* spp., *Puccinellia maritima*, and *Bolboschoenus maritimus*) (Leuschner & Ellenberger, 2017a). Dune vegetation can vary dramatically depending on the age of the dune and its distance to the sea, where young dunes are dominated by herb species such as *Cakile maritima* and *Elymus farctus,* while more mature dunes can harbour woody species from small shrubs to tall trees (e.g., *Salix repens* and *Betula pubescens*) (TMAP, 2017; Leuschner & Ellenberger, 2017b). Land use on the target islands can be described as rather extensive compared to mainland areas. Meadows with grazing sheep, cattle and horses are common. In areas surrounding and within human settlements the vegetation is a miscellaneous of opportunistic species such as *Plantago major*, escaped ornamental ones such as *Rosa rugosa*, and economically important crops such as *Triticum aestivum* (Niedringhaus et al., 2008). All 31 islands share similar maritime climatic conditions with mild winters and cool summers with moderate rainfall and strong winds.

The unique Wadden Sea of the Netherlands, Germany, and Denmark, with its islands, fauna and flora, and special environmental regimes, has been declared a UNESCO World Heritage Site (11,400 km^2) in 2009 with an extension in 2014 (UNESCO, 2022). The 14,950 km^2 of Wadden Sea are protected by a network of 11,950 km^2 of Nature Reserves (Netherlands, Denmark) and National Parks (Germany) referred to as the Wadden Sea Conservation Area (Common Wadden Sea Secretariat, 2022). The comparable setting of the 31 study islands along the European North Sea coast (figure 2), combined with their similarity in climate and topography, make them well-fit for island biogeographic studies.

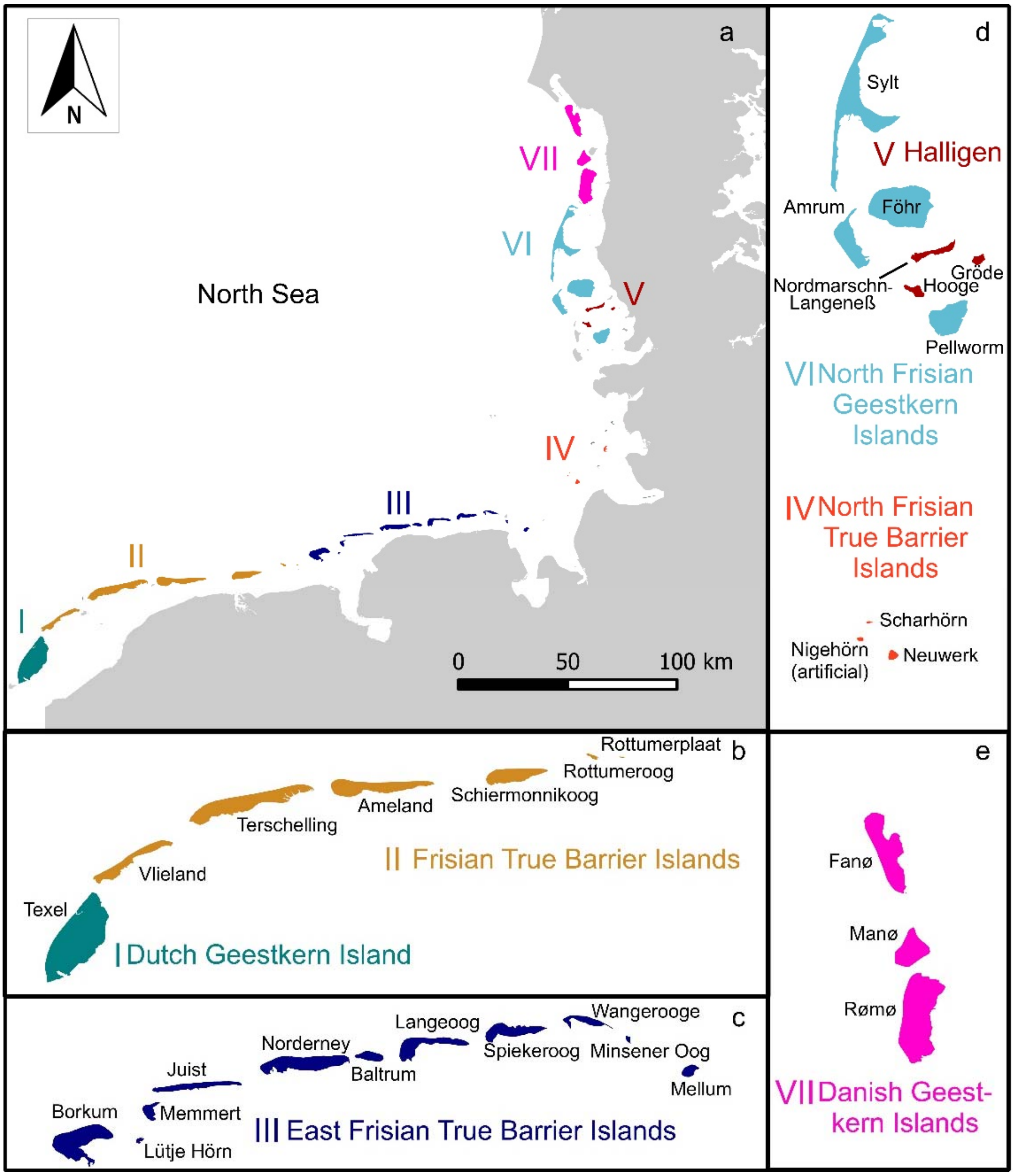

Figure 2: Overview of the study area (a) that comprises a total of 31 barrier islands, Geestkern islands, and Halligen along the North Sea coast of the Netherlands (b), Germany (c and d) and Denmark (e).

2.2 | Species occurrence data

We compiled plant species (spermatophytes and ferns) lists for the East Frisian Islands (Niedringhaus et al., 2008, considering plants present since 1980), for the West Frisian Island (NDFF 2015, considering plants since 1990), for the Danish Frisian Islands (Hartvig and Vestergaard, 2015, considering plants since 1992), and the North Frisian Islands (Hellwig, 2018; GBIF, 2020a-g; LLUR, 2020, considering plants since 1995) derived from extensive species survey by experts and complemented with information from the Global Biodiversity Information Facility (GBIF). The species data thus represents the status quo. We automatically extracted species occurrence information from LLUR (2020) using Python (Van

Rossum and Drake, 1995) and the *webbot 0.34* package. We standardised the species' names according to Plants of the World Online (2022). Sub-species and varieties were treated on species level. After name standardisation, we obtained a total of 1804 species. We then classified the species as native and non-native according to the species lists if information was provided and additionally used Tamis et al. (2004), Buchwald et al. (2013) and Haeupler and Muer (2007) for status information (in total native = 1105, non-native = 699).

2.3 | Environmental drivers

For all target islands, we gathered and calculated data on island area, isolation, and habitat heterogeneity as natural drivers, and island inhabitants, number of annual tourists, and percentage of human land use as anthropogenic drivers (table 1, table S1). We used a landscape measure of isolation (Diver, 2008), for which we calculated the percent land masses (of both neighbouring islands and the mainland) that lie within a buffer around the islands. We calculated this driver for buffers of 10 km, 20 km, 40 km, 60 km, 80 km, and 100 km (figure S1) and selected the buffer showing the highest correlation with native and non-native species richness for final modelling (100 km buffer, table S2). Habitat heterogeneity was calculated by applying the Shannon index (Pielou, 1966) to a total of 24 land use categories (CORINE Land Cover, European Environmental Agency, 2013; selection of classes), following Scherber et al. (2018). Island ontogeny, which has been proven to increase the explanatory power of models explaining insular species numbers (Whittaker et al., 2008; Boregaard et al., 2016) was not included in the study as coastal islands are commonly not places of large speciation events and island dynamics have not proven to explain species richness on some of the target barrier islands (Scherber et al., 2018).

The number of inhabitants and tourists visiting the islands per year (during pre-pandemic times) was sourced from a set of administrative and web sources (table S3). The cover of land significantly altered by humans was calculated as the percentage of land cover units (CORINE Land Cover, European Environmental Agency, 2013) that were identified as anthropogenic land use categories (selection of classes table S4) per island. We acknowledge that the diversity of non-native plant species on islands has been explained in other studies by socio-economic drivers, such as Gross Domestic Product (GDP) (Kueffer et al., 2010; Wohlwend et al., 2021). However, these studies commonly focus on oceanic islands (Wohlwend et al., 2021) and include islands at larger scales differing in GDP. As our target islands are only partly inhabited and open for tourism, form part of the European Union (EU) and are spatially very close to each other, we did not include GDP as an explanatory variable.

Table 1: Natural and anthropogenic drivers used to explain native and non-native plant species richness on 31 North Sea islands.

Driver	Measurement unit
Natural	
Area	km^2
Isolation	Landscape measure of isolation calculated as % land area within a 10 km, 20 km, 40 km, 60 km, 80 km, and 100 km buffer zone around the island (sensu Diver, 2008; figure S1). For the final model building, a buffer of 100 km was chosen, as it showed the highest correlation with species richness (table S2).

Habitat heterogeneity	Shannon index of 24 CORINE land cover classifications (Land Cover, European Environmental Agency, 2013, release from 2018) sensu Scherber et al. (2018)
Anthropogenic	
Inhabitants	Number of inhabitants per island (sources listed in table S3).
Tourist numbers	Annual number of visiting tourists per island (sources listed in table S3)
Human land use	% land used anthropogenically based on CORINE Land Cover classifications (European Environmental Agency, 2013; selection of classes table S4)

2.4 | Data analysis

We tested the premise that island species numbers are not biased due to differences in island ontogeny (i.e., true barrier island, Geestkern island, Hallig) or affiliation to different countries with an ANOVA and post-hoc Tukey HSD. For the main analysis, we chose two approaches (uni- and multivariate) applied to the same dataset to shed light on the data from different angles, which is valuable when dealing with complex ecological data. Data analysis and visualisation were conducted in R Version 4.0.5 (R Core Team, 2022). Univariate relationships between insular native and non-native species richness and natural and anthropogenic drivers were assessed by fitting generalised linear models (GLMs; Poisson family error, log link). GLMs containing anthropogenic variables were limited to inhabited islands. When fit, log-transformed variables were used for GLMs to increase model performance (assessed by Akaike Information Criterion, AIC). Model fit of GLMs was evaluated by analysing the distribution of the residuals. Pseudo R^2-values were calculated according to Nagelkerke (1991) using the package *rms* (Harrell, 2020). Additionally, GLMs were built using standardized species richness values (standardized to max = 1) to compare slopes between models describing native and non-native species richness.

Additionally, we fit structural equation models (SEM) (Grace, 2006; Shipley, 2016) to distinguish how different natural and anthropogenic drivers jointly affect native and non-native plant diversity, respectively, and to account for interrelations of drivers according to our set of hypotheses (figure 1). The advantage of SEMs is that they allow the measurement of direct and indirect effects and give account to the complexity of a system. SEMs were built based on a correlation matrix of all drivers that showed a significant univariate relationship with native and non-native plant species richness based on univariate GLMs, using the *lavaan* package (Rosseel, 2012; table S5). Multivariate normality was assessed using the *MVN* package (Korkmaz et al., 2014) to ensure that model requirements concerning data distribution (skewedness, kurtosis) are met. Accordingly, if necessary, drivers were log- or square root-transformed to meet the requirement of normal data distribution. Model fit was evaluated by ensuring that the degrees of freedom are positive and do not exceed $n(n+1)/2$, with n = number of observed variables. Additionally, we report Chi-square, root mean square error of approximation (RMSEA), standardized root mean square residual (SRMR), non-normed fit index (NNFI) and comparative fit index (CFI) to evaluate the overall model fit (Fan et al., 2016; table S6). For visualisation, non-significant paths were removed to receive the most parsimonious model. As the anthropogenic drivers are expected to strongly influence models with values of zero for non-inhabited islands, we repeated the SEMs using a subset of only inhabited islands.

3 | Results

With 1060 species, the westernmost and largest of all studied islands, Texel, exhibited the highest plant species richness, including the highest number of native (n = 824) and non-native (n = 236) species (table S1). The uninhabited East Frisian Island Lütje Hörn exhibited the lowest species number (n = 66), of which only five species were non-native and 61 species were native. Lütje Hörn also represented the smallest of the target islands. On Sylt, the highest percentage of non-native plant species was present (25,7%) while Rottumeroog showed the lowest percentage of such species (7.3%, table S1). Species richness did not differ significantly between islands affiliated with different countries (figure S2). The number of species was significantly lower on Halligen, as these islands are commonly smaller than true barrier and Geestkern islands (figure S3). On inhabited islands, a mean of 14% of the species was non-native, while on uninhabited islands, this value was lower, reaching a mean of only 9%.

The univariate analysis revealed that native and non-native insular species richness responded strongly to island area (log-log space, $p < 0.001$, Pseudo-$R^2 = 0.60$ and 0.73, respectively), isolation (calculated as the land area within an 100 km radius around the islands, $p < 0.001$, Pseudo-$R^2 = 0.30$ and 0.32, respectively) and habitat heterogeneity ($p < 0.001$, Peudo-$R^2 = 0.71$ and 0.67, respectively, figure 3). The slope describing the relationship between standardized richness values and habitat heterogeneity was similar for native and non-native species but differed slightly for area (non-native species richness increased faster with increasing area) and isolation (non-native species richness decreased faster with increasing isolation, figure S4a-c). From the set of anthropogenic variables, we found that an increase in inhabitants ($p < 0.01$ and $p < 0.001$, Psedudo-$R^2 = 0.64$ and 0.76, respectively, figure 3d) and the number of tourists visiting annually ($p < 0.01$ and 0.001, Pseudo- $R^2 = 0.64$ and 0.76, respectively, figure 3e) led to higher species richness of native and non-native species on inhabited islands. On those islands, human land use did not explain patterns of native and non-native species richness ($p > 0.05$, figure 3f). Non-native species richness increased faster compared to native species richness with increases of all three anthropogenic variables (figure S4d-f).

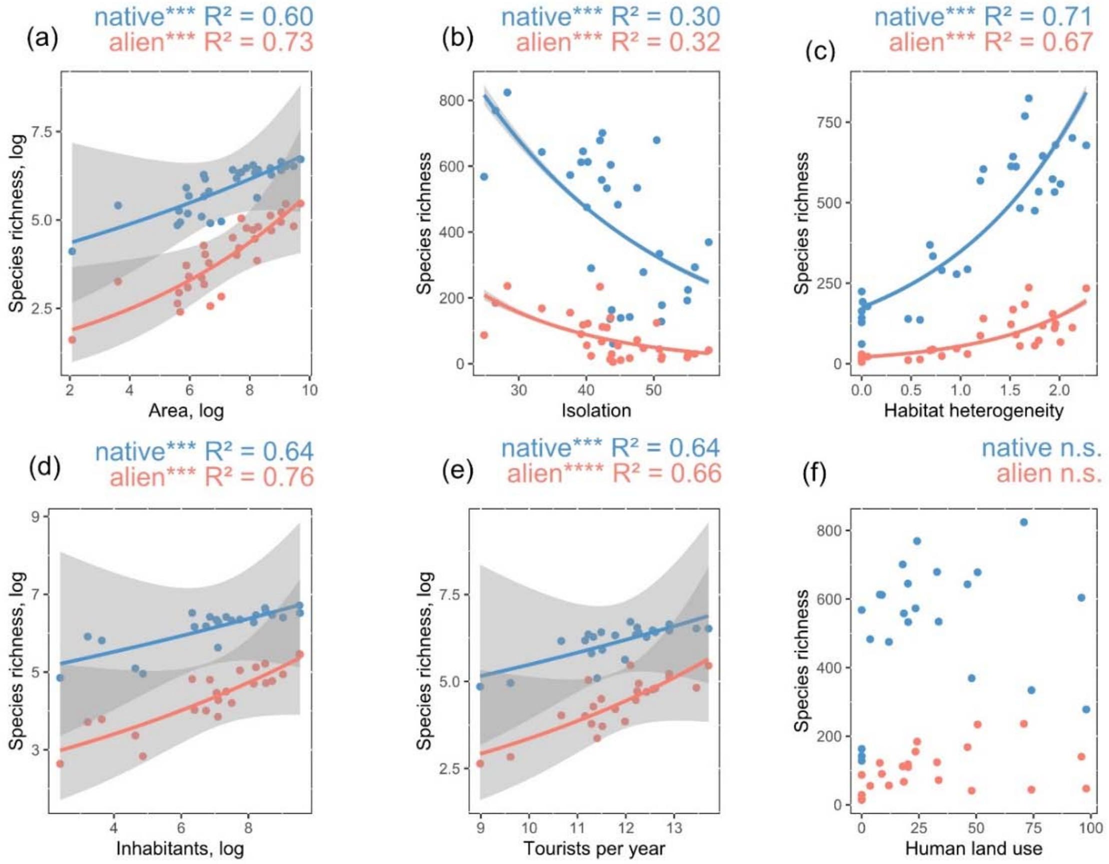

Figure 3: The univariate relationships of native (blue) and non-native (light red) insular species richness with area (log-transformed; a), isolation (b), habitat heterogeneity (c), inhabitants (log-transformed; d), tourists per year (log-transformed; e), and the percentage of human land use (f) resulting from GLMs (Poisson family error, log link). Note that the GLMs for the relationship between species richness and anthropogenic variables (d-f) were limited to inhabited islands. Grey-shaded areas indicate confidence intervals of 95% and significance levels are reported using asterisks. Note that the confidence interval in (b) and (c) is very narrow and thus hardly visible. Pseudo-R^2, according to Nagelkerke (1991), is given for significant relationships.

From the joined and interrelated analysis of natural and anthropogenic drivers potentially affecting insular plant species richness with SEMs, we can derive that incorporating driver interrelatedness adds considerable information on the processes that lead to species assemblages on the target islands (figure 4, table S7). Island area drives native plant species richness indirectly by affecting habitat heterogeneity (standardised model estimate of 0.7) and inhabitants (standardized model estimate of 0.8), which explains large amounts of the variety in plant species between islands (figure 4a). Area drives non-native plant species richness primarily by influencing the number of inhabitants (standardised model estimate 0.8) and tourists (standardised model estimate 0.8) which directly impact non-native plant species numbers (figure 4b). Isolation negatively affects native and non-native plant species richness on inhabited islands (standardised model estimate -0.2). In sum, the direct influence of habitat heterogeneity (standardised model estimate 0.5) and inhabitants (standardized model estimate 0.2) on all islands and isolation on inhabited islands (standardized model estimate -0.2), and the indirect influence of island area on habitat heterogeneity (standardized model estimate 0.7) accounted for large parts of the variation in native plant species richness (R^2 = 0.88). The number of island inhabitants (standardized model estimate 0.6) and annual tourists (standardized model estimate 0.3) directly, island area indirectly through the number of inhabitants (standardized model estimate 0.8) per island and tourists visits (standardized model estimate 0.8), and isolation directly (standardized model estimate -0.2, only on inhabited islands) accounted for most of the variation in non-native plant species (R^2 = 0.88).

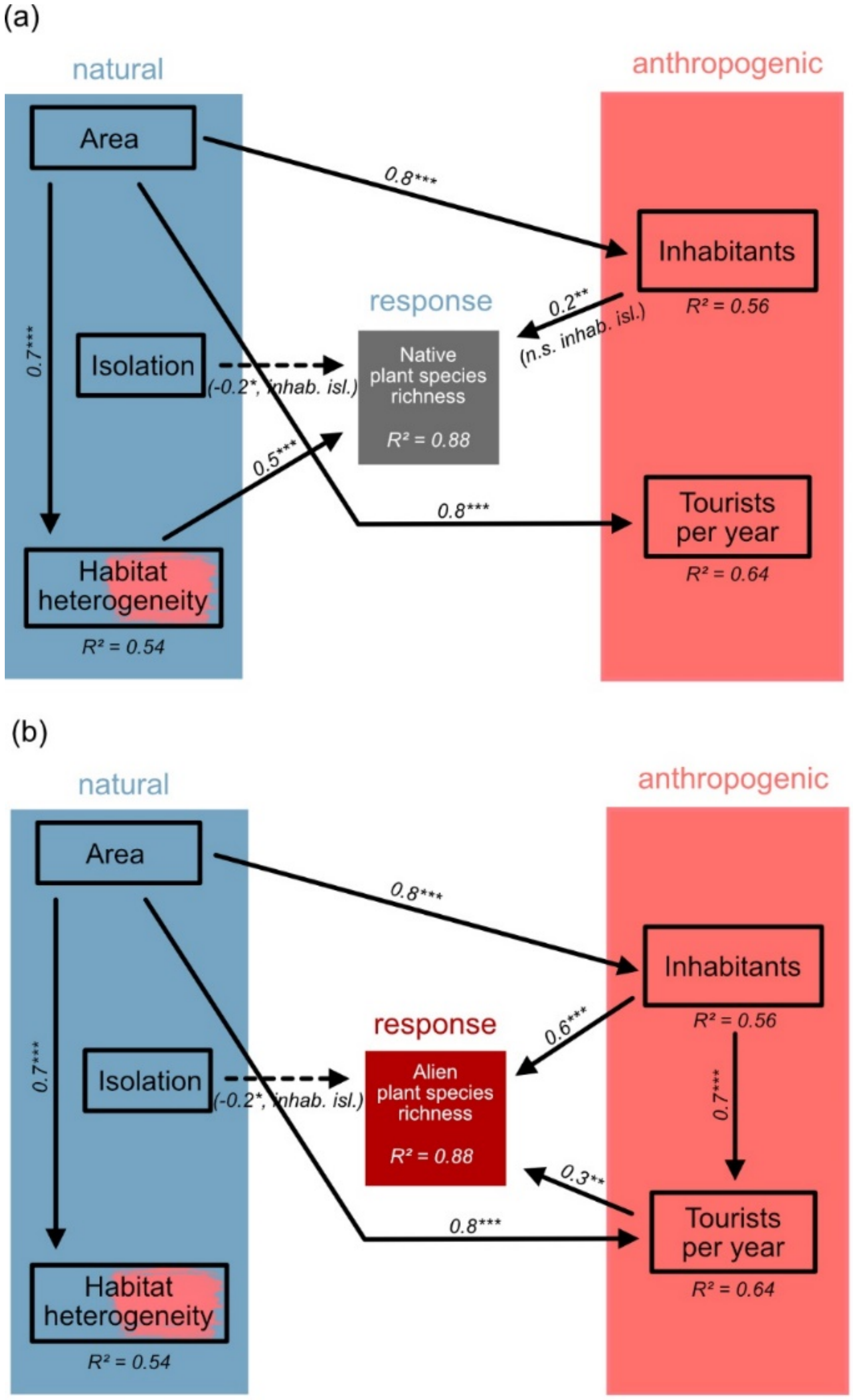

Figure 4: Structural Equation Models of natural (blue) and anthropogenic (red) drivers explaining the numbers of a) native and b) non-native species present on 31 North Sea islands. Standardised model estimates, significance levels (with asterisks) and R^2-values are given. Dashed arrows indicate results based on a SEMs reduced to inhabited islands (n = 26) for those relationships that differed from the full model in significance.

4 | Discussion

Both natural biogeographic and anthropogenic drivers explained large parts of the variance in native and non-native plant species richness on North Sea Islands. Multivariate analysis of species richness patterns revealed a complex network of interrelated drivers of species richness and offered insights into the emergence of extant insular richness patterns. European coastal islands offer an excellent natural setting for testing hypotheses in island biogeography (e.g., Scherber et al., 2018 for East Frisian Islands; Arruda-Ferreira et al., 2022 for Dutch and East Frisian Islands). All islands exhibit comparable climatic conditions and distances to the terrestrial mainland. Formation and isolation occurred during the Holocene, leaving no options for idiosyncrasies caused by speciation processes. Besides this general homogenous setting, we could identify differences in native and non-native insular plant species numbers that can be explained by a distinct set of drivers.

Univariate analysis revealed that island size was positively related to both native and non-native plant species richness and explained the largest variance of species richness on islands, which aligns with numerous studies in island biogeography (e.g., MacArthur and Wilson, 1967; Lomolino, 1982; Kreft et al., 2008; Triantis et al., 2012). For the East Frisian Islands, representing a subset of our target islands, Scherber et al. (2018) identified area as the second most important driver of overall species richness (plants and animals) after habitat heterogeneity. However, the SEMs suggest area to have an indirect effect on species richness through habitat heterogeneity and inhabitants for native plants and through island inhabitants and tourists for non-native species. In fact, native species richness was mostly directly driven by habitat heterogeneity, which aligns with Udy et al. (2021) who found this relationship globally. Thus niche-related processes seem to be the prominent underlying cause of native richness patterns in contrast to pure spatial processes (Udy et al., 2021). Conversely to Wohlwend et al. (2021), who identified area and island altitude (which relates to the 3-dimensional area of islands) to explain a large variance of naturalized species richness in the Pacific region, our SEMs suggest no direct effect of this natural biogeographic driver on non-native plants.

According to Scherber et al. (2018), habitat diversity best explained cross-taxa diversity in the East Frisian Islands, representing a subset of this study's target islands. While the univariate analysis resulted in habitat heterogeneity explaining 71% of the variance in native and 67% of the variance in non-native species, the SEMs showed that, in contrast to this general finding and to our expectations, habitat heterogeneity was not relevant in explaining insular non-native plant species richness. The high correlation of several drivers can evoke the impression of an existing relationship and the effects of single drivers can better be assessed by simultaneous application in a model. The detachment of non-native plants from habitat heterogeneity can be explained by the fact that many non-native plants on islands are often ornamentals. This aligns well with a lower percentage of non-native plants found on uninhabited islands compared to inhabited islands in this study. Non-natives thrive within the proximity of humans but would not necessarily resist the hostile conditions close to the sea where sandy soils prevail, and tides, strong winds, and salt spray only allow the survival of well-adapted plants. Nevertheless, the relation of non-native plants with habitat heterogeneity has been little explored, as richness patterns are rarely investigated separately for native and non-native species. Scherber et al. (2018), for example, did not differentiate between native and non-native species richness on the East Frisian Islands, and hidden patterns remain veiled. Studies like those by Rojas-Sandoval et al. (2020) and Tordoni et al. (2021) analyse patterns of native and non-native plants separately but do not consider habitat heterogeneity as a driver. The impact of habitat heterogeneity on plant species richness is also difficult to understand, as this driver is in its essence natural, but it can be significantly altered by anthropogenic impact. Additionally, plant population can also be diminished and impacted within natural habitats by human collection (Norton et al., 1994) or browsing, grazing, and trampling by non-native animals. To be considered as well is that for non-native plants, environmental filtering might be more critical than dispersal filtering. This point is also stressed by the little importance that isolation played in explaining native and non-native plant species richness on islands. Only a slight negative impact of isolation can be recovered for native and non-native species in the multivariate analyses and univariate analysis. The minor relevance of isolation for near-shore continental islands compared to oceanic islands has been reported before (Weigelt and Kreft, 2013) where it is attributed to the proximity of such islands to source populations. For the analysed coastal islands, the inverse species-isolation relationship reported from remote oceanic islands by Moser et al. (2018) cannot be confirmed, which can most likely be attributed to the proximity to the mainland and the very different characteristics of the here targeted coastal islands compared to remote tropical and subtropical islands addressed by Moser et al. (2018).

Interestingly, the amount of human land use per island was irrelevant for native and non-native plant species richness. We propose that native species might be unaffected by this anthropogenic driver as firstly, those plants might ostensibly be limited by the prevailing environmental conditions, i.e., the influence of strong winds, salt spray and floodings and secondly, human land use is comparatively extensive on the target islands and thus native species persist on anthropogenically used land. Thus, species occurrences might be similar in- and outside anthropogenically used areas. Additionally, some native species on North Sea barrier islands could also be synanthropic, profiting from human land use, which could compensate for a potential loss in numbers of native species in areas under human land use. This could lead to unaffected species numbers but increased turnover and has, to our knowledge, not yet been investigated for the North Sea islands targeted in this study. The reasons for the non-existence of a relationship between human land use and non-native species remain unknown.

The number of inhabitants best explained non-native species numbers on islands which can be seen as a proxy for human activities supporting the establishment of non-natives (e.g., by laying out gardens) or as a proxy for functional connectivity as humans tend to travel between the neighbouring mainland and the islands. Humans most likely function as vectors for such species and directly and indirectly introduce species that then become established on the island. This aligns with literature that confirms the positive influence of human population size and density on the number of non-native species (Denslow et al., 2009; Spear et al., 2013). For the same reasons, the number of tourists was expected to influence the number of non-native species, which was confirmed by both, the univariate and multivariate analyses. The SEMs suggest that the relationship of native species richness with the number of tourists is negligible in this case study. In contrast to non-native species, the number of native species was unaffected by the annual number of visiting tourists, but a slight influence of inhabitants could be recovered. Potential explanations are that firstly, the flora of the North Sea barrier islands is dominated by halophytes (Niedringhaus et al., 2008) and these species are well adapted to the harsh prevailing environmental near-shore conditions where human influence is marginal. Secondly, all islands are located within national parks (Common Wadden Sea Secretariat, 2022), which reduces anthropogenic pressure. The trilateral Wadden Sea agreement between the Netherlands, Denmark, and Germany has created a common framework of conservation policies and management to treat the whole Wadden Sea as one entity (Common Wadden Sea Secretariat, 2022). The unaffectedness of native species numbers by tourists could imply that management and protection concept are effective. Additionally, native species might face an extinction debt and the direct effect of, e.g., inhabitants and tourists on the one hand, and plant (and animal) invasions on the other hand might only become effective in the future (Gilbert & Levine, 2013; Cronk, 2016; Otto et al., 2017).

Although we could explain large parts of the variation in native and non-native plant species richness on North Sea Islands, additional drivers that we did not consider in our models might be influential, such as the time span of human settlement. Additionally, the border between natural and anthropogenic drivers might be blurry as drivers commonly considered as ‘natural’ might be anthropogenically impacted. Parts of an island can be uninhabitable for certain species, reducing the effective area they could occupy that can differ from the total area of an island. The effect of island isolation can be reduced by anthropogenic activities that function as vectors, thereby shortening biogeographic distances between islands and mainland areas. In addition to the six focal natural and anthropogenic biogeographic drivers, differences in species numbers between islands might also be attributable to slightly differing survey periods (Aggemyr & Cousins, 2012; Chiarucci et al., 2017), location along geographical gradients (Hawkins & Diniz-Filho, 2004), flooding frequency and intensity and therefrom resulting soil salinity. However, as species richness on true barrier islands did not differ markedly from those on Geestkerninseln (islands with mainland cores) between which soil properties differ, such island characteristics did not seem to influence species patterns significantly. Only Halligen proved to host a lower number of plant species, which can be attributed to their smaller sizes compared to the other target islands.

Biogeographic and biodiversity research is complex considering the multitude of influential natural drivers, and numerous additional anthropogenic drivers that are, in addition, highly interrelated. A recently proposed shortfall of biodiversity research is the *Hookerian* shortfall which delineates that our understanding of human-mediated changes in insular biodiversity is limited (Carine & Menezes de Sequeira 2020). The shortfall was named after Joseph Dalton Hooker, who demonstrated in the 19th century at the example of the islands Madeira and St. Helena that humans have already massively influenced the flora on those islands and that differentiating between anthropogenic changes and natural processes is challenging. He also identified islands to be well-suited to disentangle natural processes from anthropogenic influences. Our study on the Frisian Islands can be seen as a contribution to tackle this challenge and contribute to a better understanding of the emergence of biodiversity patterns in the Anthropocene.

Our aim was to disentangle the effects of natural and anthropogenic drivers on native and non-native plant species richness on islands while accounting for the interdependency of contrasting drivers at the example of 31 North Sea Islands. The double analysis approach (GLMs and SEMs) we chose had the advantage that we could illuminate our data from different sides. Such an approach is well-suited for ecological data as these are often complex and can be ambiguous. The North Sea islands serve well as an example system to challenge and develop theories in island biogeography, especially in the context of anthropogenic influences on biogeographic patterns. We could show that insular native and non-native plant species can be governed by different drivers (natives responded mostly to habitat heterogeneity; non-natives to the number of inhabitants). In general, the research landscape on anthropogenic drivers of insular species richness is growing (e.g., Rodgers III and Parker, 2003; Rojas-Sandoval et al., 2020; Irl et al., 2021; Tordoni et al., 2021; Wohlwend et al., 2021; Dimitrakopoulos et al., 2022). The interrelation of anthropogenic and biogeographic factors that drive species richness patterns should be considered when evaluating the importance of human impacts on species richness patterns for both native and non-native plant species richness (e.g., Gleditsch et al., 2023).

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Data availability statement

Data are openly available on zenodo and via https://doi.org/10.5281/zenodo.8371245 and provided in the Supporting Information.

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Supplementary Materials

Table S1: Species numbers of 31 Nort Sea Islands, their affiliation to countries (NL = Netherlands, DE = Germany, DN = Denmark) and island groups and natural and anthropogenic drivers (area, isolation expressed as land within a radius of 100 km around an island, habitat heterogeneity, number of inhabitants and tourists per year, and the percent anthropogenic land use).

Target islands			Species richness			Natural driver				Anthropogenic driver		
Island name	**Country**	**Island group**	**Total**	**Native**	**Non-native**	**Area (ha)**	**Isolation (surr. land, %)**	**Habitat hetero-geneity**	**Island type**	**Inhabitants**	**Tourists per year**	**Anthropo-genic land use**
Texel	NL	West Frisian	1054	820	234	16235	25	1.69	Mainland core	13575	178930	71
Vlieland	NL	West Frisian	652	565	87	3538	23	1.2	True barrier	1155	2.00E+05	0
Terschelling	NL	West Frisian	948	765	183	8527	26	1.65	True barrier	4888	4.00E+05	24
Ameland	NL	West Frisian	810	642	168	5942	32	1.53	True barrier	3716	4.00E+05	46
Schiermonnikoog	NL	West Frisian	729	609	120	3944	42	1.51	True barrier	947	3.00E+05	8
Rottumerplaat	NL	West Frisian	148	135	13	801	44	0.59	True barrier	0	0	0
Rottumeroog	NL	West Frisian	149	138	11	294	45	0.47	True barrier	0	0	0
Borkum	DE	East Frisian	809	699	110	3327	43	2.13	True barrier	5002	205719	18
Lütje Hörn	DE	East Frisian	65	61	4	8	45	0	True barrier	0	0	0
Memmert	DE	East Frisian	313	289	24	651	41	0.81	True barrier	1	0	0
Juist	DE	East Frisian	701	612	89	1689	38	1.56	True barrier	1534	97806	9
Norderney	DE	East Frisian	760	643	117	2673	36	1.83	True barrier	6032	283516	20
Baltrum	DE	East Frisian	529	474	55	673	37	1.75	True barrier	599	42861	12
Langeoog	DE	East Frisian	624	558	66	2076	38	2.01	True barrier	1812	130724	18
Spiekeroog	DE	East Frisian	536	482	54	1926	39	1.6	True barrier	843	70133	4
Wangerooge	DE	East Frisian	604	533	71	643	42	1.79	True barrier	1214	83104	34
Minsener Oog	DE	East Frisian	200	178	22	378	47	0.06	True barrier	0	0	0
Mellum	DE	Watten im Elbe-Weser-Dreieck	322	292	30	392	54	1.07	True barrier	1	0	0
Scharhörn	DE	Hamburgisches Wattenmeer	247	222	25	37	49	0	True barrier	1	0	0
Nigehörn	DE	Hamburgisches Wattenmeer	206	187	19	282	49	0.01	Artificial barrier	0	0	0

Neuwerk	DE	Hamburgisches Wattenmeer	407	366	41	360	53	0.69	True barrier	25	1.00E+05	48
Pellworm	DE	North Frisian	321	278	43	3802	46	0.96	Mainland core	1203	160000	98
Hooge	DE	North Frisian	186	162	24	600	41	0	Hallig	103	90000	0
Langeneß	DE	North Frisian	157	141	16	1154	44	0	Hallig	129	15000	0
Gröde	DE	North Frisian	141	127	14	268	50	0	Hallig	11	8000	0
Amrum	DE	North Frisian	716	569	147	2257	33	1.93	Mainland core	2311	75000	24
Föhr	DE	North Frisian	731	600	131	8448	41	1.23	Mainland core	8321	212709	96
Sylt	DE	North Frisian	845	668	177	9920	40	2.27	Mainland core	13818	9.00E+05	51
Rømø	DN	North Frisian	800	677	123	12886	51	1.96	Mainland core	559	7.00E+05	33
Mandø	DN	North Frisian	377	334	43	763	54	0.72	Mainland core	38	80000	74
Fanø	DN	North Frisian	642	532	110	6138	50	1.95	Mainland core	3488	250000	20

Table S2: Correlation matrix of native and non-native species richness with buffers of 10 km, 20 km, 40 km, 60 km, 80 km, and 100 km around the 31 target islands.

	Native species	Non-native species	Buffer 100 km	Buffer 80 km	Buffer 60 km	Buffer 40 km	Buffer 20 km	Buffer 10 km
Native species	1,00	0.89	-0.60	-0.60	-0.53	-0.31	-0.10	0.02
Non-native species	0.89	1,00	-0.62	-0.61	-0.53	-0.34	-0.17	-0.09
Buffer 100 km	-0.60	-0.62	1,00	0.94	0.79	0.45	0.23	0.05
Buffer 80 km	-0.60	-0.61	0.94	1,00	0.94	0.65	0.38	0.13
Buffer 60 km	-0.53	-0.53	0.79	0.94	1,00	0.84	0.59	0.31
Buffer 40 km	-0.31	-0.34	0.45	0.65	0.84	1,00	0.88	0.65
Buffer 20 km	-0.10	-0.17	0.23	0.38	0.59	0.88	1,00	0.85
Buffer 10 km	0.02	-0.09	0.05	0.13	0.31	0.65	0.85	1,00

Table S3: Sources of data on number of inhabitants and tourists visiting the islands per year.

Number of inhabitants	
Dutch Islands	https://opendata.cbs.nl
East Frisian Islands, Pellworm, Langeneß, Gröde, Sylt	https://www.statistikportal.de
Hooge, Amrum, Föhr	https://www.statistik-nord.de
Danish Islands	https://www.statistikbanken.dk
Neuwerk, Süderoog, Oland, Memmert, Mellum, Scharhörn	https://www.wikipedia.de/
Number of visiting tourists per year	
East Frisian Islands	TourismusMarketing Niedersachsen, personal communication by Thorsten Glaß
Texel	https://www.texel.net
Vlieland	https://www.nach-holland.de
Terschelling	https://core.ac.uk/
Ammeland	https://www.wadden-vakantiehuis.nl
Schiermonnikoog	https://www.holland.com
Neuwerk	https://www.ndr.de
Süderoog	https://www.rnz.de
Hooge, Langeneß, Gröde, Oland	https://halligen.de
Pellworm	https://www.spiegel.de/reise/deutschland/nordsee
Amrum, Föhr, Sylt, Rømø	https://de.statista.com
Mandø	https://www.vadehavskysten.de
Fanø	http://fanö.com/

Table S4: Classes, including codes, of CORINE land cover classification considered anthropogenic land use categories.

code	class
112	Discontinuous urban fabric
121	Industrial or commercial units and public facilities
124	Airports
142	Sport and leisure facilities
211	Non-irrigated arable land
231	Pastures, meadows and other permanent grasslands under agricultural use
242	Complex cultivation patterns
123	Port areas

Table S5: Correlation matrix of all variables used in SEMs.

	Native species	Non-native species	Area (log)	Human land use (sqrt)	Isolation (buffer 100 km)	Habitat heterogeneity	Inhabitants (sqrt)
Native species	1.00	0.890	0.801	0.620	-0.599	0.895	0.828
Non-native species	0.890	1.00	0.783	0.638	-0.620	0.749	0.918
Area (log)	0.801	0.783	1.00	0.612	-0.534	0.735	0.751
Human land use (sqrt)	0.620	0.638	0.612	1.00	-0.154	0.569	0.658
Isolation (buffer 100 km)	-0.599	-0.620	-0.534	-0.154	1.00	-0.474	-0.588
Habitat heterogeneity	0.895	0.749	0.735	0.569	-0.474	1.00	0.727
Inhabitants (sqrt)	0.828	0.918	0.751	0.658	-0.588	0.727	1.00

Table S6: Fit measures of SEMs based on all islands (n = 31) and on inhabited islands only (n = 26) for models describing native and non-native species richness. Results of the Chi-square test, degrees of freedom (df), p-value, root mean square error of approximation (RMSEA), standardized root mean square residual (SRMR), non-normed fit index (NNFI) and comparative fit index (CFI) are provided.

	All islands		Inhabited islands	
Indice	Native spec.	Non-native spec.	Native spec.	Non-native spec.
Chi-square	16.229	16.229	10.006	10.006
df	6.000	6.000	6.000	6.000
p-value	0.012	0.012	0.124	0.124
RMSEA	0.235	0.235	0.147	0.147
SRMR	0.089	0.091	0.070	0.070
NNFI	0.844	0.843	0.928	0.928
CFI	0.933	0.933	0.969	0.969

Table S7: Result of SEM based on all islands (n = 31) and on inhabited islands only (n = 26). Model estimates, significance levels (p-values) and standard values are given. The parameter area was log and the parameters inhabitants and tourists were square root transformed.

	All islands (n = 31)		Only inhabited islands (n = 26)	
Regressions	Estimate (p-value)	Standard Error	Estimate (p-value)	Standard Error
nr. natives ~ area	0.1 (0.610) n.s.	0.138	0.1 (0.459) n.s.	0.139
~ tourists	0.2 (0.072) n.s.	0.097	0.1 (0.248) n.s.	0.100
~ inhabitants	0.2 (0.025)*	0.088	0.1 (0.222) n.s.	0.097
~ isolation	-0.1 (0.063) n.s.	0.069	-0.2 (0.001)**	0.075
~ habitat heter.	0.5 (<0.001)***	0.086	0.6 (<0.001)***	0.079
inhabitants ~ area	0.8 (<0.001)***	0.119	0.8 (<0.001)***	0.117
habitat heter. ~ area	0.7 (<0.001)***	0.122	0.6 (<0.001)***	0.144
tourists ~ area	0.8 (<0.001)***	0.108	0.8 (<0.001)***	0.113
nr. non-native ~ area	0.0 (0.866) n.s.	0.139	0.1 (0.709) n.s.	0.140
~ tourists	0.3 (0.005)**	0.098	0.3 (0.004)**	0.101
~ inhabitants	0.6 (<0.001)***	0.089	0.5 (<0.001)**	0.098
~ isolation	-0.1 (0.081) n.s.	0.069	-0.2 (0.011)*	0.075
~ habitat heter.	0.0 (0.621) n.s.	0.086	0.1 (0.485) n.s.	0.079
inhabitants ~ area	0.8 (<0.001)***	0.119	0.8 (<0.001)***	0.117
habitat heter. ~ area	0.7 (<0.001)***	0.122	0.6 (<0.001)***	0.144
tourists ~ area	0.8 (<0.001)***	0.108	0.8 (<0.001)***	0.113

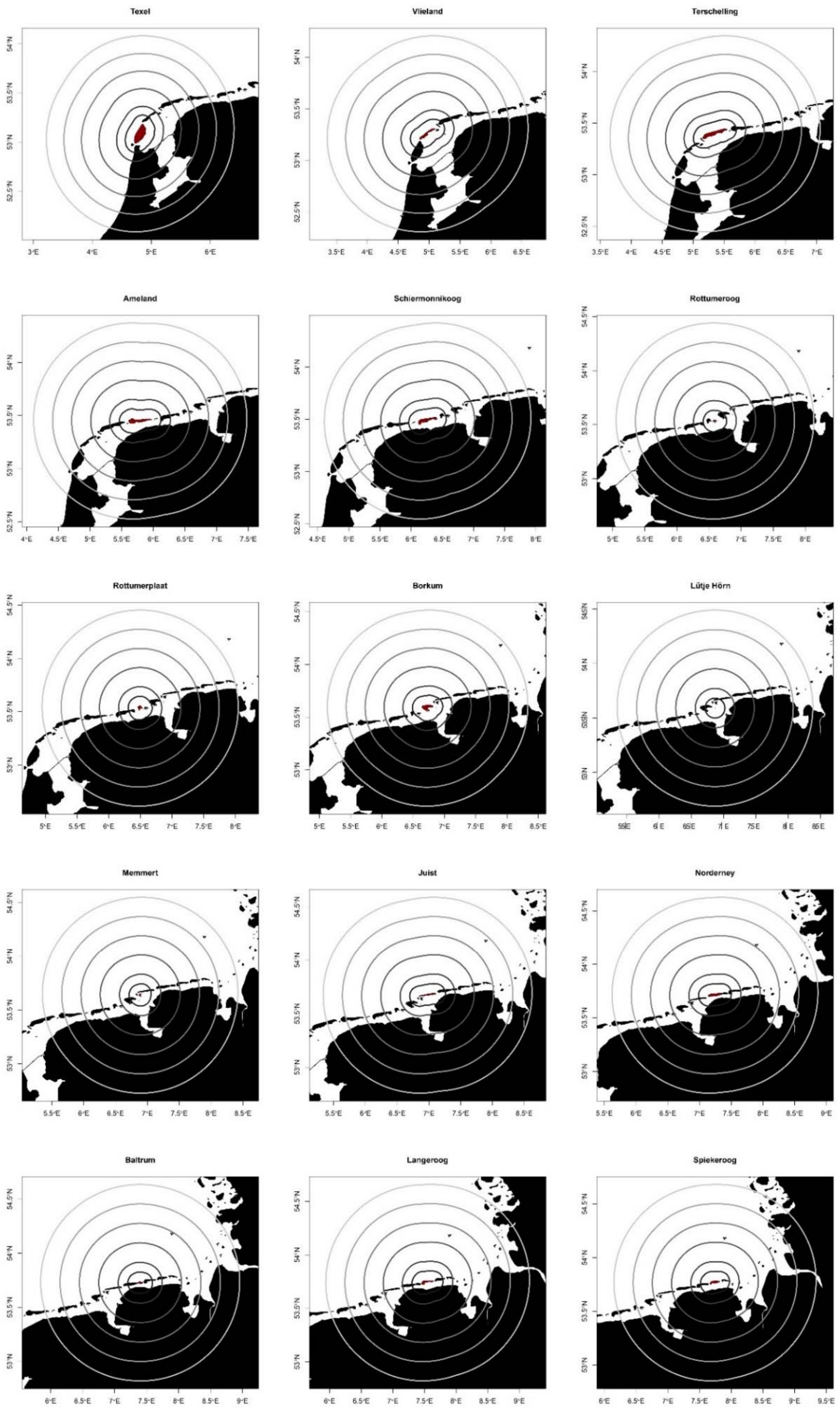

Figure S1 continued

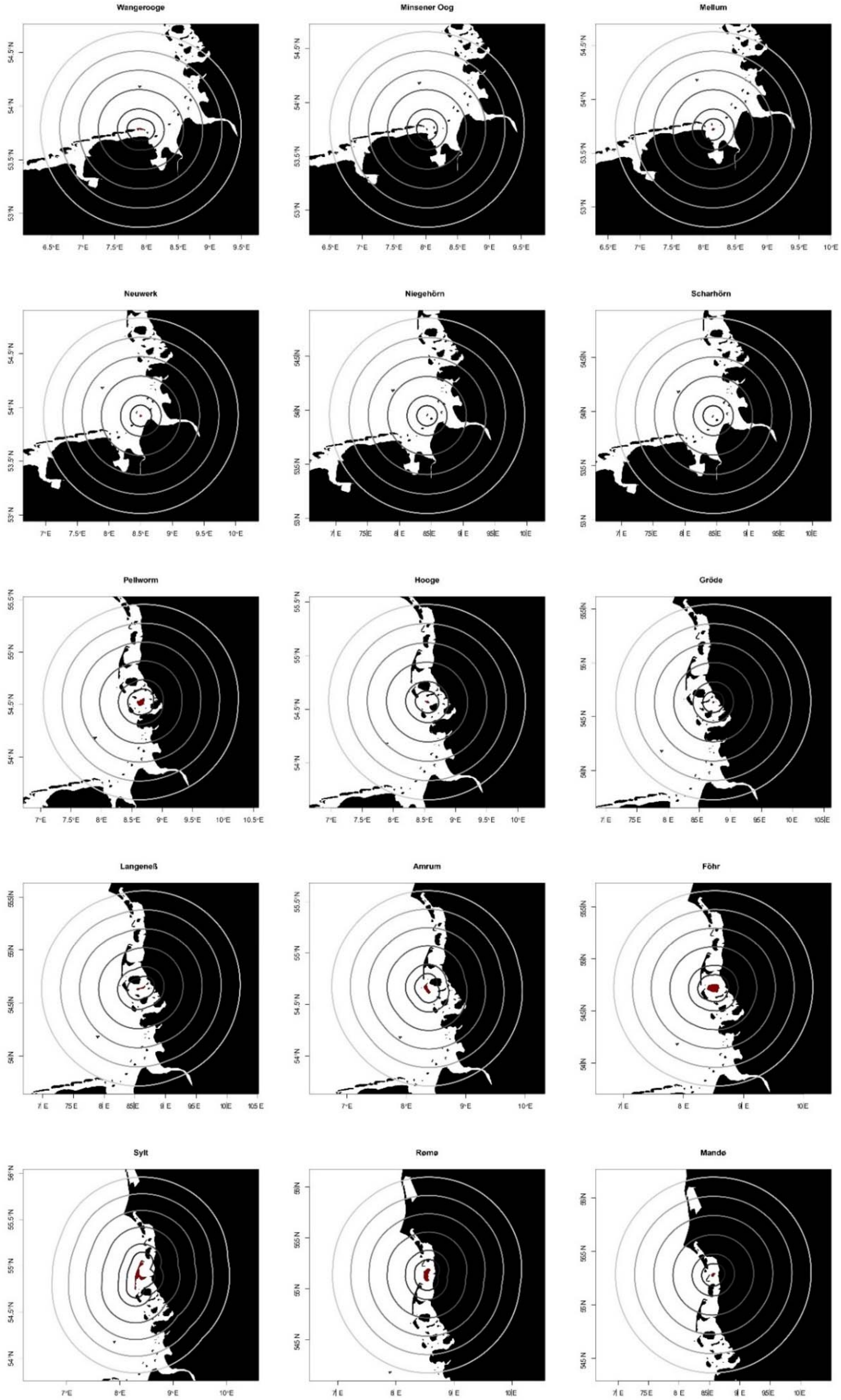

Figure S1 continued

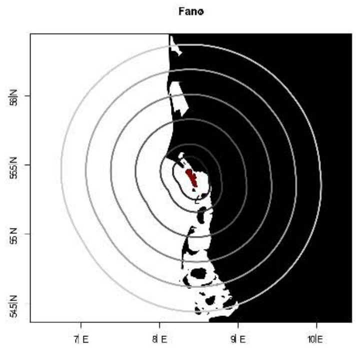

Figure S1: Studied islands (red) with buffers of 10 km, 20 km, 40 km, 60 km, 80 km, and 100 km (from dark to light grey) around the 31 target islands. Land other than the target island is displayed in black.

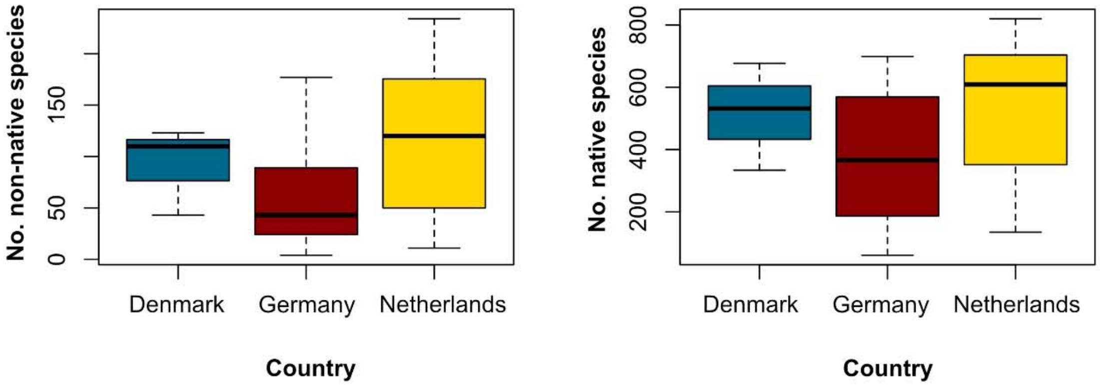

Figure S2: Numbers of non-native (left) and native (right) on North Sea islands categorized by country (Denmark, Germany, Netherlands).

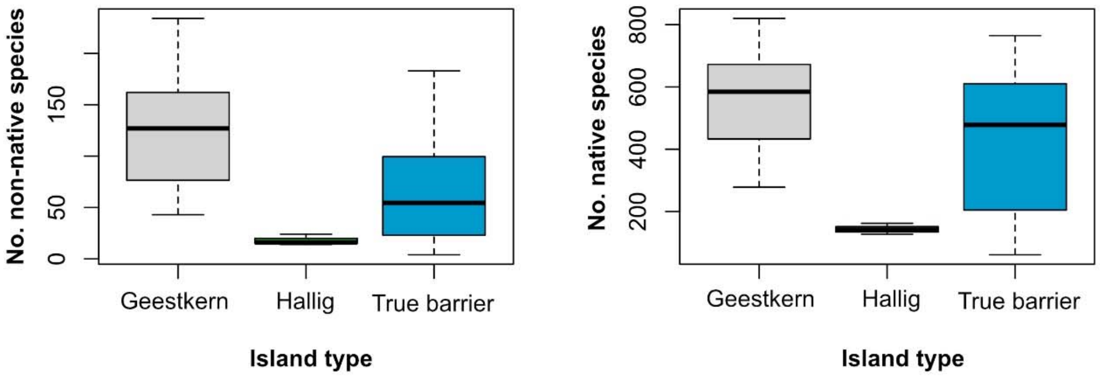

Figure S3: Numbers of non-native (left) and native (right) on North Sea islands categorized by island type (Geesterkern island, Hallig, true barrier island).

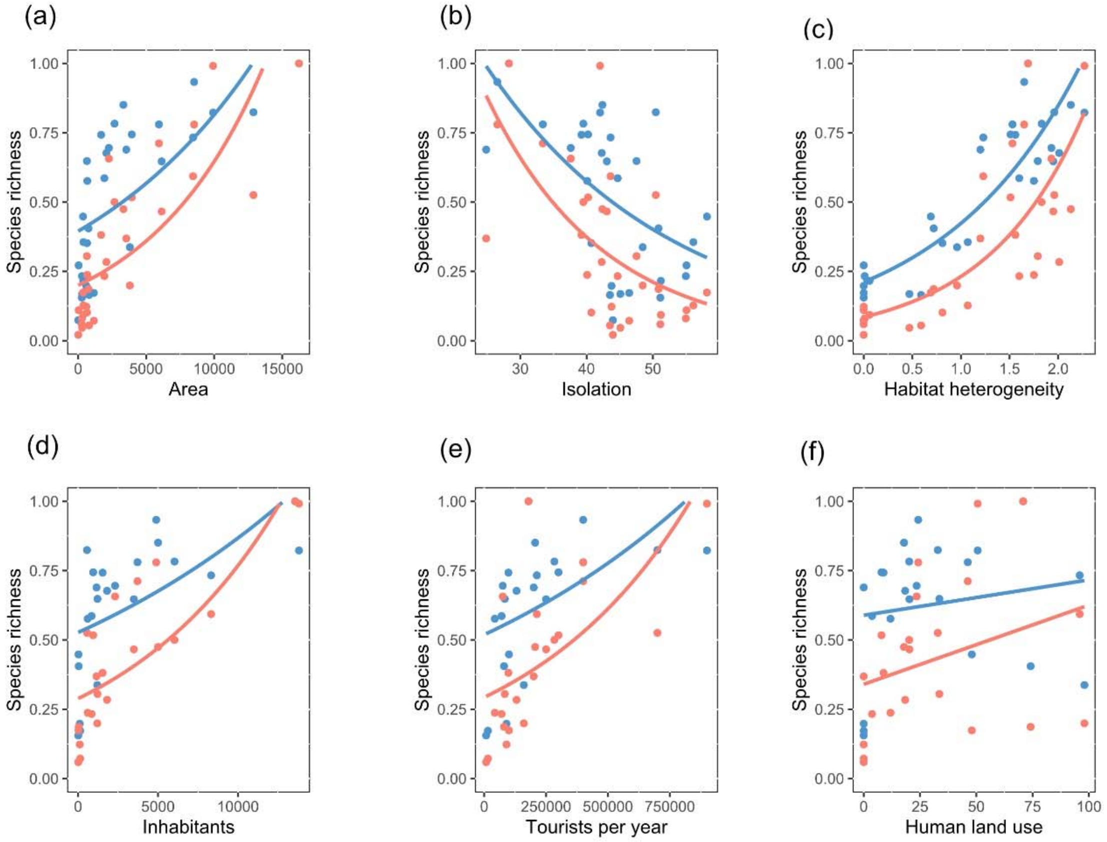

Figure S4: The univariate relationships of native (blue) and non-native (light red) standardized insular species richness (standardized to max = 1) with area (log-transformed; a), isolation (b), habitat heterogeneity (c), population density (log-transformed; d), the percentage of human land use (e) and tourists per year and area (log-transformed; f) resulting from GLMs (Poisson family error, log link). Note that the GLMs for the relationship between species richness and anthropogenic variables (d-f) were limited to inhabited islands.

Manuscript 2

Danish coastline with the island Hjelm in the background. © Anders S. Barfod

Summary

Island biogeographic studies typically focus on species numbers and disregard structures of communities or species' characteristics (Whittaker & Fernández-Palacios 2007). Here, we investigate dispersal characteristics of vascular plant species in the context of common relationships in island biogeography, namely the species-area relationship and the species-isolation relationship while also considering anthropogenic drivers of biodiversity change. Therefore, extant floral compositions on 54 Danish Islands are examined. The integration of functional ecology and island biogeography will gain further importance in future research (Schrader *et al.* 2021, 2022).

Plant dispersal characteristics shape the relationship of diversity with area and isolation

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Abstract

Aim: The relation of plant dispersal syndromes with insular species richness patters remains one of the challenges in island biogeography, especially as people have affected species distribution patterns. This study disentangles how dispersal syndromes influence the relationship of richness with area and isolation while also accounting for the human impact on island biodiversity. It builds on the potential of islands at the mesoscale and of similar origin to contribute to the ongoing discussion in island biogeography on what determines species richness and filtering.

Location: Denmark, 54 islands in the North and Baltic Sea.

Taxon: Vascular plants, including pteridophytes.

Methods: Generalized linear models (GLMs) and linear regressions are used to analyse how dispersal syndromes influence the relationships of species numbers with island area and isolation, as well as island inhabitation and human density, respectively.

Results: Species numbers, seed mass and the proportion of zoochore and anemochore species are positively related to island area while the share of water-dispersed species decreases with increasing area. Isolation is weakly related to mean seed mass but has no explaining power for species numbers and the presence of specific dispersal syndrome on the target islands. Species richness and seed mass were positively related to human presence.

Main conclusions: Human impact for centuries has not overwritten the strong relationship of species richness with area on the Danish Islands but is affecting the shape of this relationship. Island area constitutes a strong filter for different dispersal syndromes and leads to the assumption that heavier and animal-dispersed seeds are positively related to area due to the presence of more bird and mammal species. Human-induced loss of isolation caused by ongoing traffic and the connection of landmasses by bridges and ferries may be a reason for the overall low explanatory power of island isolation.

Keywords: dispersal pathways, dispersal syndromes, establishment, insular biodiversity, plant species richness, SAR

1 | Introduction

The forgotten roots of island biogeographic theory can be found in the seminal work of Alvar Palmgren in the Finnish Åland archipelago Already 50 years before MacArthur and Wilson (1967), he developed ideas similar to the equilibrium theory of island biogeography and suggested that isolation from the mainland and area balance species richness on islands (Palmgren, 1915–1917; Palmgren, 1921; Palmgren, 1927). Palmgren's (1915–1917) work on plants in the Åland archipelago inspired the Swedish scientist Olof Arrhenius to formulate the first mathematical expression of the species-area relationship (henceforth SAR) (Arrhenius, 1921), which remains one of the most essential models explaining species richness in various island systems around the world (Triantis et al., 2012). Palmgren additionally argued that the dispersal and establishment of particular species, being dependent on chance and priority effects, govern species compositions on islands (Palmgren, 1915–1917; Palmgren, 1921; von Numers & van der Maarel, 1998). This early vision initiated an intellectual debate between Palmgren on the one side and his contemporaries Paul Jaccard and Ole Eklund on the other side (Swenson, 2019; von Numers

& van der Maarel, 1998). Both Jaccard and Eklund opposed Palmgren's idea of area and isolation effects suggesting habitat availability and quality (and hence competitive exclusion) as the main drivers of species richness on islands (Eklund, 1931; Eklund, 1937; Jaccard, 1922; Järvinen, 1982; Palmgren, 1915–1917; Palmgren, 1921; Palmgren, 1925; Palmgren, 1927).

The disagreement between Palmgren, Eklund and Jaccard is symptomatic for the field of island biogeography and it has embossed the discussions on what determines insular species richness ever since (Proença & Pereira, 2013; Scherber et al., 2018; Triantis et al., 2003; Triantis et al., 2005). Several studies indicate that island area is the strongest predictor for species richness in different island systems around the world, followed by isolation (Abbott, 1974; Chown et al., 1998; Kreft et al., 2008; Lomolino, 1982). However, a number of confounding factors such as habitat diversity, island age and disturbance history have been suggested to drive species richness on islands as well (Heaney, 2000; Losos & Ricklefs, 2010; Losos & Schluter, 2000; Matthews et al., 2019; Rosenzweig, 1995; Scherber et al., 2018; Triantis et al., 2012; Whittaker et al., 2008). Thereby, the different mechanisms are not mutually exclusive and may operate either individually or in combination (Connor & McCoy, 1979; Kohn & Walsh, 1994; Ricklefs & Lovette, 1999; Rosenzweig, 1995; Triantis et al., 2003). For special island systems such as barrier islands or tiny islands, habitat diversity may have a stronger influence on species diversity than other drivers (Scherber et al., 2018; Triantis et al., 2006). Furthermore, spatial autocorrelation, latitudinal differences that translate into climatic dissimilarity (Drakare et al., 2006) and the small island effect (Burns et al., 2009; Dengler, 2010) often make generalizations on diversity patterns on islands difficult. Human alterations of islands add another layer of complexity to species assemblages on islands (Nogué et al., 2021). Revisiting Palmgren's works is a tribute to his pioneering research and frames ongoing discussions on island biogeography.

Alvar Palmgren was aware that species growing in the Åland archipelago were a filtered subsample from a larger species pool found on mainland Scandinavia (Palmgren, 1915–1917). He acknowledged that species filtering by island isolation is dependent on species-specific dispersal traits. Several decades later, seminal work by Carlquist (1966) from the Pacific further demonstrated how species composition depends on prevailing dispersal vectors and how this potentially influences evolutionary dynamics on large oceanic islands. However, despite these early indications, the role of species-specific traits involved in island colonization (i.e. dispersal vectors) and their relation to island characteristics have remained unclear. Few studies have continued this idea and applied it to island systems. Among these, Burns (2005) evaluated dispersal constraints of woody plants on Vancouver Island as a function of fruit characteristics. Another study by Heleno and Vargas (2015) that focuses on long-distance dispersal syndromes suggests sea dispersal and endozoochory as possible important traits for long-distant island colonization. Beyond the importance of zoochory as a dispersal syndrome to overcome long distances it can also result in wider distributions of species within archipelagos (Arjona et al., 2018). Substantial differences in slope and intercept of SARs among the main lineages of land plants have been linked to diaspore size, and hence, their potential for long-distance dispersal by wind (Patiño et al., 2014). Recently, Schrader et al. (2021) used functional diversity in general, including dispersal characteristics, to show that assembly processes of tree species on islands are not random and scale with area.

In this study, we return to Scandinavia to investigate SARs, species' relationships with isolation and human impact, based on dispersal traits and species compositions of plants on 54 Danish islands scattered throughout the Baltic and the North Sea including bays and fjords. We acknowledge the great potential of these islands to investigate patterns of species richness and filtering on islands of similar origin at the mesoscale. Human alterations of the islands add another layer of filtering to the analysis that we account for by taking island inhabitation and human density into the equation. The Danish islands are located in the nemoral zone of northern Europe. They constitute a geographically contrasting study site to current island biogeographic research that mostly takes place on larger archipelagos at subtropical latitudes, often of volcanic origin and with considerable evolutionary dynamics (Borregaard et al., 2015; Jõks & Pärtel, 2019; Valente et al., 2017; in geographical contrast to Korvenpää et al., 2003; MacArthur & Wilson, 1967; McMaster, 2005; Morrison, 2010; Scherber et al., 2018). As demonstrated by the influential work of Simberloff and Wilson (1969) in the Florida Keys, these smaller, less isolated barrier island systems are governed by unexplored dynamics that remain to be unveiled.

First, we investigate the relative effect of island area, isolation and human impact on plant species richness in 54 Danish saltwater and brackish water islands. After controlling for area, we expect more distant islands to have a lower species richness, with distance from the mainland being the second most important driver beside area (according to MacArthur & Wilson, 1967). Human impact is expected to increase species richness due to the introduction of agricultural and ornamental plants.

In a second step, we disentangle the driving mechanisms by analysing the potential presence of constraining dispersal filters acting on the regional species pool. Given the strong effect of island area on plant species richness (Kreft & Jetz, 2007), we suspect that island area might act as a dispersal filter (e.g. target-area effect, Lomolino, 1990). After characterizing species by traits associated with dispersal potential (seed mass as well as dispersal strategies; Heleno & Vargas, 2015), we expect (1) a positive relationship between seed mass and island area, since endozoic and epizoic plant species have heavier seeds and the overall number of mammals and birds that are typically involved in this kind of dispersal will increase as a function of island size. This translates into the expectation of (2) an increase in the percentage of zoochore species with increasing area but (3) a decrease in the percentage of hydrochore species because of the relationship between coastline and area (when coastline doubles, area roughly quadruples). Furthermore, we expect (4) the mean seed mass to decrease with increasing isolation, as it would be more likely for smaller seeds to be carried to islands that are further away; (5) the proportion of autochore species to decrease with increasing isolation, as it would be more difficult for sessile species to disperse to great distances without further adaptations.

2 | Materials and Methods

2.1 | Study area

We analyse plant species compositions from 54 major Danish islands scattered around the Danish North Sea and Baltic Sea coasts (Figure 1). These islands provide optimal conditions to test for environmental filters as they are all separated from the mainland since the last glaciation 10,000 years ago and have been gradually colonized since then (Böse et al., 2012; Mortensen et al., 2011). Salinity and tidal range influence the islands' vegetation and differ along a gradient from the North to the Baltic Sea (Moeslund et al., 2011). The islands are heavily impacted by human activity, and species assemblages are influenced by agricultural uses and human settlements (Hannus & von Numers, 2010). Acknowledging the islands' anthropogenic alteration is necessary, as a strict distinction between natural and anthropogenic impacts on island flora is impossible on the islands investigated. To account for human alterations we identified inhabited (n = 18) and uninhabited islands (n = 36) and calculated human density (number of island inhabitants per ha). The number of island inhabitants was compiled from Danmarks Statistik (2021) and for smaller islands, we used Google Earth images (© Google Earth 2021) to verify that no houses were present on the island (human density = 0) (Table S1).

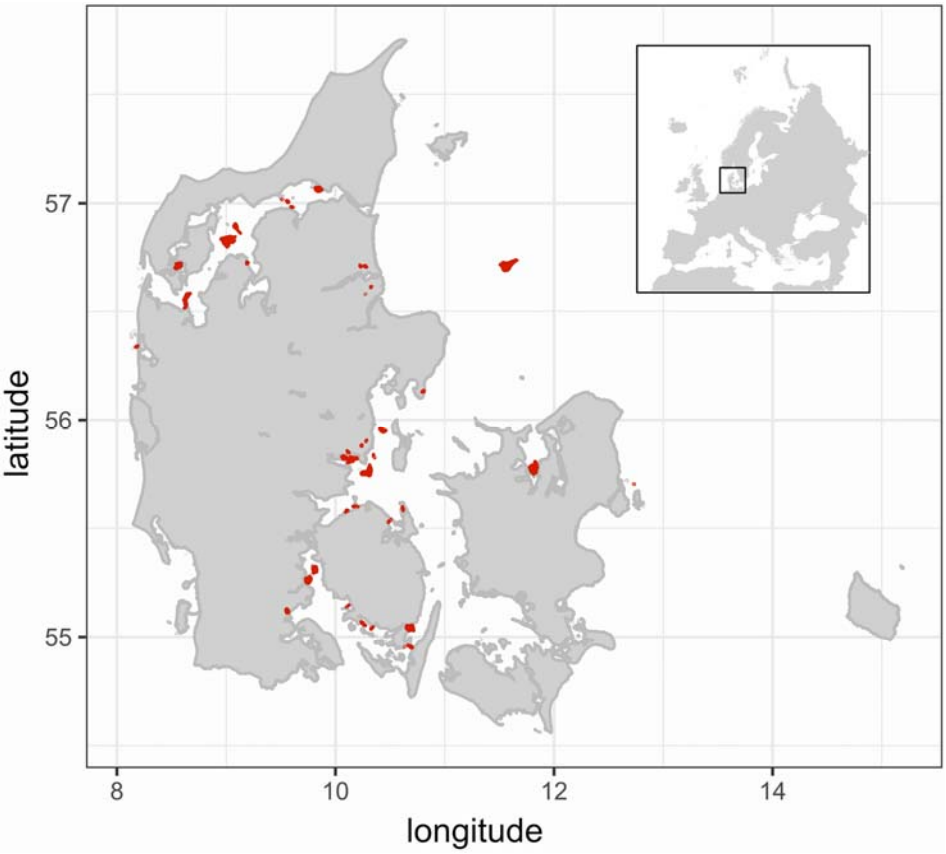

Figure 1: The investigated 54 small islands (red) are scattered along the coast of Denmark (location within Europe is indicated in the upper right overview). The map is based on a geographic coordinate system (EPSG 4326, WGS 84).

The development of the Danish landscape during the Holocene was determined by an interaction between eustatic sea rise and up-lifting of several mm per year. This led to significant changes in the number, size, and positions of islands over a short evolutionary time (von Numers & van der Maarel, 1998). The definition of an island in a shallow sea influenced by sedimentation dynamics and tidal water is far from trivial. Based on recent GIS maps and historical maps, we identified islands as bodies of permanent dryland clearly separated by water in the recent past (last 130 years). Some of the surveys by Wessberg et al. (2011) comprise a cluster of islands with several species lists. The number of islands in these clusters varies from two (e.g. Kyholm) to 23 (Treskelbakkeholm), but the smallest islets were not surveyed.

2.2 | Plant species occurrence data

This study is built on a comprehensive data set compiled by Erik Wessberg and co-workers since 1979. It became available in 2011 on the homepage of the Danish Botanical Society as a series of commented species lists, one for each of the islands or cluster of islands surveyed in total (Wessberg et al., 2011). The complete data set is appropriate for inter-island comparisons at the mesoscale since the surveys were conducted by the same group of botanists. Most of the species on the list were recorded by the authors themselves during field surveys, but they also included species recorded in literature. We removed literature records before 1950 since this year marks the beginning of the mechanization of Danish agriculture, which has profoundly impacted Danish nature. We used presence-absence data throughout because the abundances recorded in the original data were not complete for all species. It should be noted that we also include naturalized domesticated plants in the analyses, which brings the total number of taxa to 1360 (Table S1). To make the species list comparable across islands, we decided to exclude all taxonomic categories below species level and to merge agamospecies (resulting in 1201 species). The taxonomy follows the authority list for Danish species available online at www.allea rter.dk.

2.3 | Species trait data

We gathered trait information on seed mass (mg) as well as dispersal syndromes (zoochory, hydrochory, anemochory, and autochory) for the 1201 species found on the islands from databases. Sources were the Royal Botanic Gardens Kew (2016) and the LEDA database (Kleyer et al., 2008) that provided data for more than one thousand species. For the remaining species, we extracted data from the Ecological Flora of The British Isles (Fitter & Peat, 1994), BIOLFLOR (Klotz et al., 2002), BROT trait database for plant species of the Mediterranean Basin (Paula et al., 2009), and D3, The Dispersal and Diaspore Database (Hintze et al., 2013). Gaps in the data (roughly 100 species) were filled, when possible, by interpolation based on the traits of other species of the same genus, and ferns and clubmosses were assigned the smallest seed mass value in the dataset.

The data gathered was used to characterize seed mass and dispersal syndromes of each of the islands' species communities. Island community seed mass was quantified as the mean seed mass of all present species. The importance of different dispersal syndromes for reaching and establishing on the island was weighted by the relative percentage of species per island associated with each dispersal type (e.g. species A: 50% zoochory and 50% autochory).

2.4 | Analysis

The species lists of Wessberg et al. (2011) were entered manually into an Excel spreadsheet and the exact geographic position and precise boundaries were determined in GIS. This allowed us to calculate isolation (mean of 2732 m + −6508) as the shortest distance to the nearest mainland (species pool; considering the largest islands Saelland, Vendsyssel-Thyto and Fyn to be part of continental Denmark), and surface area (mean of 252 ha + −502) of the individual islands.

To test the relationship of insular species richness with area, isolation and human presence, using island inhabitation (GLM^{inhab}) or human density (GLM^{pop_dens}) as proxies, we performed GLMs (Poisson family error, log link). We tested for correlation between the continuous variables area, isolation and human density (Pearson's product–moment correlation was <0.2), which can be neglected in this instance, and log10-transformed the values of all island characteristics (adding 10^{-6} for values of zero). Independence of the categorical variable island inhabitation with area and isolation was tested with a Student's *t*-test, which revealed a significant relationship between the variables ($p < 0.001$). We therefore performed two GLMs to explain species numbers of which the GLM^{inhab} includes island inhabitation as an explanatory variable, and GLM^{pop_dens} is based on a subset of only inhabited islands, incorporating population density as an independent variable to account for human alteration of island flora. We used backwards variable selection for model building and the Akaike Information Criterion (AIC) to evaluate model fit. The fitted models were validated by plotting residuals against fitted values. The analysis was repeated with a subset of the data incorporating only spermatophytes and no pteridophytes (ferns, clubmosses and horsetails) to distinguish if the observed patterns are being driven by spores of pteridophytes or seeds of spermatophytes. As the most frequently used function to investigate SAR is the power function (Arrhenius, 1921; Triantis et al., 2012), we fitted its linear version on the log-transformed species numbers and island area to make our results comparable to other findings using the package *vegan* (Oksanen et al., 2019).

In an additional subsequent regression analysis, we decomposed species richness by dispersal syndromes (zoochory, hydrochory, autochory and anemochory) to examine their relationship with island area after log10-transforming all explanatory variables (adding 10^{-6} for values of zero). 95% confidence intervals were calculated. To investigate the presence of area-, isolation-and human-related dispersal constraints, we tested the relationship between mean seed mass per island and the percentage of zoochore, hydrochore, anemochore and autochore species with area and isolation (on all study islands, $n = 54$) and population density (only on inhabited islands, $n = 18$), respectively, using GLMs (Poisson family error, log link). Isolation-related analyses were repeated using a subset of only spermatophytes, excluding pteridophytes. Significance levels are reported as: [*] $0.05 > p > 0.01$; [**] $0.01 > p > 0.001$; [***] $p < 0.001$ throughout the analysis. Pseudo R^2 (Nagelkerke, 1991) was calculated with the package *rms* (Harrell Jr, 2020). All analyses were performed in R (version 4.0.2; R Core Team, 2020) using the packages *tidyverse* (Wickham et al., 2019), *gridExtra* (Auguie, 2017), *jtools* (Long, 2020) and *ggeffects* (Lüdecke, 2018).

3 | Results

Analyses confirm a significant and strong species-area relationship for the 54 Danish islands, a significant but less strong relationship with island inhabitation and human density on inhabited islands, but no relationship between isolation and species richness (Table S2 and S3). Human impact shapes the relationship of the global SAR as inhabited islands (model estimates: area = 0.7***, inhabitation = 0.5***) and islands with a higher population density (model estimates: area = 0.6***, inhabitation = 0.1***) show an overall higher species richness compared to uninhabited islands and less densely populated islands (Figure 2). Focusing only on spermatophytes and excluding pteridophytes revealed the same pattern (Table S3). Using the power function, the SAR has a regression slope (z) of 0.34.

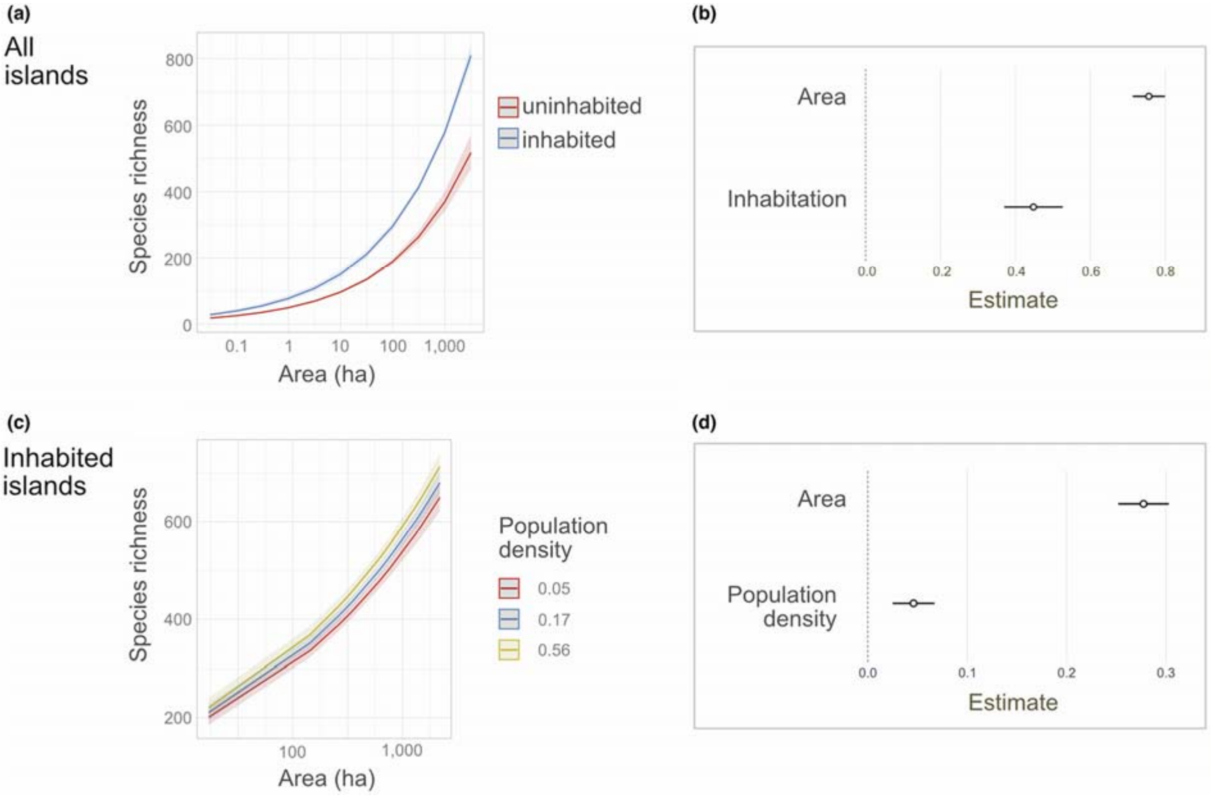

Figure 2: Relationship of plant species richness with island area and island inhabitation on all study islands (GLM^{inhab}; n = 54; top) as well as the relationship of plant species richness with area and population density (inhabitants per ha) on inhabited islands (GLM$^{pop\_dens}$; n = 18; bottom) based on GLMs. Mean model predictions of the number of species considering area and (a) island inhabitation or (c) population density as explanatory variables are displayed. 95% confidence intervals are given as shaded areas. The x-axes (area) and the legend (population density) respond to linear scale. Regression coefficient plots show the relationship of area and island inhabitation (b) or population density (d) with species numbers.

When comparing species by dispersal syndromes, the strong relationship between species richness and island area remained, with slight differences in intercepts and slopes (Figure 3). The steepest slope was calculated for anemochore species followed by autochore, zoochore and then hydrochore species (0.43 > 0.42 > 0.41 > 0.34), with overlapping confidence intervals but differing intercepts of zoochore and hydrochore species (intercept = 1.07 and 1.16, respectively) and of autochore and anemochore species (intercept = 0.66 and 0.59, respectively).

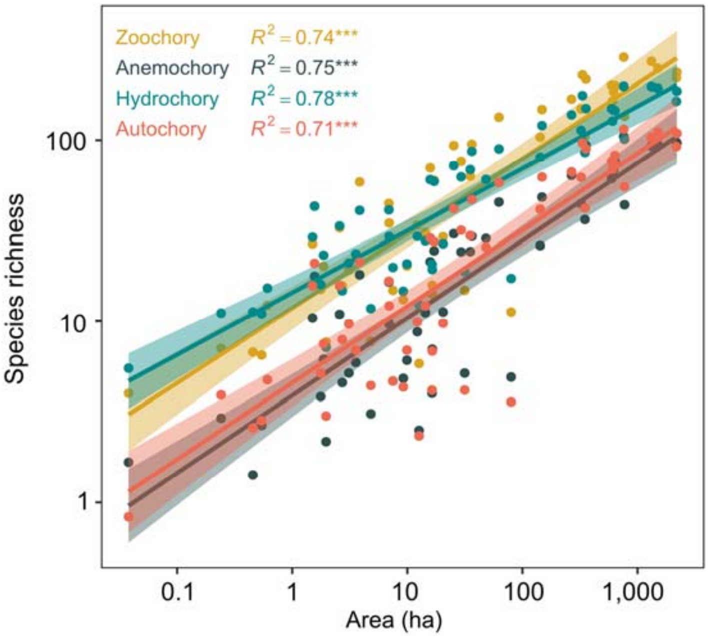

Figure 3: Relationship between species richness and island area (n = 54 Danish islands) among plant groups characterized by different dispersal syndromes in log–log space. Zoochore (R^2 = 0.74***, z = 0.41) and hydrochore (R^2 = 0.78***, z = 0.34) species exhibit higher intercept values than anemochore (R^2 = 0.75***, z = 0.43) and autochore (R^2 = 0.71***, z = 0.42) species, while slopes differ only slightly. 95% confidence interval are given as shaded areas. The axes respond to linear scale.

Mean seed mass of plant communities as well as the percentage of species with zoochore, hydrochore and anemochore dispersal syndromes were all significantly related with island area with the exception of autochore species (Figure 4a–e; Table S4). In detail, mean community seed mass was significantly increasing with island area (pseudo R^2 = 0.46***). There was a positive relationship between the proportion of zoochore species (pseudo R^2 = 0.29*) and anemochore (Pseudo R^2 = 0.29*) species with island area, while the percentage of hydrochore species declines with increasing island area (pseudo R^2 = 0.53***).

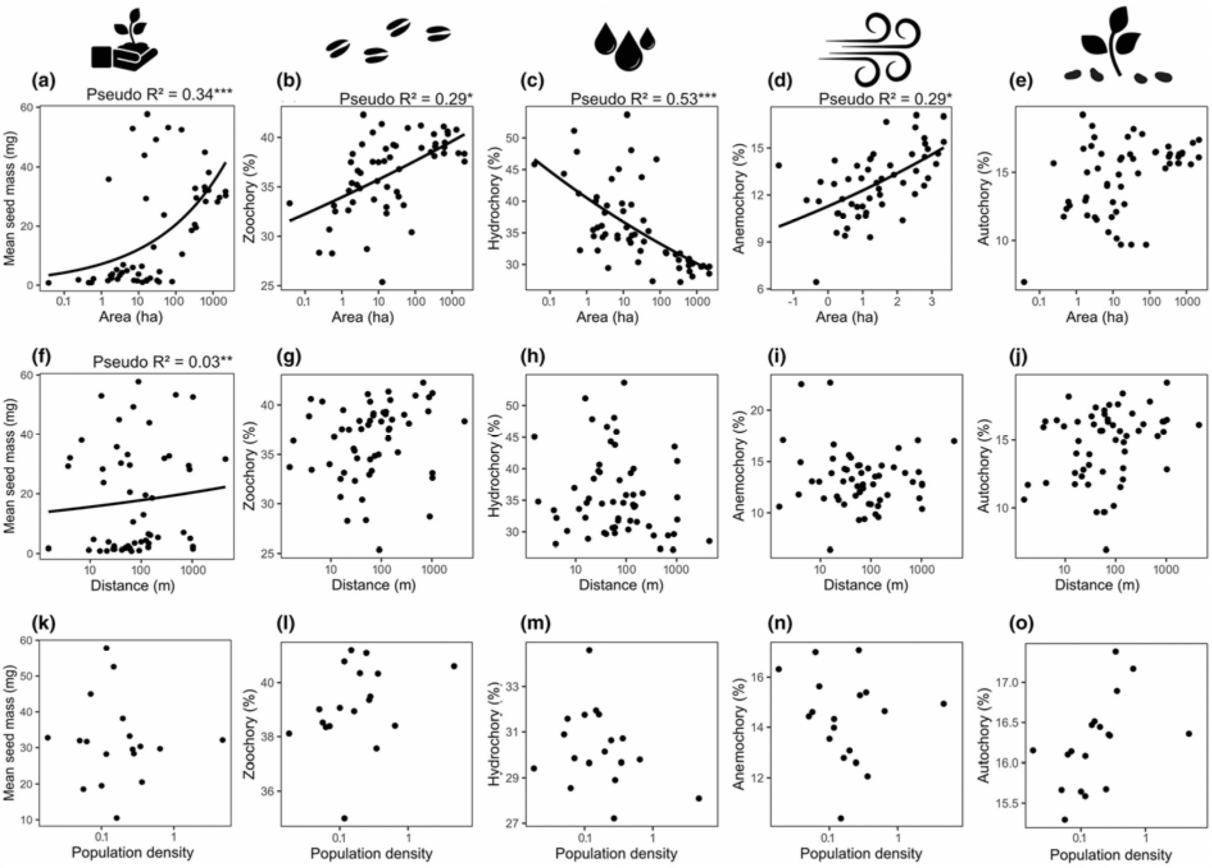

Figure 4: The upper row shows the relationship of area with (a) seed mass (pseudo R^2= 0.34***), (b) the percentage of animal (pseudo R^2= 0.29*), (c) water (pseudo R^2 = 0.53***), (d) wind (pseudo R^2= 0.29*) and (e) self-dispersed ($p > 0.05$) plant species. In the centre row, the relationship of isolation (f) with seed mass (pseudo R^2= 0.03**) and the non-significant relationships with isolation and the percentages of (g) animal, (h) water and (i) wind, and (j) self-dispersed species are displayed. Below, human density of inhabited islands is not related to (k) seed mass or (l-o) any of the dispersal syndromes ($p > 0.05$). The models related to area and isolation are based on all target islands ($n = 54$) whereas models related to population density were based only on inhabited islands ($n = 18$). Black lines and asterisks indicate significant linear relationships (GLMs; $\alpha = 0.05$) and according pseudo R^2-values are given.

Community seed mass was also found to be dependent on isolation but was less strongly associated with isolation compared to island area (pseudo R^2 = 0.03**, Figure 4f). No significant relationships between the percentage of zoochory, hydrochory, anemochory and autochory with isolation were detected ($p > 0.05$, Figure 4g–j). Human density of inhabited islands as a proxy for human impact was not related to any of the dispersal syndromes.

4 | Discussion

Despite the strong human impact for centuries on the 54 Danish islands surveyed by Wessberg et al. (2011) and targeted in this study, we recovered a strong relationship of species per island with area, confirming the global SAR pattern (Triantis et al., 2012). The slope of the regression line representing this relationship was 0.34, which lies within the common range (Triantis et al., 2012). Comparing the SARs per dispersal syndrome revealed only slight differences in slope, that might be attributed to the high variability of this relationship in general (Sólymos & Lele, 2012) or can be the result of unknown relationships between area and dispersal-related plant characteristics. In addition, SAR intercepts of plant species with hydrochore and zoochore dispersal syndromes were higher compared to anemochore and autochore species, which translates into a higher richness of water- and animal-dispersed species on islands compared to wind-and self-dispersed plant species. The difference in intercept between SARs of plants with specific dispersal syndromes most likely reflects their overall representation in the source pool and is not an effect of island characteristics or filtering. Although the dataset contained several islets (39% of all islands were smaller than 10 ha), no patterns hinting at the small island effect (Lomolino & Weiser, 2001) could be detected. Human density as a proxy for anthropogenic impact proved to partly explain richness patterns on the Danish Islands, suggesting that the human dimension should be included as an explanatory variable in such analysis. The intentional and accidental introduction of alien plant species and the creation of additional habitats (e.g. agricultural fields, meadows and gardens) can explain higher species numbers under increased human impact. However, this relationship should be interpreted carefully, as human density is likely to scale with area and small islands are commonly not inhabited. Isolation was not associated with species numbers per island, which contradicts former studies that considered it to be the second most important variable explaining the species numbers on islands (Kreft & Jetz, 2007; McMaster, 2005) considering only natural drivers of species richness. One explanation is that the targeted island systems are simply not very isolated, exhibiting a mean distance to the mainland of 2700 m and a maximum distance of 44,000 m, and lever out the impact of isolation on richness patterns. Additionally, the low explaining power of isolation may be attributed to the loss of floristic distances as humans function as vectors due to ongoing traffic and the connection of landmasses by bridges and ferries. Although the distance to the mainland remains the same, the biogeographic distance and dispersal barrier for species become smaller. Additionally, most studies investigating isolation as a predictor for species richness were limited to vascular plants (Diver, 2008; Kreft et al., 2008; Weigelt & Kreft 2012; Weigelt et al., 2015), whereas our dataset also included ferns, clubmosses and horsetails, which might be less affected by isolation as they are characterized by extremely light diaspores (Kreft et al., 2010). However, repeated analysis based only on spermatophytes showed that isolation does not explain species numbers on the targeted islands. Subsequently, pteridophytes, which represent less than 3% of all study species, do not govern richness patterns. Since isolation is weakly related to seed mass and not at all with any dispersal syndrome, all species in the species pool seem to be able to reach the islands of the study regardless of their distance to mainland, which then could lead to the observed species richness patterns. We thus have to reject our expectation that the proportion of autochore species irrevocably decreases with augmenting isolation from the mainland for the target islands.

The general tendency of island area as a significant explaining variable of species richness is also reflected in its importance for the occurrence of dispersal syndromes per island and for community seed mass. The analysis confirms the expected positive relationship between seed mass and the percentage of zoochore species with island area. Both observations might have a common explanation, and we suggest this to be a consequence of larger islands attracting more mammal and bird species supporting plant dispersal, also of heavier seeds. In accordance, Liu et al. (2019) use seed size of woody plants as a proxy for seed weight and revealed a negative trend with the island area. The explanation of the authors is that for smaller islands, birds gain more importance for dispersal compared to mammals, with birds being a vector for smaller seeds while mammals can disperse larger seeds (Liu et al., 2019). Fragmentation experiments reveal that smaller patches sustain fewer mammals (Hagen et al., 2012; Heinen et al., 2018), which can serve to explain our observations, if islands scattered along the coast of large mainland areas are considered to be a fragmented landscape. The importance of zoochory for dispersal has also been reported by Burns (2005) for woody angiosperms on Vancouver Island and Heleno and Vargas (2015) for long-distance dispersal of angiosperm species.

On islands, the occurrence of especially large seeds is a known phenomenon, which is the result of evolutionary processes (Kavanagh & Burns, 2014). The Danish islands are in this regard not comparable to true oceanic islands that have undergone a long history of isolated evolution that results in the occurrence of high percentages of endemic plants. The flora of the Danish islands does not differ largely from the species occurring on the nearby mainland (Wessberg et al., 2011). Therefore, our study setup aligns with the groundbreaking work of Simberloff and Wilson (1969) on island biogeography who conducted their experiments in the Florida Keys, which are also located close to the North American continent and thus have no long history of evolution separated from the mainland.

In contrast to the positive relationships between species richness, seed mass, the percentage of zoochore species, and area, a decrease in the percentage of hydrochore species was observed, confirming our expectation based on the fact that coastline doubles while area quadruples. Thus, an increase in island area does not result in the same increase of coastline that commonly is the habitat of hydrochore species. Unexpected is the steep relationship between the number of hydrochore species and area, considering that the number of species that are exclusively hydrochore is very low (<20%). This apparent dichotomy could be due to the relative proportions of other dispersal vectors increasing more rapidly in relation to area. However, a possible explanation could be that species not exclusively associated with hydrochory reach the island via water transport but, once on the island, their dispersal is more related to other dispersal syndromes.

Despite the large impact of humans on the investigated Danish islands, we found that area was the overriding driver of species richness patterns and also had the greatest filtering effect on plants with differing dispersal syndromes. The human impact variable increased the explanatory power when added to the models predicting insular species richness.

Expanding the set of islands commonly used in island biogeography, as has been done in this study, is needed to challenge theories of island biogeography. Although the Danish islands have undergone anthropogenic alterations, it is astonishing that the general pattern of increasing species numbers with area is strongly visible, confirming the global SAR. Decomposing this relationship by dispersal syndromes enhances the understanding of insular species patterns and filtering and taking anthropogenic variables into the equation complements the set of variables explaining species assemblages in these modern times.

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Data availability statement

Data and R script are fully available on Dryad under the following link: https://doi.org/10.5061/dryad.r2280 gbg0.

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Supporting Information

Table A1: Island characteristics, namely area, distance, number of inhabitants, and in addition the number of plant species for all 54 target islands.

	Island	Area	Distance	Nr. of inhabitants	Nr. plant species
1	Anholt	2175.1	44482	136	591
2	Hjarnø	322.8	600	117	381
3	Treskelkakkeholm	31.4	601	0	44
4	Mellempolde	16.4	299	0	23
5	Pletten	16.3	579	0	51
6	Alrø poller	3.5	1234	0	51
7	Lille plet	7.4	15	0	44
8	Alrø	770.7	67	152	63
9	Hov røn	12.2	1384	0	45
10	Svanegrunden	4.8	9109	0	346
11	Vår holm og Kyø holm	79.7	417	0	84
12	Fjandø	35.1	94	0	30
13	Egholm	605.7	368	43	38
14	Søby rev	6.9	1506	0	189
15	Agerø	349.0	1210	35	440
16	Stenrevet	0.5	212	0	89
17	Stenklipperne	2.7	1372	0	277
18	Livø	331.9	3523	6	24
19	Mågeøerne	9.9	228	0	45
20	Tunø	356.1	8518	96	619
21	Lindholm	48.2	182	0	84
22	Barsø	266.6	1631	15	22
23	Venø	635.2	175	178	56
24	Bågø	619.4	2839	31	568
25	Ejlinge	15.7	37	0	38
26	Dræet	29.3	700	0	13
27	Leammer	6.9	165	0	176
28	Kyholm	0.2	496	0	451
29	Ægholm	1.8	294	0	520
30	Trindelen	0.4	155	0	484
31	Fur	2195.0	400	757	184
32	Drætteholm	1.7	1402	0	198
33	Siø	142.5	10295	21	120
34	Bjørnø	147.8	692	24	26
35	Endelave	1321.3	8834	154	58
36	Hjelm	62.5	4753	0	2
37	Årø	595.6	540	146	648
38	Vigø	17.0	880	NA	41
39	Horsehoved	2.5	2125	0	260
40	Mejlø	36.3	116	0	387
41	Flakfortet	3.8	6754	0	683
42	Orø	1501.2	596	968	334
43	Thurø	758.4	40	3584	243

44	Store Rotholm	14.3	1439	0	57
45	Lille Rotholm	1.9	996	0	128
46	Hornsgård holm	9.2	283	0	501
47	Tøtten	0.03	644	0	174
48	Klosterholm	20.4	553	0	95
49	Startøtterne	12.6	911	0	263
50	Store Svelmø	25.2	1106	0	83
51	Græsholmen	3.1	742	0	38
52	Lille Svelmø	1.5	332	0	141
53	Store Rallen	1.5	10297	0	670
54	Lille Rallen	0.6	10287	0	728

Table A2: Summary statistics of stepwise variable selection of GLM^{inhab} using area (log10 area [ha]), isolation (log distances [m]) and island inhabitation as parameters to explain species richness (nr. species) and based on spermatophytes and pteridophytes (top) and only on spermatopyhtes (bottom). Degrees of freedom (Df), deviance and Akaike Information Criteron (AIC) are given.

Model: Nr. species (spermatophytes & pteridophytes) ~ area + distance + island inhabitation			
Start: AIC=1971.77			
	Df	Deviance	AIC
Isolation	1	1604.2	1970.6
Full model	-	1603.4	1971.8
Island inhabitation	1	1727.0	2093.4
Area	1	2945.3	3311.7
Model: Nr. species ~ area + island inhabitation			
Step: AIC=1970.6			
	Df	Deviance	AIC
Full model		1604.2	1970.6
Island inhabitation	1	1730.9	2095.3
Area	1	2945.8	3310.2
Model: Nr. species (pteridophytes) ~ area + distance + island inhabitation			
Start: AIC=1939.78			
	Df	Deviance	AIC
Isolation	1	1572.2	1938.2
Full model	-	1571.8	1939.8
Island inhabitation	1	1694.8	2060.8
Area	1	2872.3	3238.3
Model: Nr. species ~ area + island inhabitation			
Step: AIC=1938.18			
	Df	Deviance	AIC
Full model		1572.2	1938.2
Island inhabitation	1	1697.7	2061.7
Area	1	2873.4	3237.4

Table A3: Output of generalized linear models (GLM^{inhab}, GLM^{pop_dens}) based on final variable selection describing the relationship of species richness (nr. species) with area (log10 area [ha]) and inhabited islands (island inhabitation) or population density (log 10 inhabitants per ha). Model results are given for the entire set of plant species (spermatophytes and pteridophytes) (top) and for a subset of only spermatophytes (bottom). Model estimates, standard error and p-value are given. Bold letters indicate significant relationships.

	Estimate	Standard Error	P-value
Model: Nr. species (spermatophytes & pteridophytes) ~ area + island inhabitation			
Intercept	3.897	0.027	<0.001
Area	0.672	0.019	<0.001
Inhabited islands	0.448	0.040	<0.001
Model: Nr. species (spermatophytes & pteridophytes) ~ area + population density			
Intercept	4.732	0.077	<0.001
Area	0.556	0.026	<0.001
Population density	0.088	0.021	<0.001
Model: Nr. species (spermatophytes) ~ area + island inhabitation			
Intercept	3.898	0.027	<0.001
Area	0.665	0.020	<0.001
Inhabited islands	0.448	0.040	<0.001
Model: Nr. species (spermatophytes) ~ area + population density			
Intercept	4.747	0.078	<0.001
Area	0.546	0.026	<0.001
Population density	0.094	0.021	<0.001

Table A4: Output of generalised linear models describing the relationship of community seed mass (seed weight [mg]) and dispersal syndromes zoochory, hydrochory, anemochory and autochory (%) with area (log10 area [ha]), isolation (log10 distances [m]), inhabited islands (island inhabitation) and population density (log10 inhabitants per ha). Model results are given for the entire set of plant species (spermatophytes and pteridophytes) (top). Distance-related analysis were repeated based on a subset of only spermatophytes (bottom). Model estimates, standard error and p-value are given. Bold letters indicate significant relationships.

	Estimate	Standard Error	P-value
Models based on entire plant data set, including spermatophytes and pteridophytes			
Model: Seed weight ~ area			
Intercept	4.441	0.029	<0.001
Area	0.666	0.011	<0.001
Model: Zoochory ~ area			
Intercept	3.527	0.037	<0.001
Area	0.050	0.020	0.014
Model: Hydrochory ~ area			
Intercept	3.722	0.034	<0.001
Area	-0.106	0.020	<0.001
Model: Anemochory ~ area			
Intercept	2.429	0.064	<0.001
Area	0.083	0.034	0.015
Model: Autochory ~ area			
Intercept	2.607	0.059	<0.001
Area	0.061	0.032	0.055
Model: Seed weight ~ isolation			
Intercept	5.451	0.039	<0.001
Isolation	0.151	0.012	<0.001
Model: Zoochory ~ isolation			
Intercept	3.535	0.097	<0.001

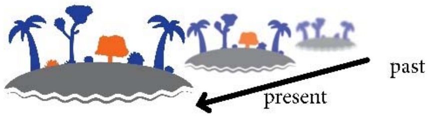
Isolation	0.022	0.033	0.508
Model: Hydrochory ~ isolation			
Intercept	3.753	0.097	<0.001
Isolation	-0.060	0.033	0.071
Model: Anemochory ~ isolation			
Intercept	2.442	0.164	<0.001
Isolation	0.037	0.055	0.500
Model: Autochory ~ isolation			
Intercept	2.544	0.153	<0.001
Isolation	0.052	0.051	0.312
Model: Seed weight ~ population density			
Intercept	6.531	0.016	<0.001
Population density	0.375	0.019	<0.001
Model: Zoochory ~ population density			
Intercept	3.685	0.068	<0.001
Population density	0.026	0.074	0.727
Model: Hydrochory ~ population density			
Intercept	3.390	0.079	<0.001
Population density	-0.033	0.085	0.694
Model: Anemochory ~ population density			
Intercept	2.640	0.115	<0.001
Population density	-0.029	0.123	0.815
Model: Autochory ~ population density			
Intercept	2.800	0.106	<0.001
Population density	0.023	0.115	0.845
Isolation-related models only with spermatophytes, excluding pteridophytes			
Model: Seed weight ~ isolation			
Intercept	5.432	0.039	<0.001
Isolation	0.158	0.012	<0.001
Model: Zoochory ~ isolation			
Intercept	3.531	0.097	<0.001
Isolation	0.026	0.033	0.418
Model: Hydrochory ~ isolation			
Intercept	3.752	0.097	<0.001
Isolation	-0.057	0.033	0.081
Model: Anemochory ~ isolation			
Intercept	2.421	0.169	<0.001
Isolation	0.026	0.057	0.642
Model: Autochory ~ isolation			
Intercept	2.545	0.152	<0.001
Isolation	0.056	0.051	0.275

Manuscript 3

Extant species richness on islands is well known. However, past trajectories are largely unknown, and the picture becomes blurry when trying to reconstruct biodiversity timelines encompassing decades, centuries, or millennia. Here, an artistic representation of the Scalesia forest on Santa Cruz, Galápagos, is shown. © Anna Walentowitz

Summary

To add a temporal perspective on anthropogenic biodiversity changes on islands to this doctoral thesis, this manuscript provides a palaeoecological perspective on human-induced vegetation changes in island floras globally. The aim was to study the timing, trajectories, and magnitude of non-native vegetation change on islands. To do so, matching of fossil pollen data with status information from extant plant species checklists was first applied. Such novel unconventional approaches based on palaeoecological data are needed to gain long-term perspectives on anthropogenically induced biodiversity changes (Willis & Birks 2006; Nogué *et al.* 2017). This study provides evidence that the onset of non-native vegetation on islands dates back longer (1000 years) than has been deduced from scientific written records and censuses (500 years, Seebens *et al.* 2017). We provide much needed baseline information on island naturalness that can inform biodiversity conservation and ecosystem restoration.



Long-term trajectories of non-native vegetation on islands globally

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Abstract

Human-mediated changes in island vegetation are, among others, largely caused by the introduction and establishment of non-native species. However, data on past changes in non-native plant species abundance that predate historical documentation and censuses are scarce. Islands are among the few places where we can track human arrival in natural systems allowing us to reveal changes in vegetation dynamics with the arrival of non-native species. We matched fossil pollen data with botanical status information (native, non-native), and quantified the timing, trajectories and magnitude of non-native plant vegetational change on 29 islands over the past 5000 years. We recorded a proportional increase in pollen of non-native plant taxa within the last 1000 years. Individual island trajectories are context-dependent and linked to island settlement histories. Our data show that non-native plant introductions have a longer and more dynamic history than is generally recognized, with critical implications for biodiversity baselines and invasion biology.

Keywords

Anthropocene, biodiversity, biological invasions, fossil pollen, alien species, novel ecosystems, island biogeography.

1 | Introduction

Humans have become the overwhelming force behind changes in island biodiversity in the Anthropocene (Russell & Kueffer, 2019). Many native island biotas continue to decline in diversity and numerous species are heading towards extinction (Bellard et al., 2017; Spatz et al., 2017), in part because islands have also become hotspots of non-native species introductions (Dawson et al., 2017). A total of 26% of all islands have already accumulated more non-native than native vascular plant species (Essl et al., 2019). Further, new evidence shows that vegetation turnover rates increased 11-fold since human settlement on islands (Nogué et al., 2021), leading to the emergence of novel ecosystems characterized by altered species compositions and structural features (e.g. Devkota et al., 2020; Ewel et al., 2013).

For some islands, substantial restoration actions and conservation efforts are being advocated and undertaken to protect endemic island biodiversity, such as invasive species eradication (Jones et al., 2016; Kaiser-Bunbury et al., 2010; Tapia et al., 2022). On other islands where traditional societies have been living for millennia or centuries, the revitalization of traditional land management approaches counter to modern industrial land-use practices may be resulting in better conservation outcomes for endangered species (Fletcher et al., 2021; Russell & Kueffer, 2019). Tracing the transition from natural dynamics to a human-dominated world to obtain palaeoecologically derived baseline information is necessary if achievable ecosystem restoration and conservation goals are desired (Barak et al., 2016; Nogué et al., 2017; Willis & Birks, 2006).

Islands exhibit unique histories of human-mediated vegetation change depending on (1) the onset of initial and subsequent human colonization events, and (2) the associated type and impact of land use and non-native species introductions (throughout this article colonization refers to humans, not colonization by other species). Human arrival on an island is thus a key event determining subsequent biodiversity change (Nogué et al., 2021; Russell & Kueffer, 2019). Overall, evidence suggests that biodiversity changes due to 'natural' drivers of change (e.g. climate, volcanism) have been overwhelmed by the impacts of anthropogenic drivers after the first arrival of people (Russell & Kueffer, 2019;

Wilmshurst et al., 1997). Habitat destruction, unsustainable exploitation of resources and the introduction of non-native species (including diseases associated with novel microorganisms and pathogens) has resulted in extinction of local populations or species (Wood et al., 2017). The spread of non-native species in contemporary times and projections into the future show that biological invasions are an especially important driver of island biodiversity change (Fernández-Palacios et al., 2021; Leclerc et al., 2018; Lenzner et al., 2020; Russell & Kueffer, 2019). With the advent of European colonization worldwide (after 1492 AD), ongoing land-use change, globalized trade and subsequent increased urbanization amplified these changes (Fernández-Palacios et al., 2021; Russell & Kueffer, 2019; Steibl et al., 2021). An extreme example of modern human-driven biodiversity alteration can be found on the volcanic island of Ascension (South Atlantic Ocean), where in an attempt to green the island, artificial ecosystems consisting almost entirely of non-native species were established in the nineteenth century (Wilkinson, 2004). Largely treeless areas were transformed into novel ecosystems of tropical cloud forests dominated by non-native species (Wilkinson, 2004). This landscape transformation has led to severe reductions in native plants and extinctions, and the potential for future extinctions (Cronk, 1997).

Trends in biodiversity change on islands can be highly context dependent, resulting in differences in ecosystem transformation and biodiversity change. The large island of New Guinea was settled by people more than 50,000 years ago, but retains the world's richest island flora (Cámara-Leret et al., 2020). Fiji and Vanuatu were first colonized 3000 BP and New Zealand around 750 BP, resulting in contrasting ecosystem transformation and biodiversity change, for example, deforestation and reduced native species' population sizes or extinctions (Ash, 1992; Lebot & Sam, 2019; Wilmshurst et al., 2011). By contrast, the Galápagos Islands were settled in the nineteenth and twentieth centuries (Tye, 2006), which is comparatively late in human history, with numerous endemic species currently facing extinction (Bush et al., 2022).

Besides anthropogenic pressures, the biogeographical and environmental properties of islands are known to shape their susceptibility to invasion (Blackburn et al., 2016; Essl et al., 2019; Helmus et al., 2014; Moser et al., 2018). More isolated islands, such as the Hawaiian group (approximately 3650 km from the nearest mainland) or the Tongan Islands (approximately 3340 km) (Moser et al., 2018; Weigelt et al., 2013), are more prone to the establishment of non-native species than less isolated island systems such as the Canaries (96 km) (Fernández-Palacios et al., 2022). The main explanations are that isolated islands exhibit lower competition among the few native species for available resources resulting in an often naïve native flora and fauna that can be poor in characteristics that make them less competitive against introduced non-natives (Allen et al., 2006; Whittaker & Fernández-Palacios, 2007). As a consequence, islands have accumulated high numbers of non-native species from a wide range of taxonomic groups, including groups previously absent from islands (Moser et al., 2018), often with severe impacts on native species (Bellard et al., 2017). While recent work has shown that the accumulation of non-native species has been prolific in recent decades on continents as well as islands (Seebens et al., 2017), it remains unknown when and how many non-native species were introduced to islands in previous centuries and millennia.

Fossil pollen time-series from chronologically dated sedimentary sequences offer the opportunity to unravel the dynamics of non-native species over millennia. Palaeoecological approaches have already been successful in reconstructing how island vegetation responded to climate change and initial human settlements, for example, on the islands of La Gomera (Canary Islands, Nogué et al., 2013) and São Nicolau (Cabo Verde, Castilla-Beltrán et al., 2020). Such analyses provide information on biodiversity baselines and trajectories of change after human colonization, both important to inform conservation management and policy and to understand the future direction of this biodiversity change (Bush et al., 2022; Castilla-Beltrán et al., 2020; Nogué et al., 2017; van Leeuwen et al., 2008; Willis & Birks, 2006).

We have compiled and integrated a global data set containing fossil pollen data for 29 islands covering the last 5000 years, plant census information for non-native species occurrences, and timing of human settlement. Using this data set, we investigate the timing, trajectory and magnitude of insular non-native vegetation abundance, with fossil pollen as the proxy. Across islands, we expect an increasing trend of non-native pollen towards the present. We expect the timing and magnitude of this increase to differ among individual islands, depending on individual human settlement histories.

2 | Material and Methods

2.1 | Study areas

Islands are well suited as study systems to reconstruct the vegetation history of non-native taxa as they represent isolated areas with discrete boundaries, and thus, the attribution of fossil pollen taxa to resident plant species is more straightforward than it is for mainland areas. In addition, fossil pollen time-series from isolated island systems contain low percentages of pollen taxa derived from long-distance transport (e.g. ±1.2% on Marion Island, Scott & van Zinderen Barker, 1985; or 3–5% in the Galápagos Islands, van der Knaap et al., 2012). This study focuses on 29 generally small islands worldwide that range from true oceanic islands (n = 24; 0.23–2040 km^2), some in archipelago settings (e.g. Gran Canaria, Tenerife and La Gomera in the Canary Islands), to other islands of volcanic origin and continental islands (n = 5; 2–102,387 km^2; e.g. Tawhiti Rahi, New Caledonia; Table S1). Human arrival falls within the period covered by most of the investigated time-series, allowing us to trace the transition of pollen composition from natural dynamics into human-dominated island systems.

2.2 | Data acquisition and preparation

For each island, we assembled fossil pollen data from radiocarbon-dated sedimentary sequences, up-to-date plant species checklists and complementary literature comprising status information of species (native, non-native; Figure 1, Table S1). The cores were collected from a variety of environments (e.g. crater bog on Pico, Azores; swamp on Ha'afeva, Tonga; see sources listed in Table S1).

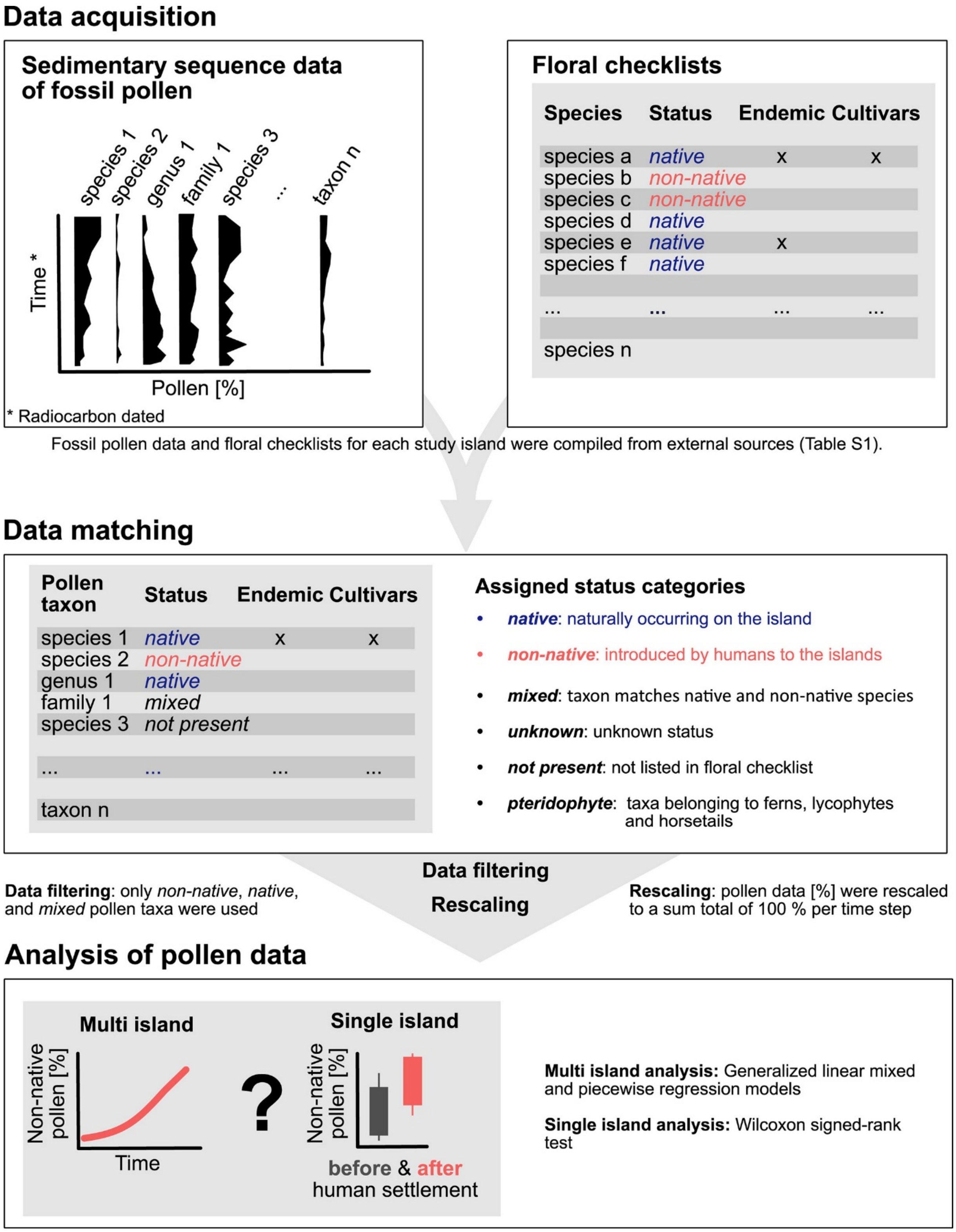

Figure 1: Schematic flow chart describing data acquisition, matching and analysis. The methodology developed aims at combining long-term fossil pollen data at variable levels of taxonomic resolution with biogeographic status information (native, non-native) of extant island floras as derived from checklists to gain insights into palaeoecological trends of non-native vegetation on 29 islands globally.

Fossil pollen taxa are identified at different taxonomic levels because closely related species or genera can have morphologically similar pollen. For example, within the plant families Brassicaceae, Caryophyllaceae, Cyperaceae and Poaceae, pollen is morphologically indistinct and can often only be identified to family level (Faegri, 1989; Tweddle et al., 2005). In contrast, pollen grains from many plant genera can be identified to species, thus, the fossil pollen taxa range from species to genera or even family levels to accommodate the ability of palynologists to identify pollen grains to the highest taxonomic level possible.

The published sedimentary sequences from all islands included in this study were chronologically dated using, for example, radiocarbon dating techniques and by building age-depth models (see individual sources of fossil pollen data, Table S1). As calibrated and standardized age information for all sequences, we used published age-depth models calibrated according to IntCal20 (Reimer et al., 2020, northern hemisphere) and SHCal20 (Hogg et al., 2020, southern hemisphere) (see individual sources of pollen data in Table S1). For the sequence from Santa Cruz, additional ^{210}Pb dating was undertaken to account for high accumulation rates in the upper part of the peat core (Froyd et al., 2014). In this study, time is provided as calibrated (cal.) years BP, using 1950 CE as year zero (Walker et al., 2009; cut-off sensu Nogué et al., 2021). We focus on the last 5000 cal. year BP. According to current information available, few remote islands were colonized before this date, given constraints on ocean voyaging technology (Leppard et al., 2022).

For all islands, we collected up-to-date checklists of vascular plant species that include information on the biogeographic status (*native* and *non-native*; written in italics if referring to status categories in the data set) of extant island floras (see Table S1). For islands in archipelago settings (e.g. Azores, Canary Islands), plant species checklists at archipelago level were used. Infraspecific taxa such as subspecies or varieties were disregarded, and hybrids were excluded from the analyses. It is important to highlight that plant species extinctions prior to checklists (mostly due to human encroachment) might not have been documented. Therefore, additional palaeoecological and botanical literature on known extinct or extirpated native plant taxa was used to complement extant plant species checklists (e.g. *Quercus* sp. in Canary Islands, de Nascimento et al., 2009; *Notanthera heterophylla* on Alexander Selkirk and Robinson Crusoe, Stuessy et al., 2017; *Stachytarpheta fallax* on Cabo Verde; Romeiras et al., 2016; see sources listed in Table S1). The categories used to describe the biogeographic status of plant species (e.g. 'indigenous', 'native', 'invasive' and 'possibly non-native') differed among checklists. To overcome this inconsistency, we reduced the different categories to just two: *non-native* and *native*, based on whether a plant species was associated with human presence on an island (*non-native*) or not (*native*). The native category also included extinct native taxa.

To match fossil pollen taxa which refer to different extant plant taxa at species, genus or family level with the extant plant species checklist data, we used three steps (Figure 1):

1. **Matching:** To attribute biogeographic status levels from extant checklists of vascular plant species to the pollen (and spore) taxa, we assigned six categories: (i) *Pteridophyte* (spore-producing; belonging to ferns, lycophytes or horsetails), (ii) *non-native* (introduced by humans to an island), (iii) *native* (naturally occurring on an island), (vi) *mixed* (pollen matching both native and non-native species), (v) *unknown* (status not provided in the plant species checklist) and (vi) *not present* (taxon was not represented in the plant species checklist). Matching was done manually by comparing single pollen taxa with all species of the corresponding extant plant species checklist or, for extinct plant taxa, relevant literature. To attribute the status categories, we first matched pollen taxa at species level with the species occurring on the respective islands. In the second step, pollen

taxa at genus and family levels were matched with all species from the island flora belonging to the corresponding genus or family respectively. For non-matching taxa, taxonomy and nomenclature were checked manually for synonyms in Plants of the World Online (POWO, 2022). If all species from the corresponding genus or family had the same biogeographic status (i.e. all being either *native* or *non-native*), we assigned this status level to the corresponding pollen type. As an example, on the Galápagos Islands, the pollen type *Scalesia* corresponds to a genus of the same name. The pollen is therefore classified as *native*, as all species of the genus reported from the Galápagos are native to the archipelago. In the same archipelago, the pollen type *Cinchona* is *considered non-native* as it matches only with a plant species that is non-native on the islands (Froyd et al., 2010). If a pollen type at genus or family level was matched with both native and non-native species of an island flora, it was assigned to the category *mixed*.

2. **Filtering:** This article is based only on pollen taxa and therefore spore-producing taxa classified as *pteridophytes* were not included in the final data set. Their sexual reproduction and dispersal strategy leads to the massive production of spores as propagules that could likely mask patterns of other less abundant pollen grains. Pollen taxa classified as *unknown* were discarded as their status was unclear. If pollen was classified as *not present* in the current island flora, it was excluded from the analysis as it most likely represented long-distance dispersal or represented unknown extinct island taxa. The final data set comprised only fossil pollen data with the assigned biogeographic status levels *native*, *non-native* and *mixed*.

   Six islands (i.e. Hispaniola, Iceland, La Gomera, New Caledonia, Nightingale Island and Robinson Crusoe) were excluded from further analyses. This was done because the pollen data of these islands contained taxonomically poorly resolved or largely uncategorizable pollen taxa which hampered the assignment of *native* and *non-native* taxa (Table S1, Figure S1). Additionally, we excluded pollen data from Foa and Ha'afeva (Tonga) from further analysis, as the stratigraphic data had a very low temporal resolution (Figure S2). Thus, the final data set used here derived from 21 islands and 14 archipelagos and comprises percentage data for *non-native*, *native* and *mixed* pollen at discrete timesteps of varying length from records of up to 5000 cal. years BP. The data set represents a total of 665 plant taxa.

3. **Rescaling:** After filtering, the data set was rescaled to allow for an analysis of relative changes in non-native plant abundance on islands using two different approaches. In the first, the count or percentage data of *non-native*, *native* and *mixed* pollen grains was rescaled to 100% per time step (data set$_{\text{lower}}$). In a second approach, only the data of *non-native* and *native* pollen grains were used for rescaling (data set$_{\text{upper}}$). Pollen taxa classified as *mixed*, comprising both native and non-native taxa, are likely to represent more native taxa in early settlement periods. Therefore, the consideration of both scaling approaches provides the opportunity to analyse the upper (not considering pollen classified as *mixed*) and lower (including pollen classified as *mixed*) boundaries of non-native pollen abundances on islands.

Data on *endemic* and *cultivar* pollen were also considered, as endemic species are often negatively affected by human encroachment (e.g. displacement by non-natives), and *cultivar* species represent a subcategory of non-native species directly used by humans. We therefore marked *endemic* pollen taxa (i.e. native taxa limited to an island or archipelago) and *cultivars* (e.g. *Zea mays*), following the same procedure as described in data matching step 1. The information was taken from the extant plant species checklists (Table S1). Here, no rescaling was applied, and the data are presented as raw percentage data of the entire sedimentary sequence.

The onset of permanent human settlement on each island was retrieved from a range of archaeological sources to provide complementary environmental information for subsequent analysis (sources listed in Table S1).

2.3 | Analysis

Data were analysed both jointly for all islands (multi-island analysis) and separately for each island (single-island analysis; Figure 1). Analysis and visualization were performed with the R software (R Core Team, 2022). All 21 islands with successful matching procedures and sufficient temporal resolution (i.e. minimum 25 total records and minimum five records per millennium) were included in the multi- and single island analysis.

All multi-island analyses were applied to data set$_{upper}$ and data set$_{lower}$ to account for the upper and lower limits in non-native vegetational change. Trajectories of non-native pollen in time were visualized using local polynomial regression fitting. To analyse overall non-native pollen trajectories in time, three methods were applied.

> a) A linear mixed effect model (LMM) was fit by restricted maximum likelihood using the *lme4* package (*lmer* function; Bates et al., 2015) to reveal temporal patterns of non-native pollen (as a proxy for the abundance of non-native vegetation) in time. Sums of non-native pollen per timestep were included simultaneously from all 21 islands with successful matching. Time (cal. years BP) was set as a fixed effect and islands additionally included as a random effect. The response variable was log-transformed to meet the requirements of a linear model and the residuals were checked for normal distribution to ensure goodness of fit.
>
> b) Additionally, a piecewise regression model (using a Bayesian information criterion) was fit to the data with the package *segmented* (*segmented* function; Muggeo, 2017) to extract break points and abrupt changes in non-native pollen trajectories. This analysis was limited to the last 2000 cal. years BP, as for this time frame, the data resolution was best and single island sequences overlapped the most (Figure S3).
>
> c) To link percentage data of *non-native* pollen (and thus the abundance of non-native vegetation) with taxonomic richness, we calculated the correlation (Pearson's r) of the percentage of *non-native* pollen and number of pollen taxa per time step jointly for all islands.

As complementary analyses, the overall trend of *endemic* and *cultivar* pollen in time was analysed using LMMs, applying the same model settings as presented above. The analysis was limited to timesteps where cultivar or endemic pollen was represented and for *cultivar*, pollen is presented only for the last 2000 cal. years BP due to limited data (Figure S3).

To put single islands trajectories in the context of individual human settlement histories and quantify magnitudes of change, the percentage of non-native pollen before and after human settlement was compared using Wilcoxon signed-rank sum tests. Trajectories of non-native pollen in time were visualized using a moving window approach (means of 250 years are shown) and boxplots.

3 | Results

We found substantial changes in the abundance of non-native vegetation on islands through time as expressed by their proportion of pollen (LMM $p < 0.001$, Table S2). When all 21 islands are analysed jointly, pollen values of taxa assigned to non-native flora show a tendency to increase starting ca. 1000 cal. years BP for both, upper and lower limit scenarios (Figure 2a). We identified break points at 102 cal. years BP (data set$_{\mathrm{upper}}$) and 575 cal. years BP (data set$_{\mathrm{lower}}$) before which the percentage of non-native pollen amounted to an average of 2% to 7% and after which these percentages reached 5% to 19% (Figure 2b, Table S2 & S3). This trend shows no sign of a deceleration towards the present.

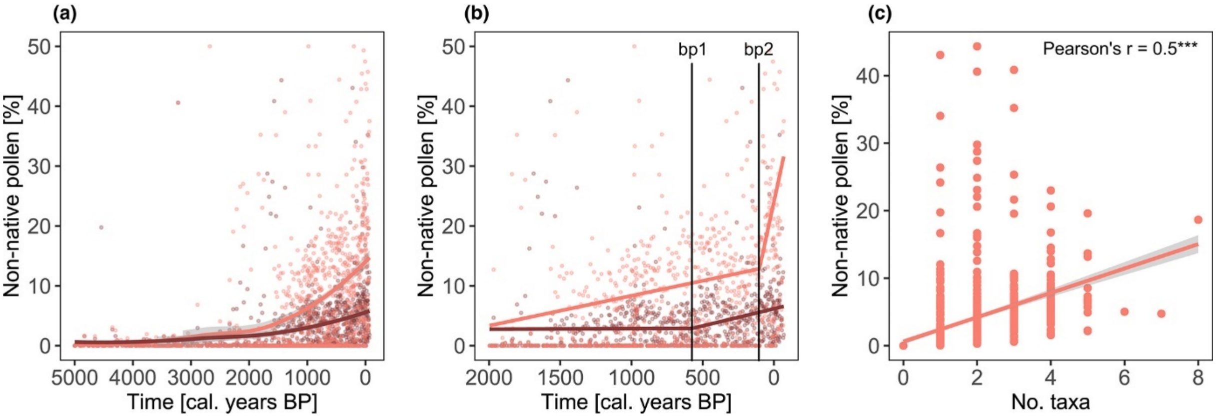

Figure 2: (a) Percentage of pollen of non-native vegetation for the past 5000 calibrated years Before Present (cal. years BP) for 21 islands, represent the maximum (light red, data set$_{\mathrm{upper}}$) and minimum (dark red, data set$_{\mathrm{lower}}$) limits of non-native vegetation abundances. For trend visualization, a local polynomial regression was fitted with a 95% confidence interval (cut-off at 50% non-native pollen, outliers are not shown). (b) Pollen of non-native vegetation for the last 2000 cal. years BP, showing piecewise regression models (using Bayesian information criterion) of non-native pollen in time (cal. years BP) with resulting break points at 575 (break point 1, bp1) and 102 (break point 2, bp2) cal. years BP (cut-off at 50% non-native pollen, outliers are not shown). Scale is limited to 2000 cal. years BP. (c) To investigate if pollen abundance translates into species richness, the percentage of non-native pollen was regressed against the number of pollen taxa during each time step and for all 21 islands (Pearson's $r = 0.5$, $p < 0.001$, based on data set$_{\mathrm{lower}}$).

The percentage of non-native pollen and the number of non-native pollen taxa was correlated with 0.5 (data set$_{\mathrm{lower}}$, Pearson's r and $p < 0.001$) and 0.4 (data set$_{\mathrm{upper}}$, Pearson's r and $p < 0.001$; Figure 2c). The percentage of pollen from endemic taxa decreases almost continuously towards the present (LMM, $p < 0.001$; Table S4, Figure S4a). Cultivar pollen abundance decreases faster towards the present compared with endemic pollen abundance (LMM, $p < 0.001$; Table S5, Figure S4b).

The timing, trajectory and magnitude of change in non-native pollen varies substantially between islands across the data set (Figure 3). Specifically, most islands show an increasing trend of non-native pollen over time that starts with the onset of human settlement (i.e. Flores, Great Mercury, Mo'orea, Raivavae, Rimatara, São Nicolau, Tawhiti Rahi and Tristan da Cunha). Besides a post-settlement increase in non-native pollen, several islands exhibit an increasing trend in non-native pollen slightly before the onset of human settlement (i.e. Alexander Selkirk, Brava, Gran Canaria, Maui, Mauritius, Pico, Rapa Iti, San Cristóbal and Santa Cruz). In addition, three islands show trends without clear directionality (i.e. Santo Antão, Tenerife and Uta Vava'u). Finally, for Vanuatu, only post-settlement fossil pollen data were available and a comparison with pre-settlement times was not possible. Still, the island shows an increase of non-native pollen towards the present. In total, 14 islands exhibit significantly more non-native pollen post-settlement compared to pre-settlement times. The patterns were similar for data $\text{set}_{\text{lower}}$ and data $\text{set}_{\text{upper}}$ (see Figure S5). On average, the islands recorded 1–6% non-native pollen preceding permanent human settlement and 5–16% non-native pollen after the onset of human settlement history (based data $\text{set}_{\text{lower}}$ and data $\text{set}_{\text{upper}}$ respectively). The percentage values of non-native pollen taxa for all islands increases towards the present, reaching average values of 8–25% (based data $\text{set}_{\text{lower}}$ and data $\text{set}_{\text{upper}}$ respectively). The magnitudes of non-native pollen on islands during human settlement times vary from below 5% (i.e. Rapa Iti, Tristan da Cunha) to more than 20% (i.e. Alexander Selkirk, Gran Canaria, Mo'orea and Raivavae).

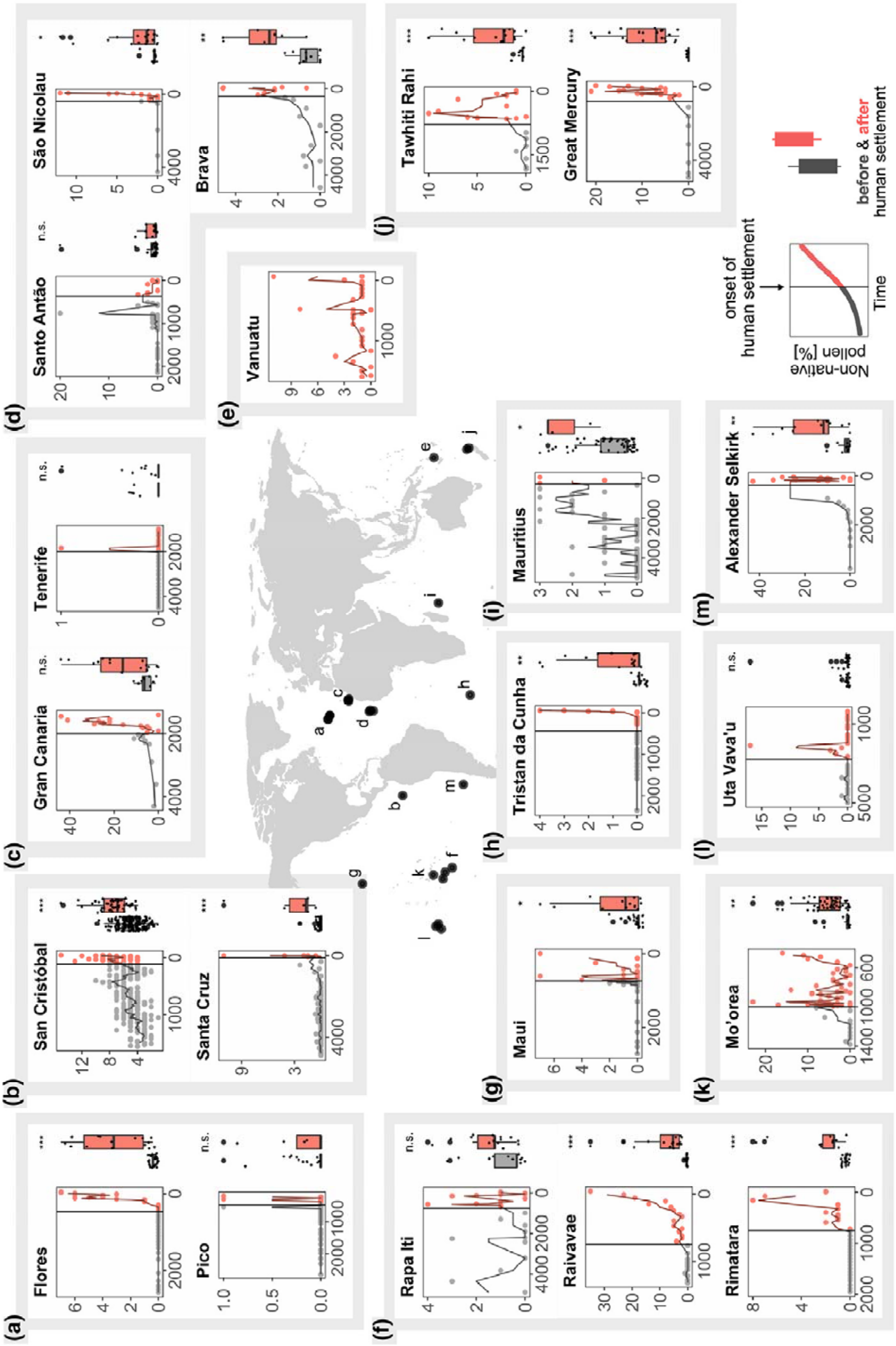
(a)
Flores
***
Pico
n.s.
(b)
San Cristóbal
***
Santa Cruz
***
(c)
Gran Canaria
n.s.
Tenerife
n.s.
(d)
Santo Antão
n.s.
São Nicolau
*
Brava
**
(e)
Vanuatu
(f)
Rapa Iti
n.s.
Raivavae
***
Rimatara
***
(g)
Maui
*
(h)
Tristan da Cunha
**
(i)
Mauritius
*
(j)
Tawhiti Rahi
***
Great Mercury
***
(k)
Mo'orea
**
(l)
Uta Vava'u
n.s.
(m)
Alexander Selkirk
**
a
b
c
d
e
f
g
h
i
j
k
l
m
Non-native pollen [%]
Time
onset of human settlement
before & after human settlement

Figure 3: A total of 5000 calibrated years Before Present of trajectories of non-native pollen for 21 islands globally. The onset of human settlement is indicated by a black vertical line. A comparison of non-native pollen taxa (%) before and after human settlement is provided as boxplots. Significance levels are indicated by asterisks (Wilcoxon signed-rank sum tests). Colours in grey correspond to data points before and colours in red to data points after human settlement. Plot legends are provided at the bottom-right. Note that for Vanuatu, pollen data are only available for a time frame after human settlement, and consequently, no comparison of non-native pollen before and after the human settlement is possible. Figures are based on data $\text{set}_{\text{lower}}$ and results for data $\text{set}_{\text{upper}}$ presented in Figure S5. Note furthermore that on Rapa Iti, patterns in non-native pollen before human arrival can most likely be attributed to contamination with *Pinus* pollen at the coring site (Prebble et al., 2019).

4 | Discussion

Palaeoecological data reveal an increasing trend in non-native pollen proportions on islands globally starting approx. 1000 cal. years BP and continuing to increase towards the present. The analysis of single islands shows that the onset of non-native vegetation and their magnitude of change differ among islands. This is likely related to the individual human settlement histories of these islands. Using pollen of non-native plant species as proxies for the abundance of non-native species translates into substantial vegetational changes due to human-mediated species introductions.

This increase in non-native vegetation during the last millennium diverges from currently available global data sets based on published first records of non-native species. Most of these records focus on the past 500 years, with reliable data largely being constrained to the last 200 years (Seebens et al., 2017; global, not specific to islands). The temporal divergence between palaeoecological trends of non-native plants presented in this article and the published scientific written records indicates that advances in the understanding of the dimensions, importance and impacts of long-term biodiversity change caused by non-native plants on islands can be fostered by palaeoecological data. In addition, we found that towards the present 8–25% of pollen grains may be attributed to non-native plant taxa. Although pollen percentages reflect plant abundances only indirectly (e.g. due to palynologically silent taxa or differing pollen productivity, Birks & Birks, 1980), this increase in non-native vegetation underlines the scale of human-mediated species' introductions and the potential impact they may have on islands. Importantly, these biodiversity changes seem accelerated towards the present. In addition, previous studies have demonstrated that plant species richness is reflected in pollen taxonomic richness (Birks et al., 2016) and the positive relationship in our data (Figure 2c) appears to confirm this for islands as well. Most likely, increasing abundance of non-native vegetation is the result of both ongoing introductions and expansions of present non-native species. Differences in pollen productivity between species might also hamper a higher correlation between non-native pollen percentages and the number of taxa.

Anthropogenic forces add another layer to the ever-changing nature of islands and have relatively recently (in geological timescales) emerged as dominant drivers in ecological systems (Fernández-Palacios et al., 2021). As the result of numerous human-mediated introductions of non-native species, novel species assemblages and ecosystems have established on islands globally (e.g. Russell & Kueffer, 2019). For example, the sweet chestnut (*Castanea sativa*) forests on La Palma (Canary Islands), initially planted for agricultural purposes, are increasingly replacing parts of the laurel forest, naturally dominated by Macaronesian-endemic species, such as *Ilex canariensis*, *Laurus novocanariensis* or *Persea barbujana* (Beierkuhnlein et al., 2021; Devkota et al., 2020). In the Galápagos Islands, large blackberry (*Rubus niveus*) or guava (*Psidium guajava*) populations are thriving where once endemic species (e.g. *Scalesia pedunculata* on Santa Cruz) were dominant (Urquía et al., 2019; Walentowitz et al., 2021). Our findings open a new perspective on the timing of the development and the extent of novel species assemblages that seem to emerge up to 1000 years earlier than historical records suggest. Furthermore, our results contribute to the discourse on the naturalness of extant island biodiversity around questions like what can be considered as 'natural' island biodiversity if non-native vegetation started to increase about one millennium ago? Our results demonstrate the power of long-term palaeoecological records that extend beyond the written record and observations to help distinguish between natural patterns and those affected or caused by non-native vegetation, and ultimately by human encroachment.

Our findings support the notion of the *Hookerian* shortfall, as the botanist Joseph Dalton Hooker already raised the question in the nineteenth century of how islands can be considered as 'natural laboratories' in light of the impacts of human activities (Carine & Menezes de Sequeira, 2020). An example from the Galápagos Islands illustrates this shortfall: According to our findings, non-native vegetation accounted for about 6–9% of their flora by the time Charles Darwin visited the archipelago in the year 1835. Thus, even Charles Darwin most likely visited an archipelago where novel plant communities were already present, and the flora had in addition to the introduced non-native plants been impacted by the removal and inter-island translocation of tortoises by whalers and the introduction of non-native herbivores (Bush et al., 2022). The human-influenced nature in the Galápagos Islands continues to influence conservation management in the archipelago, which does not fully consider the long-term perspective on change in species compositions (Bush et al., 2022). This example illustrates how information on the temporal abundance and trajectories of non-native vegetation, determined through palaeoecological data, is required to determine the degree of naturalness of island vegetation, facilitate the establishment of baseline information and to identify introduced taxa (e.g. Bush et al., 2014; Gillson, 2022; van der Knaap et al., 2012). Especially on islands, where expensive conservation and restoration efforts are being undertaken to preserve native biodiversity and recover unique ecosystems (e.g. Jones et al., 2016), the establishment of such baselines is imperative to inform such efforts (Barak et al., 2016; Bush et al., 2022; Nogué et al., 2017; Willis & Birks, 2006).

Despite non-native species being currently omnipresent and widespread in island systems globally (Essl et al., 2019), the timing of introduction and trajectories of their expansion differ substantially between islands and archipelagos. Here, we use the onset of human settlement to explain differences in trajectories. For a widely dispersed suite of islands, namely Flores, Great Mercury, Mo'orea, Raivavae, Rimatara, São Nicolau, Tawhiti Rahi and Tristan da Cunha, the onset of rising trends in non-native vegetation coincides with the onset of permanent human settlement in the islands. Similar trajectories are exhibited by Alexander Selkirk, Brava, Gran Canaria, Maui, Mauritius, Pico, Rapa Iti, San Cristóbal and Santa Cruz, but with the difference that these nine islands show increasing trends in non-native vegetation before the onset of human settlement. This divergence might be attributed to impacts by known earlier presences of people before permanent settlement, or it could mean that more robust chronological data is required for the initial human colonization period. In Galápagos, permanent settlement on the islands occurred comparatively late in human history (Tye, 2006). While the archipelago had already been discovered in 1573 AD, the scarcity of freshwater hampered permanent colonization. Nevertheless, earlier occasional visits by pirates, mariners and whalers impacted the vegetation by both accidentally and intentionally introducing non-native species long before the onset of permanent settlements in the nineteenth century (Bush et al., 2022). Furthermore, pollen records from islands that were never permanently settled but temporarily exploited by humans for resources have also revealed plant introductions, such as the subantarctic Auckland Islands, demonstrating the sensitivity of the method (Wilmshurst et al., 2015). In addition to human-mediated introductions, it is important to consider other environmental factors, such as legacies of land-use change, local extinctions of species, ecological cascading effects or ecosystem conversion by introduced mammals. These are just some examples of potential drivers considered to be causing increases in non-native plant species (Anderson et al., 2011; Bush et al., 2022; Castilla-Beltrán et al., 2020; Fernández-Palacios et al., 2021; Kueffer et al., 2010; Prebble et al., 2019). Furthermore, interrelations between natural forces, such as climate change (e.g. de Boer et al., 2013) and volcanic impacts (Castilla-Beltrán et al., 2021, 2023) with human history could be of interest.

Mismatches between settlement dates and onsets of the rise of non-native vegetation or non-directional changes in non-native pollen percentages might, besides island characteristics or the presence of people before permanent settlement, also be attributable to data and methodological limitations. Inaccuracies and uncertainties in radiocarbon dating might be one potential reason for mismatches, differences in pollen source area resulting from variability in depositional environments and the type and size of coring sites, for example, small bogs to large lakes (Jacobson & Bradshaw, 1981) may also influence early detection of the presence of non-native species in our records (see Table S1). Inadequate pollen grain identification or inaccurate assessment of species' status (e.g. native or non-native) in botanical checklists (e.g. van Leeuwen et al., 2008) are additional pitfalls. In this article, we demonstrate that while pollen identification issues are a source of uncertainty, the palaeoecological data quality on the attribution of species as native or non-native is constantly increasing (Coffey et al., 2011; van Leeuwen et al., 2008). Additionally, our analysis is driven by pollen taxa that were clearly attributable as non-native (see methods). This constrained any insights being gained from large and biodiverse islands (e.g. Hispaniola, New Caledonia) for which our matching procedure resulted in coarse categories, but it provides a robust and rather conservative estimate of the phenomenon. Coarse taxonomic resolution might also be the reason we observed trends without clear directionality for Santo Antão, Tenerife and Uta Vava'u. In New Zealand (Sutton et al., 2008), Cook Islands (e.g. Kirch & Ellison, 1994; Sear et al., 2020) and Rapa Nui (Rull, 2016), cases have been made for earlier human contact than information obtained from archaeological evidence for human settlement, based on the putative presence of non-native pollen, or other palynological signatures. However, in the case of New Zealand, with the addition of more palaeoecological records and novel proxies with robust radiocarbon-dated chronologies (e.g. Wilmshurst et al., 2008), along with the large number of early archaeological sites with robust chronological information, these early claims are no longer supported by data (Wilmshurst et al., 2011).

Russell and Kueffer (2019) describe islands as microcosms in which we can observe biodiversity changes in the Anthropocene and can develop strategies to cope with these changes. In line with this, we have demonstrated the utility of fossil pollen data to improve existing biodiversity baselines on islands. Other proxy data have the potential to reveal similar global trends (e.g. for macroinvertebrate extinctions and introductions; Liebherr & Porch, 2015; Prebble et al., 2016). The temporal divergence between palaeoecological trends of non-native plants presented in this article and the published scientific written records indicates that little is known about the dimensions, importance and impacts of long-term biodiversity change caused by non-native plants on islands. In addition, our results support the idea that human impacts on islands may occur before permanent settlement (Bush et al., 2022; Raposeiro et al., 2021). However, it is still not well understood why some islands appear to be more impacted by these early introductions than others. Overall, our findings suggest that incorporating a long-term perspective into the management of non-native vegetation on oceanic islands will lead to more informed management decisions and robust conservation outcomes. Such information is much needed to contextualize ecological restoration and research related to novel ecosystems.

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Data accessibility statement

All data and code are fully accessible via Zenodo: https://zenodo.org/badge/latestdoi/566995168.

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Supplementary Information

Table S1: Studied islands, sources of pollen, floral data (extant checklists of plant species and supplementary literature) and human settlement dates. Information on matching success of pollen and floral data (related to the categories *non-native* and *native*) is given. Updated age-depth models (according to IntCal20 and SHCal20 calibration curves for the northern and southern hemisphere, respectively) were provided by Nogué et al. 2021 if not declared otherwise.

Island	Pollen data	Island floral data	Human settlement data	Depositional context	Matching success
Alexander Selkirk	Haberle 2003	Carvallo & Castro 2017, Stuessey et al. 2018	Anderson et al. 2002	Shallow depression on the southern slopes of Cerro de Los Inocentes at 800 – 1200 m a.s.l.	yes
Brava (Cabo Verde)	Castilla-Beltrán et al. 2021, information on age-depth model is being provided	Arechavaleta et al. 2005, Romeiras et al. 2016	Patterson 1988	Volcanic caldera located at ~1200 m a.s.l.	yes
Foa (Tonga)	Flenley et al. 1999, digitalized by Strandberg (2022) and Strandberg et al. (in prep.), information on age-depth model is being provided	Fall & Drezner 2019	Burley et al. 2015	Swamp at low elevations (3 m a.s.l.)	yes
Flores (Azores)	Connor et al. 2012	Borges et al. 2016, Connor et al. 2012	Schaefer 2005, Rull et al. 2017	Crater lake formed by Strombolian eruption (530 m a.s.l.)	yes
Gran Canaria (Canary Islands)	de Nascimento et al. 2016	Beierkuhnlein et al. 2021, de Nascimento et al. 2020	Velasco et al. 2019, de Nascimento et al. 2020	Laguna de Valleseco (870 m a.s.l.)	yes
Great Mercury Island (Ahuahu, Mercury Islands)	Holdaway et al. 2019, Prebble et al. 2019	Wright 1976; New Zealand Plant Conservation Network 2022	Wilmshurst et al. 2008	Small catchment wetlands	yes
Ha'afeva (Tonga)	Flenley et al. 1999, digitalized by Strandberg (2022) and Strandberg et al. (in prep.), information on age-depth model is being provided	Fall & Drezner 2019	Burley et al. 2015	Swamp at low elevations (7 m a.s.l.)	yes

Hispaniola (Greater Antilles)	Crausbay et al. 2015	Smithonian National Museum of Natural History 2022	Cooke et al. 2017	Small forest hollow at 2455 m a.s.l. (Cordillera Central)	no
Iceland	Halsdóttir 1987	Kristinsson 2008; Alsos et al. 2015, 2016	Halsdóttir 1987	Lake at low elevations	no
La Gomera (Canary Islands)	Nogué et al. 2013	Beierkuhnlein et al. 2021	Velasco et al. 2019, de Nascimento et al. 2020	Former lake at the base of an old crater at 1250 m a.s.l. (La Laguna Grande)	no
Maui (Hawaii)	Pau et al. 2012	Pacific Island Network et al. 2017; IUCN 2022	Rieth et al. 2011	Lagoon in Keālia Pond region at low elevations	yes
Mauritius	de Boer et al. 2013	PIER 2018, Government of Mauritius 2020	Cheke 2008	Crater (Kanaka Crater) at 560 m a.s.l.	yes
Mo'orea (Society Islands, French Polynesia)	Stevenson et al. 2017	Whistler 2015, CABI 2022, MDFP 2022	Kahn & Sinoto 2017, Wilmshurst et al. 2011	Lake near the coast (Lake Temae) at low elevations	yes
New Caledonia (here: Grande Terre)	Stevenson et al. 2001	Munziger et al. 2022, CEN 2018, Lebot 1999	Reith & Cochrane 2017	Backswamp of river (Plum Swamp) at 10 m a.s.l.	no
Nightingale Island	Ljung & Björck 2007	Roux et al. 1992	Headland 1989	Bog in in-filled lake at 150 m a.s.l.	no
Pico (Azores)	Connor et al. 2012	Borges et al. 2016, Connor et al. 2012	Schaefer 2005, Rull et al. 2017	*Sphagnum* bog (873 m a.s.l.)	yes
Raivavae (Austral Islands, French Polynesia)	Prebble et al. 2019	Florence 2004, Prebble et al. 2019, Hassler 2022	Wilmshurst et al. 2011	Marsh at 0-3 m a.s.l.	yes
Rapa Iti (Austral Islands, French Polynesia)	Prebble et al. 2019, Kennett et al. 2006, Prebble et al. 2014	Florence 2004, Prebble et al. 2019, Hassler 2022	Wilmshurst et al. 2011	Marsh at 0-3 m a.s.l.	yes
Rimatara (Austral Islands, French Polynesia)	Prebble & Wilmshurst 2019	Hassler 2022, Prebble & Wilmshurst 2019	Wilmshurst et al. 2011	Swamp at 84 m a.s.l. (Maunutu Swamp)	yes
Robinson Crusoe	Anderson et al. 2002, Haberle 2009	Carvallo & Castro 2017, Stuessey et al. 2018	Anderson et al. 2002	130 m a.s.l.	no

San Cristóbal (Galápagos)	Restrepo et al. 2012	Jaramillo et al. 2021	Colinvaux & Schofield 1976, Froyd et al. 2010	Crater lake (El Junco) at 679 m a.s.l.	yes
Santa Cruz (Galápagos)	Froyd et al. 2014; age-depth model updated with SHCal20 calibration curve	Jaramillo et al. 2021	Colinvaux & Schofield 1976, Froyd et al. 2010	*Sphagnum* bog (East Bog) at 739 m a.s.l.)	yes
Santo Antão (Cabo Verde)	Castilla-Beltrán et al. 2019	Arechavaleta et al. 2005, Romeiras et al. 2016	Patterson 1988	Volcanic caldera (Cova de Paúl) at ~1200 m a.s.l.	yes
São Nicolau (Cabo Verde)	Castilla-Beltrán et al. 2020	Arechavaleta et al. 2005, Romeiras et al. 2016	Patterson 1988	Volcanic caldera at ~ 1000 m a.s.l.	yes
Tawhiti Rahi (Poor Knights Islands)	Wilmshurst et al. 2014	Wilton et al. 2016	Wilmshurst et al. 2014	Moist depression at head of an ephemeral stream (30 m a.s.l.)	yes
Tenerife (Canary Islands	de Nascimento et al. 2009	Beierkuhnlein et al. 2021, de Nascimento et al. 2020	de Nascimento et al. 2020, Rando et al. 2014	Former lake bed in the city of La Laguna at 560 m a.s.l.	yes
Tristan da Cunha	Ljung et al. 2006	Wage & Dickson 1965	Headland 1989	Bog in overgrown lake (Hillpiece Bog) at 62 m a.s.l.	yes
Uta Vava'u (Tonga)	Strandberg (2022), Strandberg et al. (in prep.)	Fall & Drezner 2019	Burley et al. 2015	Marsh at low elevations (4 m a.s.l.)	yes
Vanuatu (here: Efate)	Strandberg (2022), Strandberg et al. (submitted)	Plunkett et al. 2022	Petchey et al. 2014	Lake (Lake Emaotul) at 119 m a.s.l.	yes

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Table S2: Model description and summary of linear mixed effect model with non-native pollen [%] as a response, time as an explanatory variable and islands as a random effect. Model fit was done using the *lme4* package (Bates *et al.*, 2015) based on $\text{dataset}_{\text{lower}}$ and $\text{dataset}_{\text{upper}}$.

Parameter	Coefficient	CI	CI_low	CI_high	T	df_error	p	Effects	Group	Fit
$\text{dataset}^{\text{lower}}$										
(Intercept)	1,171755	0,95	0,927159	1,416352	9,401334	948	3,92E-20	fixed		
time	-0,0003	0,95	-0,00034	-0,00026	-14,2157	948	1,02E-41	fixed		
	0,56915	0,95						random	island	
	0,571261	0,95						random	Residual	
AIC										3587,184
AICc										3587,226
BIC										3606,618
R2 (conditional)										0,360739
R2 (marginal)										0,07016
Sigma										0,571261
$\text{dataset}^{\text{upper}}$										
(Intercept)	1,851071	0,95	1,475168	2,226974	9,663859	948	3,90E-21	fixed		
time	-0,00045	0,95	-0,00051	-0,00039	-14,1225	948	3,06E-41	fixed		
	0,876423	0,95						random	island	
	0,85988	0,95						random	Residual	
AIC										5312,952
AICc										5312,994
BIC										5332,386
R2 (conditional)										5629,255
R2 (marginal)										5629,255
Sigma										0,85988

Table S3: Model description and summary of piecewise regression model (Bayesian Information Criterion) with non-native pollen as a response and time (limited to 2000 cal. years BP) as an explanatory variable. Model fit was done using the *segmented* package (Muggeo, 2017) based on $\text{dataset}_{\text{lower}}$ and $\text{dataset}_{\text{upper}}$.

Parameter	Coefficient	CI	CI_low	CI_high	Statistic	df_error	p	Std. Coefficient	Std. Coefficient low	Std. Coefficient high	Fit
$\text{dataset}^{\text{lower}}$											
(Intercept)	6,17658	0,95	5,379591	6,973569	15,21355	766	7,23E-46	6,17658	5,379591	6,973569	
time	-0,00573	0,95	-0,00847	-0,003	-4,10926	766	4,40E-05	-0,00573	-0,00847	-0,003	
U1 time	0,005656	0,95	0,002608	0,008703	3,643003	766	0,000288	0,005656	0,002608	0,008703	
psi1 time	0	0,95	-248,751	248,7512	0	766	1	0	-248,751	248,7512	
AIC											4694,598
BIC											4717,83
R2											0,060309
R2 (adj.)											0,056629
Sigma											5,08153
$\text{dataset}^{\text{upper}}$											
(Intercept)	24,03917	0,95	21,15948	26,91886	16,38737	766	5,77E-52	24,03917	21,15948	26,91886	
time	-0,10969	0,95	-0,17018	-0,0492	-3,5598	766	0,000394	-0,10969	-0,17018	-0,0492	
U1 time	0,104682	0,95	0,044141	0,165224	3,394346	766	0,000723	0,104682	0,044141	0,165224	
psi1 time	0	0,95	-61,2703	61,27031	0	766	1	0	-61,2703	61,27031	
AIC											6450,952
BIC											6474,184
R2											0,118093
R2 (adj.)											0,114639
Sigma											15,89655

Table S4: Model description and summary of linear mixed effect model with pollen of endemic taxa [%] as a response, time as an explanatory variable and islands as a random effect. Model fit was done using the *lme4* (Bates *et al.*, 2015) package.

Parameter	Coefficient	CI	CI_low	CI_high	T		df_error	p	Effects	Group	Fit
(Intercept)	0,898089	0,95	0,436234	1,359945	3,816041	954	0,000144	0,436234	fixed		
time	7,69E-05	0,95	4,10E-05	0,000113	4,20504	954	2,86E-05	4,10E-05	fixed		
	1,118111	0,95							random	island	
	0,494995	0,95							random	Residual	
AIC											3835,864
AICc											3835,906
BIC											3855,324
R2 (conditiol)											0,740359
R2 (margil)											0,005332
Sigma											0,494995

Table S5: Model description and summary of linear mixed effect model with pollen of cultivars [%] as a response, time as an explanatory variable and islands as a random effect. Model fit was done using the *lme4* (Bates *et al.*, 2015) package.

Parameter	Coefficient	CI	CI_low	CI_high	T	df_error	p	Effects	Group	Fit
(Intercept)	0,256024	0,95	0,073144	0,438904	2,747366	948	0,006122	fixed		
time	-5,50E-05	0,95	-7,37E-05	-3,63E-05	-5,77908	948	1,02E-08	fixed		
	0,439082	0,95						random	island	
	0,255954	0,95						random	Residual	
AIC										483,9341
AICc										483,9764
BIC										503,3684
R2 (conditiol)										0,750487
R2 (margil)										0,016214
Sigma										0,255954

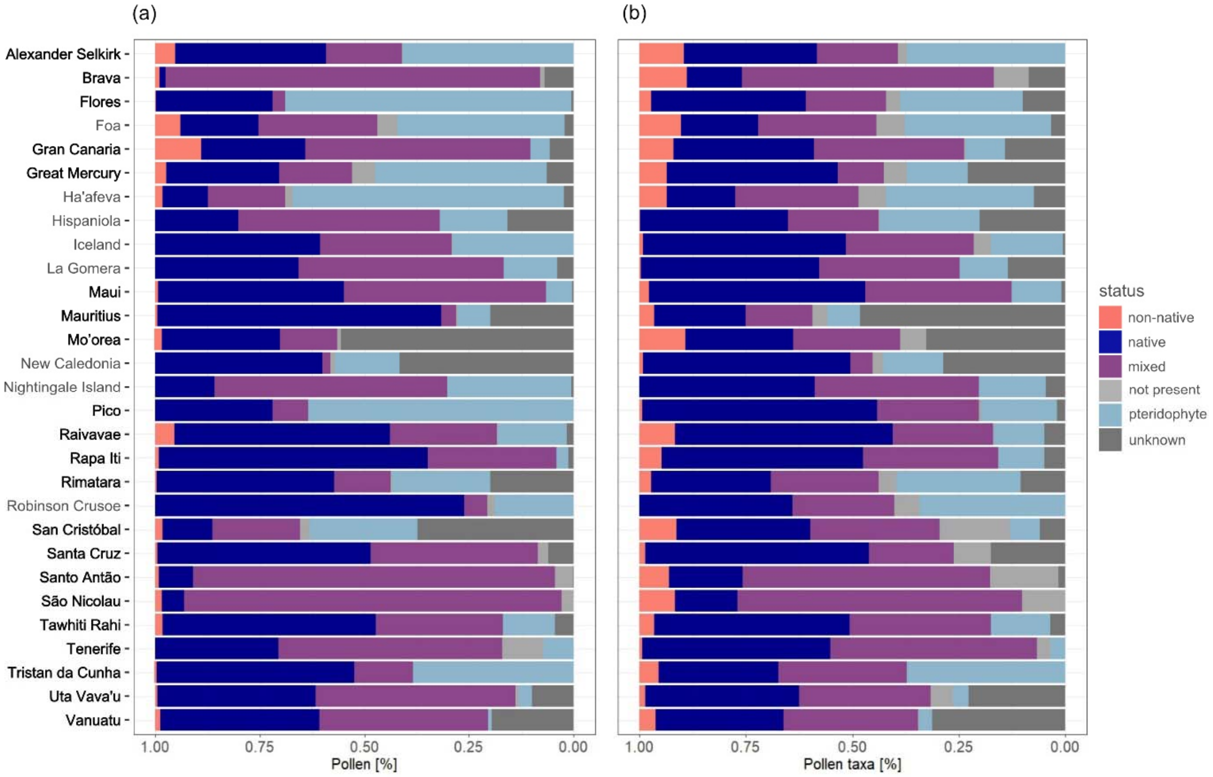

Figure S1: a) The proportion of pollen taxa divided into the categories *non-native*, *native*, *mixed*, *not present*, *pteridophytes* and *unknown* for all 29 studied islands. The information given is based on the number of pollen taxa during all time steps of a sedimentary sequence. b) The proportion of pollen abundance (= proportion of pollen grains) per category (non-native, native, mixed, not present, pteridophyte and unknown) for all study islands. The information given is based on the pollen proportions [%] and the entire time series of the underlying sedimentary sequence. The 22 islands included in the analysis due to successful data matching procedures are written in bold.

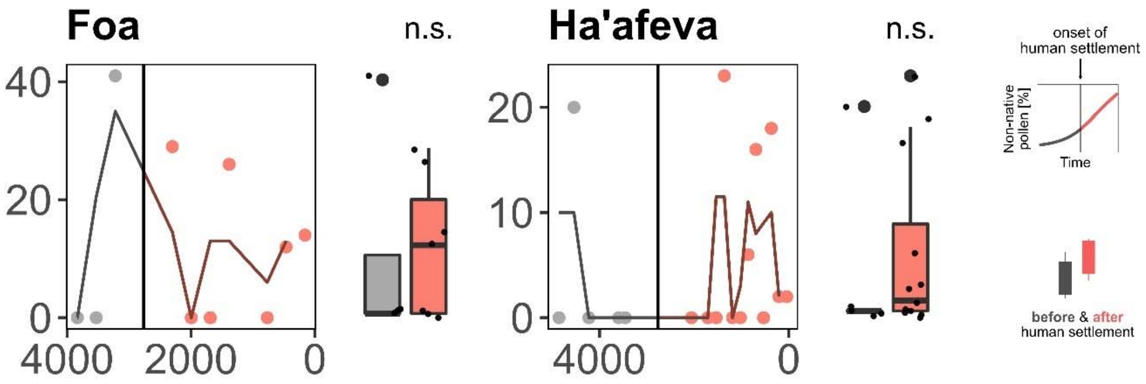

Figure S2: Fossil pollen data from sediment sequences from Foa and Ha’afeva (Tonga) were removed from the main analysis due to low temporal resolution of the data. Additionally, for Ha’afeva we detected high percentages of non-native pollen before the onset of human settlement that can be attributed to *Gardenia* pollen (Flenley et al. 1999). While the authors of the record discuss the presence of *Gardenia* in the context of Tongan human settlement history, no explanation is given for the occurrence of *Gardenia* pollen at earlier times. Here, we cannot differentiate whether an incorrect pollen grain identification or status attribution is limiting the interpretation of non-native pollen trajectories on Ha’afeva. Figures are based on dataset$_{lower}$.

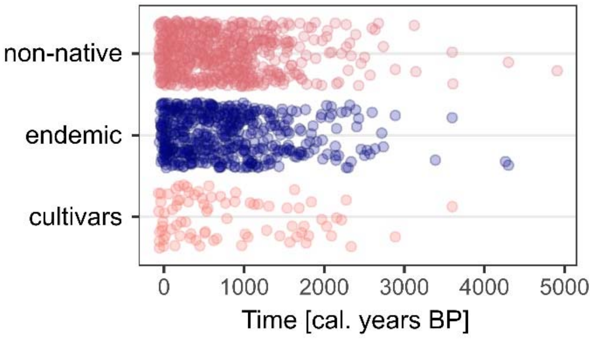

Figure S3: To assess the temporal data resolution, pollen records in time [cal. years BP] of *non-native*, *endemic* and *cultivar* pollen were plotted simultaneously for all islands and time steps. The number of data records is high from 2000 cal. years BP.

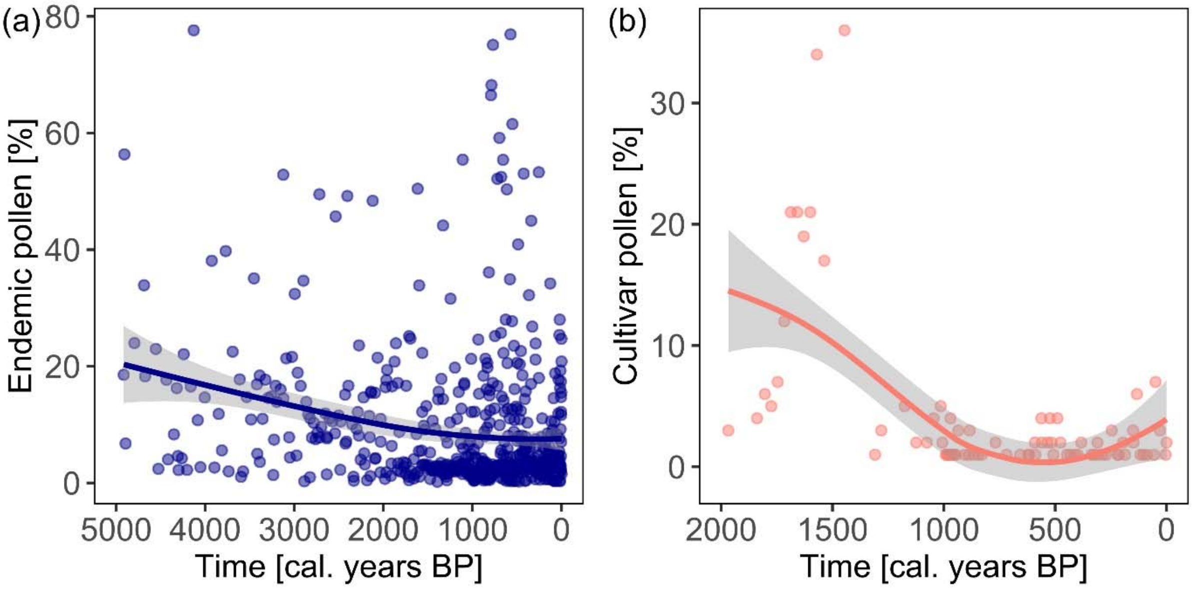

Figure S4: a) Percentage of pollen grains from *endemic* taxa in time (cal. years BP) dating back to 5000 cal. years BP that show a decreasing temporal trend. b) Percentage of pollen from *cultivars* in time (cal. years BP) dating back to 2000 cal. years BP show a decreasing temporal trend as well. For trend visualization a local polynomial regression was fitted with a 95% confidence interval.

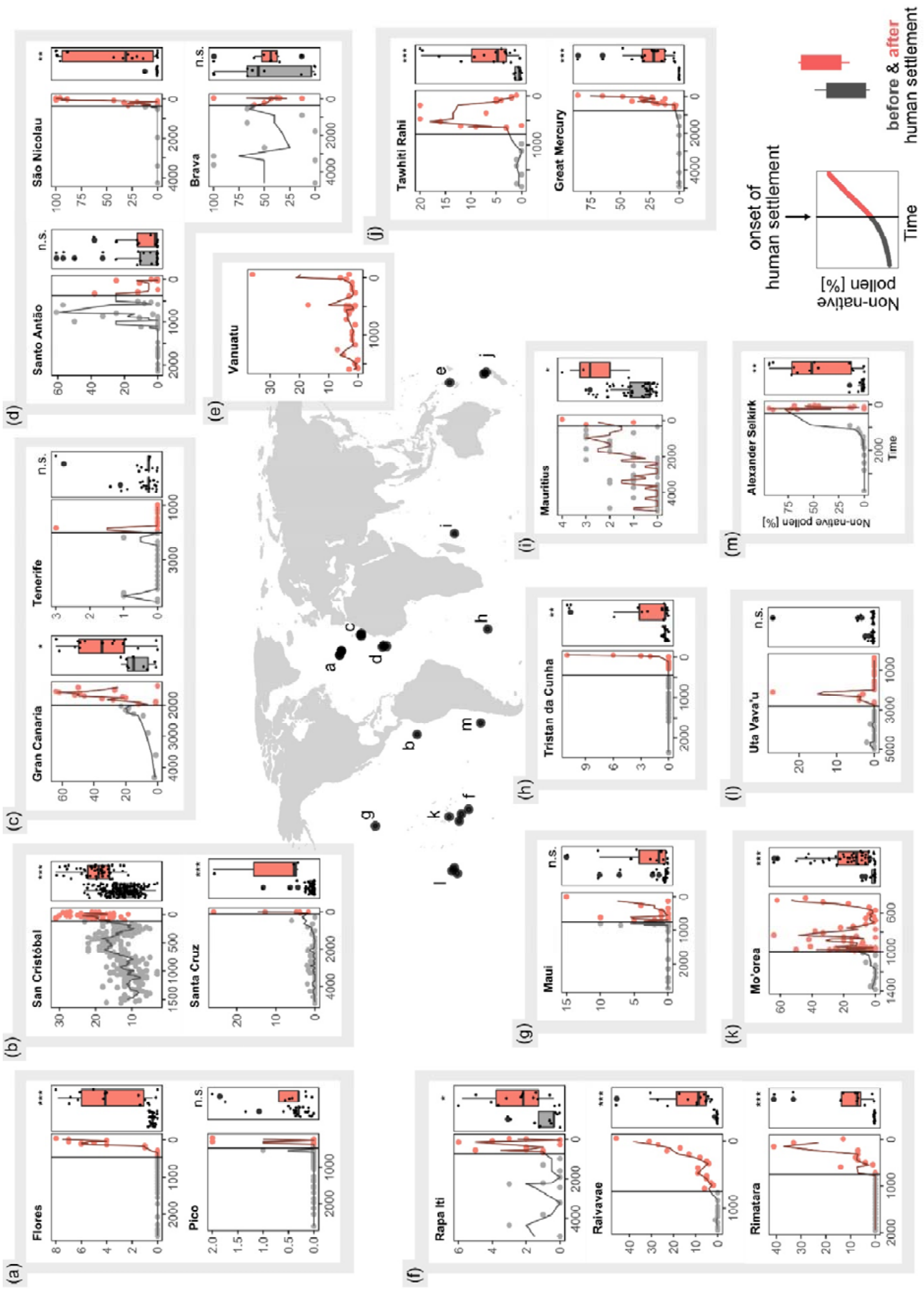

Figure S5 continued

Figure S5: Trajectories of the percentage of non-native pollen taxa found in records covering the last 5000 years (cal. years BP) for 21 islands globally. Human settlement is indicated by a black vertical line. A comparison of non-native pollen taxa [%] before and after human settlement is provided as boxplots. Significance levels are indicated by asterisks (Wilcoxon signed-rank sum tests). Colours in grey respond to data points before and colours in red to data points after human settlement. Plot legends are provided at the bottom-right. Note that for Vanuatu pollen data are only available for a period after human settlement and consequently no comparison of non-native pollen before and after the human settlement is possible. Results are based on dataset$_{upper}$. Note furthermore that on Rapa Iti, patterns in non-native pollen before human arrival can most likely be attributed to contamination with *Pinus* pollen at the coring site (Prebble *et al.*, 2019).

Manuscript 4


The invasive grass species *Pennisetum setaceum* tolerates even the dry conditions of coastal La Palma, Canary Islands. © Anna Walentowitz

Summary

Invasive species have been identified to be a major agent of biodiversity change in the Anthropocene (Kueffer 2017). With this case study, we assess the invasion of the grass species *Pennisetum setaceum* (also known under its synonym *Cenchrus setaceus*, POWO 2022) on La Palma (Canary Islands). The invasion gains relevance in the context of high endemism on La Palma (Beierkuhnlein *et al.* 2021) and therefore potential negative implications on insular biodiversity (Fernández-Palacios *et al.* 2021). Here, correlative species distribution modelling is used to project the potential distribution of this graminoid invader on La Palma. Implication for biodiversity conservation on La Palma are discussed.

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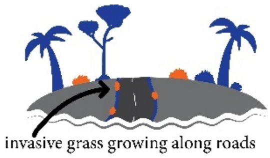

Graminoid Invasion in an Insular Endemism Hotspot and Its Protected Areas

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Abstract

Invasive plant species are increasingly altering species composition and the functioning of ecosystems from a local to a global scale. The grass species *Pennisetum setaceum* has recently raised concerns as an invader on different archipelagos worldwide. Among these affected archipelagos are the Canary Islands, which are a hotspot of endemism. Consequently, conservation managers and stakeholders are interested in the potential spreading of this species in the archipelago. We identify the current extent of the suitable habitat for *P. setaceum* on the island of La Palma to assess how it affects island ecosystems, protected areas (PAs), and endemic plant species richness. We recorded in situ occurrences of *P. setaceum* from 2010 to 2018 and compiled additional ones from databases at a 500 m × 500 m resolution. To assess the current suitable habitat and possible distribution patterns of *P. setaceum* on the island, we built an ensemble model. We projected habitat suitability for island ecosystems and PAs and identified risks for total as well as endemic plant species richness. The suitable habitat for *P. setaceum* is calculated to cover 34.7% of the surface of La Palma. In open ecosystems at low to mid elevations, where native ecosystems are already under pressure by land use and human activities, the spread of the invader will likely lead to additional threats to endemic plant species. Forest ecosystems (e.g., broadleaved evergreen and coniferous forests) are not likely to be affected by the spread of *P. setaceum* because of its heliophilous nature. Our projection of suitable habitat of *P. setaceum* within ecosystems and PAs on La Palma supports conservationists and policymakers in prioritizing management and control measures and acts as an example for the potential threat of this graminoid invader on other islands.

Keywords: alien; biodiversity; African fountain grass; non-native; *Pennisetum setaceum*; species distribution modeling; invasibility; exotic; invasive; endemism

1 | Introduction

On many islands, humans have substantially altered species composition and functioning of ecosystems. A major driver of these changes is invasive species [1]. Wealthy islands with large human populations, such as the Canary Islands, host higher numbers of invasive species compared to less wealthy islands with a low GDP (gross domestic product) as recent large-scale analyses reveal [2,3]. Biological invasions on islands have even led to the reversal of fundamental biogeographic patterns, such as the species-isolation relationship [4]. Thus, understanding the patterns of distribution and spread of invasive species is particularly relevant for islands.

Islands are generally species-poor, mostly due to their isolation and in some cases also due to their young age [5]. However, they can harbor high numbers of endemic plant species [6] and thus contribute far above average to global biodiversity. Therefore, islands are of priority interest for conservation, especially in the context of rapid species and biodiversity loss [7]. Although islands only cover approximately 5% of the global terrestrial surface, they host around 17% of all plant species [8]. The Canary Islands are no exception, and they are known for their richness in endemic plant species [6,9].

Unfortunately, island biota is known to exhibit extraordinarily high extinction rates [10,11]. Island floras are already under pressure by changes in climate because of their isolation, small distribution area, and small populations [12]. This vulnerability is exacerbated by the introduction of alien and invasive species, which become the main driver of these losses [13,14]. On the Canary Islands, many endemic plant species are currently considered highly endangered as a result of invasive species [15,16,17,18].

The survival of endangered endemics will largely depend on adequately controlling invasive species based on scientifically sound knowledge of their distribution, population dynamics, and ecology.

Precise information on distributions of introduced plant species is scarce. A timely and sound monitoring of invaders with high temporal and spatial resolutions is often lacking, also because of the immense workload and financial resources that are required for such an assessment [19]. However, the development of conservation projects requires spatial information about invasive species to assure the responsible use of ever-scarce financial resources and the effectiveness of the applied measures.

Species distribution models (SDMs) are an established and powerful tool to assess the potential occurrences of species [20,21]. They are mostly applied to identify the potential range of native species with long-term established populations. However, an increasing number of studies use SDMs to predict the distribution of invasive species, e.g., [22-24]. SDMs correlate known species occurrence records with environmental variables, making it possible to 1) provide information about suitable environments, and to 2) map the potential species' distributions.

General concerns about the modeling of invasive species' distributions have been voiced because of the potential nonequilibrium distributions of these species [25,26]. Furthermore, it is likely that the precision of modeling is strongly influenced by the phase of invasion with more stochastic model outputs in early stages [27]. However, West et al. have validated SDMs of invasive species with field data and confirmed the realistic modeling of processes. In addition, modeling invasive species can be informative when estimates about the potential distribution of an invader are urgently needed for conservation management [28].

Pennisetum setaceum ((Forssk.) Chiov. (Poaceae) is included in the List of Invasive Alien Species of Union concern that is part of the 2020 Biodiversity Strategy of the European Union [29] which implements the Biodiversity Targets of the Convention on Biological Diversity (CBD). Target 5 of the EU Biodiversity Strategy aims at controlling, eradicating, or containing invasive species that have been identified to threaten biodiversity in the EU [29]. *P. setaceum* is a known invader in Hawaii, New Caledonia, Australia, and South Africa [30] and, in consequence, efforts to control the further spread of the species should be given high priority.

In recent years, *P. setaceum* has been identified as a rapidly spreading invasive plant in the Canary Islands as well as on La Palma (Palomares-Martínez, personal observation) [31,32], yet its potential threat remains unclear. La Palma hosts various areas with differing protection status, including the Caldera de Taburiente National Park. The entire island is also a World Biosphere Reserve of the UNESCO (United Nations Educational and Cultural Organization). La Palma is a highly suited target island because it offers a large range of habitats and a diverse set of endemic species [33] where we intend to fill the knowledge gap on the invasion of *P. setaceum*. Specifically, we aim at (a) modeling its potential occurrence, (b) analyzing its distribution patterns, and (c) evaluating its habitat suitability with regard to ecosystems, endemic plant species richness, and location of protected areas on La Palma.

2 | Materials and Methods

La Palma is an oceanic island located in the Atlantic Ocean off the coast of northwest Africa and belongs to the Canary Islands (Spain, Figure 1). It contains high elevations and, therefore, exhibits strong environmental gradients, e.g., in temperature and precipitation [34]. The highest peak, Roque de los Muchachos (2426 m a.s.l.), is located in the northern part of the island. Precipitation is mainly driven by trade winds coming from the northeast causing humid conditions in the windward part of the island [34]. Several vegetation zones are structuring the island. The dry and hot zone is located below the dew point at elevations up to 800 m a.s.l. and is dominated by coastal and succulent vegetation [35]. The zone within the clouds is characterized by broadleaved evergreen vegetation composed of laurel and tree heath forests [36,37]. Laurel forests are mainly restricted to the northeastern slopes of La Palma where precipitation is high [34]. Canary pine forests range between altitudes of 800 to 2000 m a.s.l. [35]. Higher elevations above 2000 m are mainly covered by subalpine mountainous shrub species [35]. In total, 176 archipelago endemic plant species and 40 single island endemics (SIE) can be encountered on La Palma [36]. The Canary Islands have been inhabited for millennia by aborigine peoples and later by Europeans [38], who introduced hundreds of non-native plants [39]. Currently, La Palma has a population of approximately 80,000 people and is visited by more than 250,000 tourists per year [40]. In modern times of prospering tourism, frequent air traffic and cruise ship embarkments are major pathways for plant introductions [41].

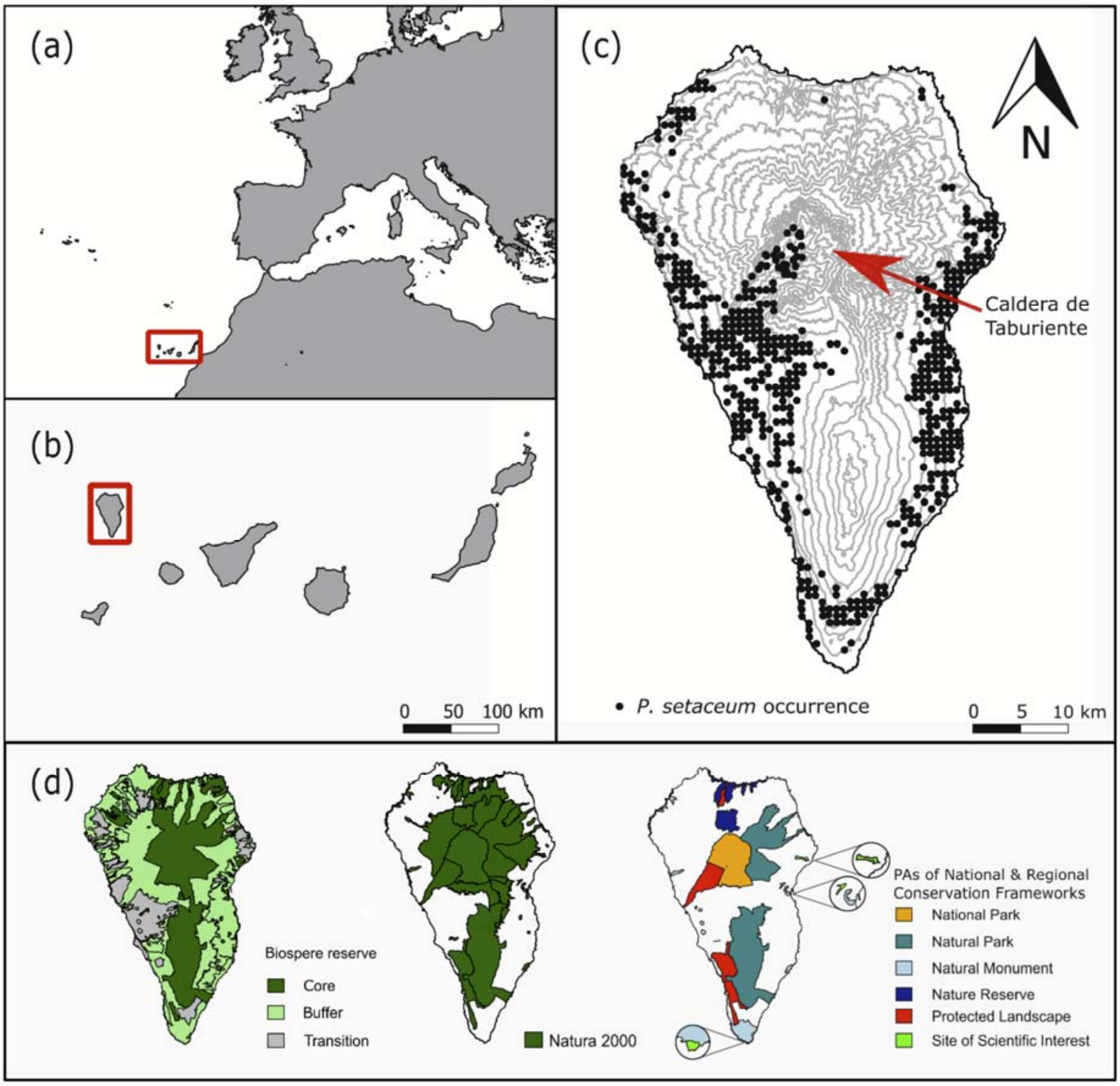

Figure 1: Location of the Canary Islands (a) and the position of La Palma within the archipelago (b). Distribution of *Pennisetum setaceum* occurrence points after correction for autocorrelation ($n_{thinned} = 561$) that was used for species distribution modeling (c). Biosphere reserve (left, d), Natura2000 sites (middle, d), and nationally and regionally designated protected areas (right, d).

Pennisetum setaceum (Figure 2) originates from northern Africa and the Middle East but is now present on most continents and many oceanic islands in the Pacific and Atlantic Ocean [30,42]. The invader is suspected to have arrived in La Palma during the construction of the new airport in the 1970s [43,44]. It shows several traits that are common among invaders, like drought-tolerance [45,46]. Furthermore, it is a C4 apomictic bunchgrass [47] and polyploid ($2n = 27$), which increases the plasticity of the species [48]. Polyploidy maintains genetic diversity within the species by the use of duplicated loci from apomictic seeds, even when the diversity among individuals is low [48]. This might explain its success as an invader despite low genetic diversity. *Pennisetum setaceum* is dependent on recruitment from seeds, as it has no vegetative propagation [47]. Seeds stay viable for up to 10 years (Acevedo Rodríguez, personal observation) and germinate without light [49].

Figure 2: The Crimson fountain grass *Pennisetum setaceum* as an invader on La Palma.

2.1 | Compilation of data sets

A dataset with occurrence data of *P. setaceum* on La Palma ($n_{\text{total}} = 786$) was compiled from four sources:

1. Occurrence data from the National Park Directorate of La Palma for *P. setaceum* within the National Park “La Caldera de Taburiente” from 2016, $n = 55$.
2. Fieldwork based occurrence data collected at a yearly basis from 2010 to 2018, $n = 19$.
3. Entries in the GBIF (Global Biodiversity Information Facility) database [50] for *P. setaceum* (only geo-referenced data; basis of record: observation, human observation) from 2012 till 2017, $n = 21$.

4. Occurrence data from the Atlantis database [51]. From this raster data, we created centroids within each pixel of *P. setaceum* occurrence with the highest precision level and a resolution of 500 × 500 m to extract occurrence points, $n = 691$.

We corrected for spatial correlation by spatially thinning the occurrence points in R Studio Version 3.5.3 [52] with the package spThin [53]. Based on a PCR of all occurrence points we selected a thinning parameter of 3.5 to avoid spatial clumping ($n_{\text{thinned}} = 561$, Figure 1c).

To model the distribution of *P. setaceum* on La Palma, we selected a set of environmental variables that account for climatic, topographic, and anthropogenic aspects (Table 1, Figure A1). We used data on elevation, slope, and aspect (its components northness and eastness have been used for modeling) as topographic information. For climate, we used mean annual temperature, mean annual precipitation, and solar radiation. For model building, the anthropogenic variables 'nearest road' and 'nearest settlement' were chosen. The variable geological age was used as a proxy for bedrock nature, which is of importance for the vegetation on a young volcanic island like La Palma. We accounted for collinearity (Pearson correlation coefficient threshold of $|r| = 0.7$ (sensu [54]) of the variables selected for modeling and removed mean annual temperature and nearest settlement from the analysis as these variables highly correlated with elevation. We decided to consider elevation in the modeling process and to drop the other variables because first, temperature interpolations are based on elevation linked with just a few weather stations on the island and second, elevation is more important for SDMs than the environmental variable 'nearest settlement'.

Table 1: Environmental variables used for species distribution modelling of suitable habitat of *P. setaceum* on La Palma, including also the calculations of variables and the source.

Category	Variable	Calculation of variables	Souces
Topography	Elevation	Rasterized at a resolution of 0.5 x 0.5 km deriving from a digital elevation model (DEM) of 2 x 2 m.	Original Data: Cabildo Insular de La Palma, [33]
	Slope	Calculations were based on a DEM of 2 x 2 m. Resolution was rescaled to 0.5 x 0.5 km.	Original Data: Cabildo Insular de La Palma, Calculations [33]
	Aspect (northness, eastness)	Calculations were based on a DEM of 2 x 2 m. Resolution was rescaled to 0.5 x 0.5 km. Northness was calculated as cos(aspect) and eastness as sin(aspect).	Original Data: Cabildo Insular de La Palma, Calculations [33]
Parent material	Geological age	Resolution was rescaled to 0.5 x 0.5 km.	Cabildo Insular de La Palma, [32]
Climate data	Mean annual precipitation	Interpolation (Linear regression kriging), using data collected from meteorological stations for the Canary Islands (n = 214). Time span from 1969 to 1998. Resolution was rescaled to 0.5 x 0.5 km.	Original Data: Cabildo Insular de La Palma, Calculations [33]
	Solar radiation	Calculation from DEM 100x100m using a standard diffuse atmosphere and based on latitude, elevation, slope	Original Data: Cabildo Insular de La Palma, Calculations [33]

		and aspect. Resolution was rescaled to 0.5 x 0.5 km.	
Infrastructure	Nearest road	Resolution was rescaled to 0.5 x 0.5 km.	[33]
Land cover	Vegetation types (coniferous forest, broadleaved evergreen forest, scrubland, cultivated land, barren land)	Rasterized at a resolution of 0.5 x 0.5 km	Original Data: Cabildo Insular de La Palma, [33]

2.2 | Ensemble modelling

An ensemble model to project the suitable habitat of *P. setaceum* on La Palma was created with the package biomod2 [55]. The spatial analysis was carried out at a resolution of 500 × 500 m.

Ensemble methods improve the accuracy of predictive models by synthesizing the results of single models into a single score [56]. For model building, we used presence-only data and thus used three sets of 561 randomly chosen pseudo-absences with 10 replications. An ensemble model was built based on a generalized linear model (GLM), gradient boosting machine (GBM), random forest (RF), and maximum entropy model (MaxEnt). One hundred evaluation runs were made using a 70/30 data plot approach advocated by Araújo et al. [57]. The ensemble model was built using AUC (area under the relative operating characteristic curve) as an evaluation metric. In total 3902 models with AUC > 0.7 were included in the ensemble model building. Ensemble predictions were calculated using the mean of the single models. The ensemble model prediction had a good predictive ability with AUC = 0.9 and TSS (true skill statistic) = 0.7. The AUC cutoff (threshold minimizing the absolute difference between sensitivity and specificity) of the mean was used as a threshold to transform the projection of suitable habitat for *P. setaceum* derived from the ensemble model into a binary presence–absence map (sensu) [58]. Further calculations were based on this binary map.

2.3 | Projecting habitat suitability onto ecosystems, PAs and endemic plant species richness

Modeling results were processed for further assessment and compared with the distribution of ecosystems, species richness, and PAs on La Palma. All data were tested for normal distribution with the Shapiro–Wilk test. To compare differences in mean annual temperature and the distance to the nearest settlement of suitable and unsuitable habitat for *P. setaceum*, a Mann–Whitney U test was used considering a non-normal distribution of the data.

For post-modeling analysis, the environmental variables 'mean annual temperature' and 'nearest settlement' were included but had been excluded beforehand from the model building. For the environmental variables 'mean annual temperature', 'annual precipitation', 'elevation', 'nearest road,' and 'nearest settlement,' we extracted minimum and maximum values to depict the range these variables cover on La Palma. We calculated the percentages of these environmental gradients which we identified as suitable habitat for *P. setaceum*.

We derived raster maps of total plant species richness and SIE richness from Irl et al. [33]. Therein the presence/absence data of native vascular and endemic perennial plant species from 890 plots on La

Palma were interpolated into richness maps. The resolution was upscaled to our model resolution of 500 × 500 m. We compared SIE richness and total plant species richness of projected suitable and unsuitable habitat for *P. setaceum*.

To evaluate modeling results in combination with designated areas of different protection status we considered the locations of the core, buffer, and transition zone of the biosphere reserve [59], Natura 2000 sites defined by the EU Habitat Directive [60], and nationally/ regionally designated protected areas, which include the national park, protected landscapes, natural parks, natural monuments, sites of scientific interest, and nature reserves [61]. The vector data was rasterized and scaled to 500 × 500 m. We calculated the projected suitable habitat for *P. setaceum* within designated areas of each protection status (cover in % and km²).

3 | Results

Under current climatic conditions, 34.7% of the land surface of La Palma is identified to be suitable habitat for *P. setaceum*. This suitable habitat for *P. setaceum* is located mainly along the coasts and enters via the Barranco de las Angustias into the Caldera de Taburiente National Park on the leeward side of La Palma (Figure 3 and Figure A2).

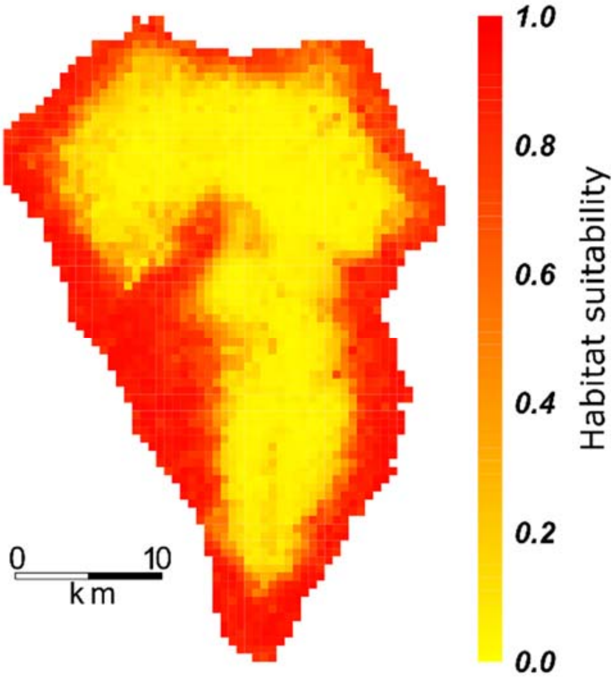

Figure 3: Projected suitable habitat conditions of *P. setaceum* on La Palma based on the ensemble model of generalized linear model (GLM), gradient boosting machine (GBM), random forest (RF), and maximum entropy model (MaxEnt). Habitat suitability ranges from 1 (high probability of occurrence, red) to 0 (low probability of occurrence, yellow).

For the single model algorithms GLM, GBM, RF, and MaxEnt, on which the ensemble model is built, we calculated the mean variable importance. In all models, elevation had the highest variable importance, followed by distance to the nearest road and mean annual precipitation (Table 2).

Table 2: Variable importance for the single model algorithms (GLM, MaxEnt, RF, and GBM) of the ensemble modeling approach. The three most important variables for each model are written in bold. Variables are ranked from highest (1.) to lowest (9.) importance.

Variable	GLM	MaxEnt	RF	GBM
1. Elevation	**0.963**	**0.573**	**0.480**	**0.676**
2. Precipitation	0.043	**0.245**	**0.155**	**0.162**
3. Nearest road	**0.180**	**0.225**	0.073	**0.071**
4. Solar radiation	**0.153**	0.104	**0.080**	0.061
5. Slope	0.012	0.137	0.034	0.017
6. Vegetation	0.022	0.051	0.027	0.006
7. Northness	0.000	0.070	0.021	0.008
8. Eastness	0.000	0.090	0.013	0.002
9. Geological age	0.000	0.063	0.023	0.007

Projected occurrences of *P. setaceum* were detected more frequently in proximity to human settlements at a mean distance of 1118 m. In contrast, projected species absence pixels had a mean distance of 2168 m to human settlements (Mann–Whitney U test, $p_{\text{settlement}} < 0.0001$, Figure 4a). The invasive grass species typically occurred at mean annual temperatures of 17.3 °C. In contrast, projected species absence pixels had a temperature of 14.9 °C (Mann–Whitney U test, $p_{\text{temp}} < 0.001$, Figure 4b). Mean annual temperature of suitable habitat of the invasive grass species ranged between 11.9 °C and 19.7 °C (Figure 5). Areas of projected suitable habitat for *P. setaceum* ranged between an elevation of 41 m and 800 m, with some exceptional occurrences at 1214 m. These high elevational projected occurrences were located without exception in the Caldera de Taburiente. For projected species presence, the precipitation varied between 212 mm/year and 901 mm/year. The distance of areas suitable for the invasive grass species to the nearest road ranged between 3 m and 2445 m. The projected suitable habitat for *P. setaceum* covers the entire gradient of the variables 'nearest road' and 'nearest settlement'. We projected unsuitable habitat for *P. setaceum* on La Palma to be found in areas with low temperature, high precipitation, and high elevation.

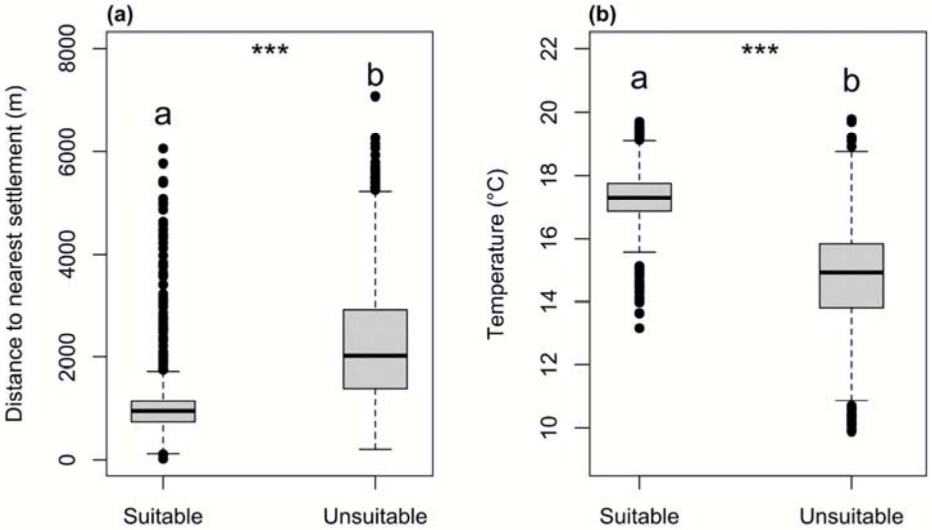

Figure 4: (a) Pixels that were modeled as suitable habitat for *P. setaceum* show smaller distances to the nearest settlement compared to pixels without *P. setaceum*. (b) Average mean annual temperatures of pixels with *P. setaceum* presence are considerably higher compared to pixels where the species is absent. Highly significant results are indicated by three asterisks.

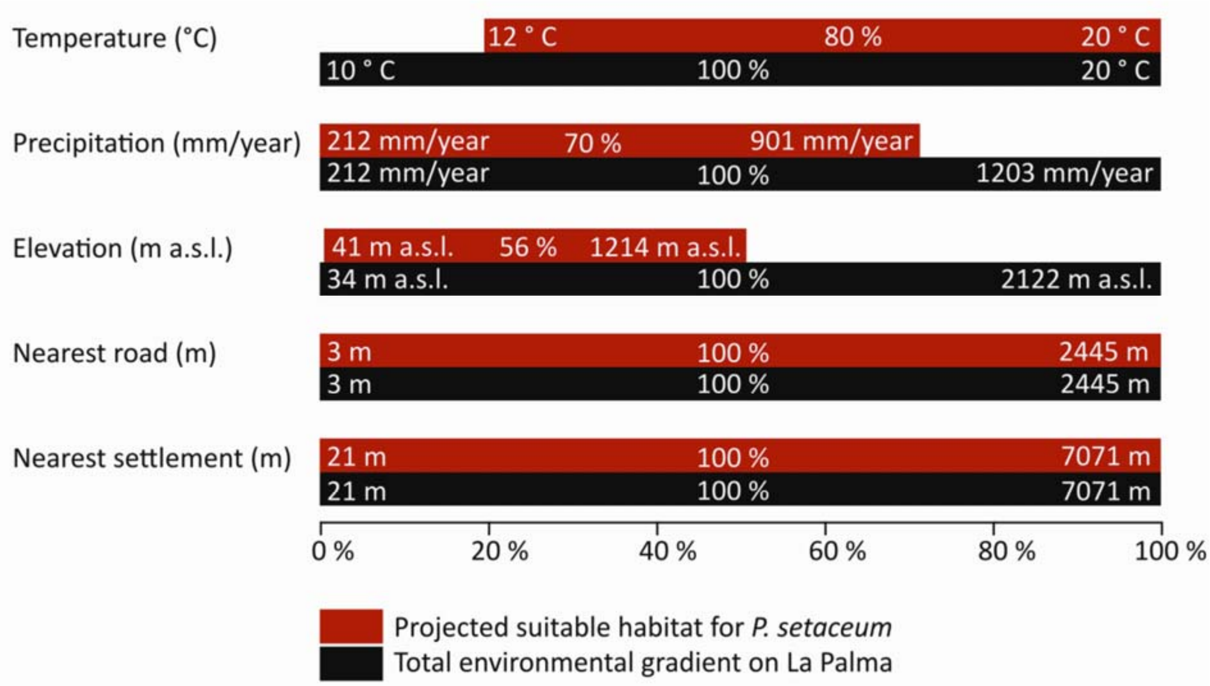

Figure 5: Total environmental gradients of mean annual temperature, annual precipitation, elevation, nearest road, and nearest settlement on La Palma (black bar). Red bars show the range of the environmental gradients projected to represent a suitable habitat for *P. setaceum* on La Palma. Note that the gradients elevation, nearest settlement, and nearest road do not start at zero due to calculations made on the bases of mean values for pixels the size of 500 × 500 m.

Total species richness of SIE was significantly lower in areas of suitable habitat for *P. setaceum* compared to areas classified as unsuitable (Mann–Whitney U test, $p\text{SIE} < 0.001$, Figure 6a). However, total species richness was higher in areas suitable for *P. setaceum* compared to areas classified as unsuitable for the grass species (Mann–Whitney U test, $p_{\text{richness}} < 0.001$, Figure 6b). *Pinus canariensis* forests cover large areas on La Palma and are poor in plant species diversity. We projected only a small area of this forest type to be suitable habitat for *P. setaceum*. Thus, when comparing total plant species richness between suitable and unsuitable habitat for *P. setaceum*, the *P. canariensis* forest might account for differences. When we excluded this ecosystem from our analysis no differences in species richness between suitable and unsuitable habitat for *P. setaceum* were found (Mann–Whitney U test, $p_{\text{richness-no-pinus}} = 0.391$, Figure 6c). Additionally, we projected coniferous and broadleaved evergreen forests to be suitable habitat for *P. setaceum* only at very low percentages while scrubland, cultivated land, and bare soil were more strongly affected (Table 3).

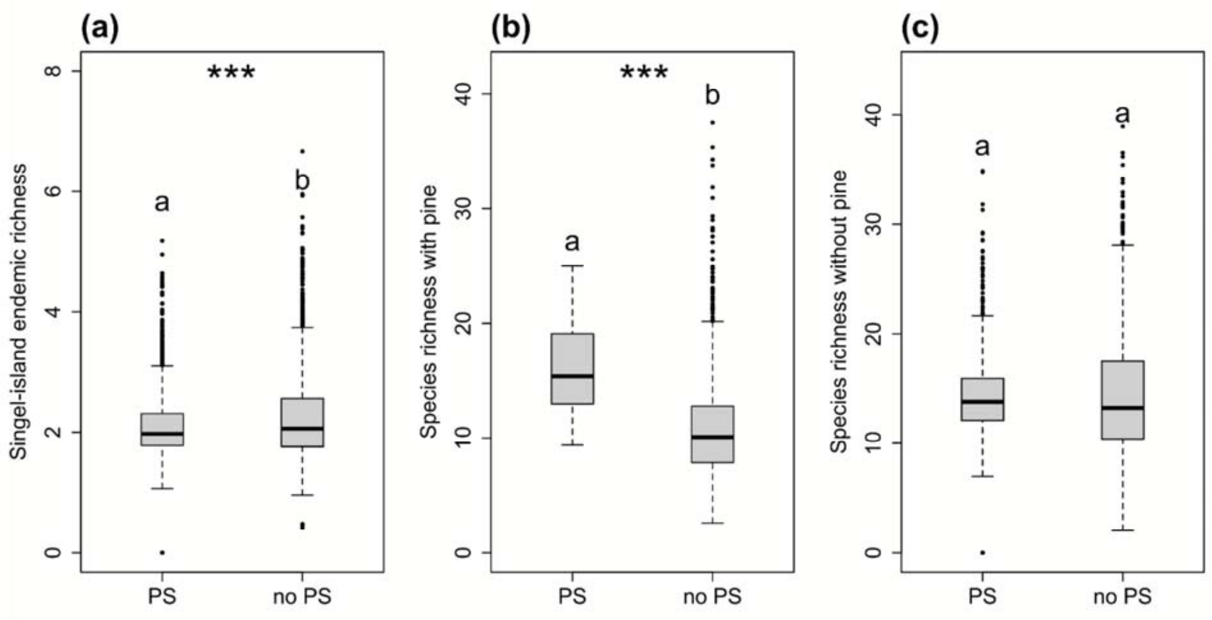

Figure 6: (a) Single island endemic plant species richness in projected suitable and unsuitable habitat for *P. setaceum*. (b) Total species richness in areas suitable and unsuitable for *P. setaceum*. (c) Species richness of unsuitable compared to suitable habitat excluding the *Pinus canariensis* forest. Highly significant results are indicated by three asterisks.

Table 3: Projected suitable habitat for *P. setaceum* within the coniferous forest, broadleaved evergreen forest, shrubland, cultivated land, and bare soil of La Palma as total cover of ecosystem, total suitable habitat for *P. setaceum*, and percentage cover of suitable habitat for *P. setaceum*.

Ecosystem	Total cover in km^2	Suitable habitat for *P. setaceum*
Coniferous forest	224 km^2	20 km^2 (9%)
Broadleaved evergreen forest	99 km^2	1 km^2 (1%)
Scrubland	78 km^2	51 km^2 (65%)
Cultivated land	214 km^2	130 km^2 (61%)
Bare soil	34 km^2	22 km^2 (65%)

While within the core of the La Palma Biosphere Reserve only 6.2% of the area was potential habitat for *P. setaceum*, the coverage reached 33.2% in the buffer zone and 67.1% in the transition zone of the biosphere reserve (Figure 7). Within Natura 2000 protected areas, a projected suitable habitat for *P. setaceum* of 8.6% was calculated. For the Caldera de Taburiente National Park, the natural parks, and nature reserves, low coverages of *P. setaceum* below 17% were detected. For other protected areas such as protected landscapes or natural monuments, the potential coverage with *P. setaceum* was far higher, reaching 63.0% and 93.1%, respectively.

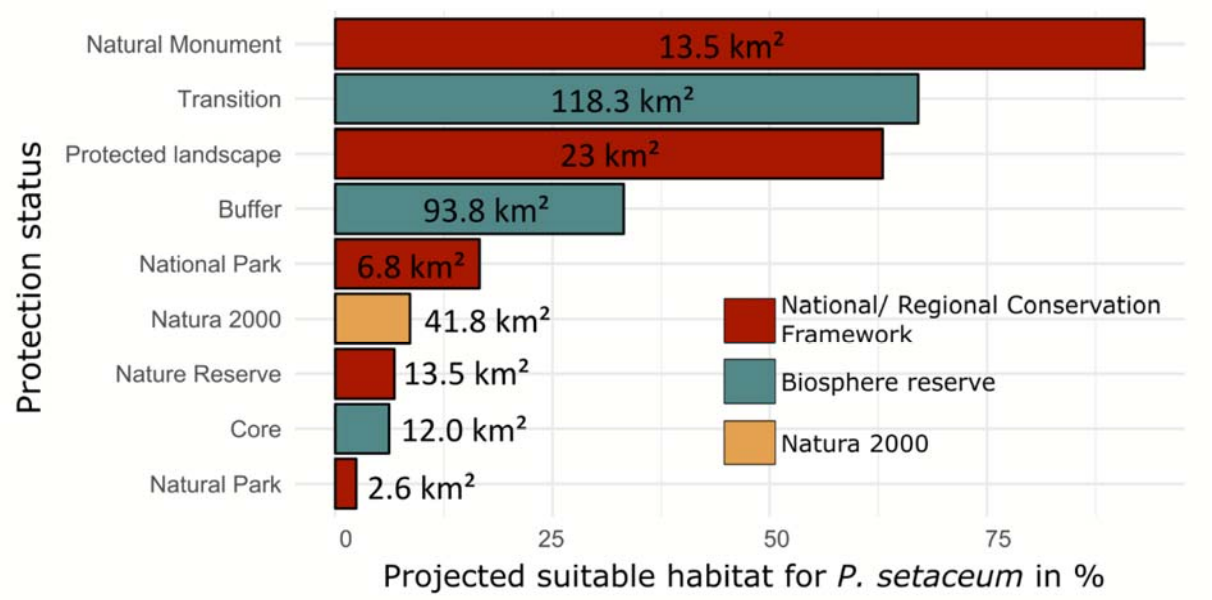

Figure 7: Projected suitable habitat for *P. setaceum* in protected areas on La Palma in coverage percent and area in km^2.

4 | Discussion

Our study is the first published assessment of the distribution and potential threat of the graminoid invader *P. setaceum* on La Palma. We find that about one-third of the surface of La Palma is potentially suitable for *P. setaceum*. The projected suitable habitat covers wide environmental gradients on the island, except for areas at very high elevations (or low temperatures) and with high amounts of precipitation. This raises major concerns for large parts of the vegetation of this island. Invasion by *P. setaceum* may considerably affect local ecosystems and native biodiversity. This threat demands priority control measures, especially in arid areas at low elevations and areas with high conservation value.

The importance of anthropogenic variables, e.g., the distance to the nearest road or settlement for the distribution of *P. setaceum*, indicates that this plant benefits from human infrastructure and activity. This is in accordance with findings from South Africa where roads strongly promote its dispersal [45,46,62,63] and relates to the dispersal of seeds by wind and car drag. Additionally, this graminoid invader is adapted to aridity typical for disturbed, sun-exposed sites in the vicinity of roads and settlements [63]. Furthermore, *P. setaceum* is favored by horticulturalists as an ornamental plant which adds to its success on anthropogenically influenced sites [64,65]. Recently, an exceptional occurrence of *P. setaceum* has been located in the northern coastal parts of La Palma (personal observation, Palomares-Martínez). However, the surroundings are anthropogenic habitats with occurrences of exotics of the genera *Furcraea* and *Opuntia*, which emphasizes the importance of disturbed areas for the dispersal of *P. setaceum*.

Elevation was the most important variable explaining the distribution of *P. setaceum* on La Palma in all model algorithms (GLM, GBM, RF, and MaxEnt) combined for the ensemble model. Our model shows a higher elevation of projected suitable habitat for *P. setaceum* within the Caldera de Taburiente compared to the rest of the island. As elevation is a proxy for temperature, microclimatic differences in temperature, caused by the protection from cool oceanic winds within the Caldera, can help to explain these findings. Furthermore, strong tropical storms from the southwest might be a factor to elucidate the high occurrences of *P. setaceum* within the Caldera de Taburiente. After storms, leaves of *Persea americana* and *Musa* sp., both agricultural plants occurring in the vicinity of the coast, have been recorded up to 2423 m a.s.l. (Acevedo Rodríguez, personal observation). Recently, occurrences of the invasive grass have been found at altitudes of 1500 m in the "Barranco Risco Liso", located within the Caldera de Taburiente.

The elevational distribution pattern of *P. setaceum* hints at environmental factors playing a role in the distribution of this grass species that have not been considered in the modeling of this invasive species in this study. In the sheltered environment of the Caldera, thermal updraft might explain the differing elevational pattern of projected suitable habitat. The dispersal of P*. setaceum* is exclusively dependent on apomictic seeds and thus assessing the wind dispersal potential of the diaspores in combination with local wind patterns could help explaining these patterns [48,66]. Precise spatial information on predominant wind direction and topographically induced turbulence is not available for La Palma. Future provision of such maps can enhance model quality of anemochorous invasive plants.

Touristic activity within the National Park might explain the extend of the projected suitable habitat for *P. setaceum* within the Caldera de Taburiente. Tourism and recreational activities can influence the spread of non-native species [41]. Unpaved paths used by hikers are dispersal pathways for species such as *P. setaceum* [67].

For conservation efforts, the impact of invaders on natives and particularly on endemic species is of importance [68]. Remarkably, the number of endemic plant species on La Palma is significantly lower in areas identified as suitable habitat for *P. setaceum* compared to unsuitable areas. We can draw from this that there is little concern for this invasive grass species to outcompete or displace endemic plants on La Palma due to lower SIE richness in these areas. The latter is in accordance with general distribution patterns of endemic and invasive plant species on high-elevation islands [33,69]. While high elevations host the highest number of endemic species [69] and the aggregation of rare endemics most vulnerable to extinction aggregate there as well [59], non-native species richness peaks at elevations around 500 m [69]. Mean elevation of projected suitable habitat for *P. setaceum* was 543 m and matches this pattern quite precisely. *P. setaceum* is a C4 plant and thus well adapted to arid and semi-arid habitats [70], which explains the low coverage by suitable habitat for *P. setaceum* of broadleaved evergreen forest on La Palma. These broadleaved evergreen forests are mainly laurel forest communities (monteverde), located in the northeastern part of La Palma where some SIE and high numbers of Macaronesian plant endemics can be encountered [59]. The main occurrences of laurel forest coincide with high precipitation and humid localities exposed to trade winds. There are transition zones between laurel forest and the Erica-Morella-Forest (fayal-brezal) but also distinct ecotones of the pine forest driving diversity patterns linked with particular ecosystems [71].

Even though total species richness seemed to differ between projected suitable and unsuitable habitats for *P. setaceum*, we could show that this pattern was distorted by the *P. canariensis* forest on La Palma. The closed canopy of the forest prevents *P. setaceum* invasion and this forest type additionally contains lower species numbers compared to other ecosystems on the Canary Islands [72]. *P. setaceum* derives from arid areas of the Middle East and northern Africa where lush evergreen forest is scarce which can explain this pattern [42]. Additionally, *P. canariensis* forests historically have a high fire frequency of dominant pine species being fire-tolerant and having the ability to resprout after fire [73]. *Pennisetum setaceum* seeds lying on the soil surface can be killed by forest fires [47] and on the short run frequent forest fires seem to help to stop invasions of this graminoid. However, seeds buried deeper in the soil can survive these forest fires [47] and the native flora and fauna can be affected negatively by this hazard.

Additionally, disturbances of natural systems (deforestation, human-caused low fire frequencies) might aid the graminoid invader in establishing within or in proximity to forest ecosystems and should be accounted for when developing conservation measures concerning *P. setaceum*.

A common disturbance on islands is the browsing of introduced herbivores. However, *P. setaceum* seems not to be negatively affected by browsing, although the graminoid mainly occurs at low elevations where introduced rabbit density is high [18]. Very likely, this results from the sharp blades of the plant using silica phytoliths as a mechanical defense against herbivory [74].

Another relevant aspect of conservation is the impact of invaders on protected areas aiming to promote and conserve endemic and native biodiversity. La Palma hosts different protected areas with different levels of protection status, as well as a UNESCO Biosphere Reserve, which covers the entire island. The specific aim of biosphere reserves is the conservation of ecosystems, species, and genetic variation [75]. We found the biosphere core area, where most rare and potentially endangered endemics are found [59], to be influenced very little by *P. setaceum* and, therefore, we currently do not see great concern for plant diversity within this area. The projected suitable habitat for *P. setaceum* in the transition area of the biosphere reserve, natural monuments, and protected landscapes reached covers of more than 60%. However, our study constitutes a snapshot in time, while biological invasions are dynamic processes that change with time and interact with their environment. A future spread of *P. setaceum* as a result of niche shifts via adaptation [26] and/or climate change [12] cannot be ruled out.

Evidence-based conservation allows conservationists and policymakers to focus conservation efforts and resources on problematic species that cause unwanted ecological changes or economic losses. Proceeding this way prevents misspending conservation funds on restoration measures, i.e., the eradication and control of invasive species that do not pose threats to biodiversity and human wellbeing [76]. Our identification of suitable habitat for *P. setaceum* on La Palma is a basis for conservationists and policy makers to prioritize conservation actions and to utilize conservation funds efficiently to maintain and protect plant species diversity on La Palma.

We suggest that immediate control measures (e.g., manual and chemical species removal efforts) should take place to prevent a further spread of *P. setaceum* into PAs and endanger unique endemic species. A specific focus should be put on potential vectors and invasion pathways, e.g., along roads and hiking paths. Furthermore, the control should be carried out from the border of its current distribution to avoid further spreading. Prioritized control in areas of high conservation value is recommended because monetary and labor resources are limited. Engagement of citizens, public administrations, and volunteers by means of environmental education would be useful to raise awareness and facilitate monitoring and controlling both in PAs and private land. Prohibiting the commercial use of *P. setaceum* lowers propagule pressure and is thus another instrument to control further spreading of the graminoid. Furthermore, we recommend implementing a monitoring system for this species in order to enable quick response times in terms of management and control of *P. setaceum*, if further spreading into areas of great biodiversity and ecological value is observed.

Our study on the distribution of *P. setaceum* as well as environmental and anthropogenic influence factors on the spread of this global invader constitutes a model case study for further islands and regions where this species has been identified as (potentially) problematic.

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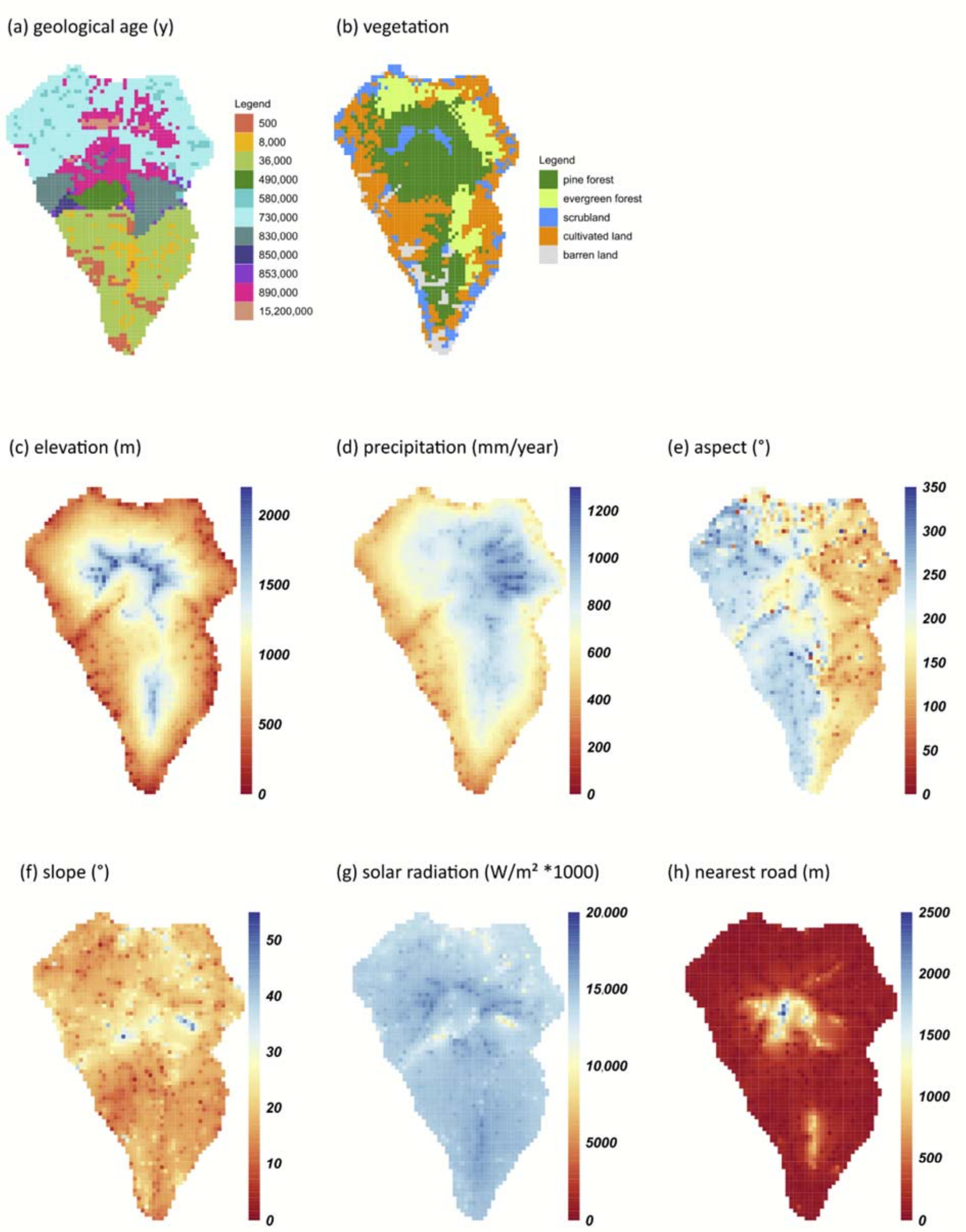
Appendix A


(a) geological age (y)

(b) vegetation

(c) elevation (m)

(d) precipitation (mm/year)

(e) aspect (°)

(f) slope (°)

(g) solar radiation (W/m² *1000)

(h) nearest road (m)

Figure A1: Environmental variables used for building the ensemble model for *P. setaceum* on La Palma: geological age (a), vegetation (b), elevation (c), mean annual precipitation (d), aspect (e), slope (f), solar radiation (g), and the distance to the nearest road (h).

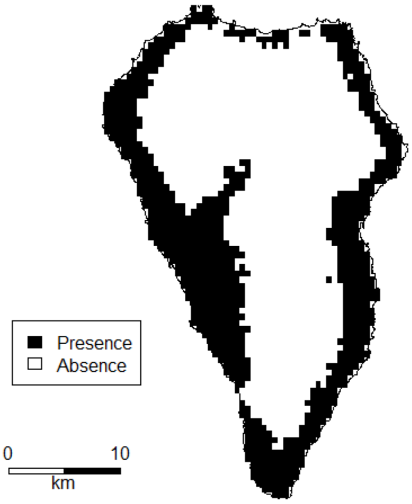


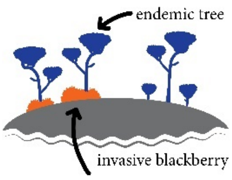
Figure A2: Projected suitable habitat of *P. setaceum* on La Palma as a result of the ensemble model based on a GLM, GBM, GF, and MaxEnt model. Conversion of the modeled habitat suitability into a presence/absence-based map on 0/1 was done using the AUC (area under the relative operating characteristic curve) cutoff of the weighted mean with a threshold value of 509.5, scaled to 0.5095 in Figure 2.

Manuscript 5

Field work to assess the natural regeneration of *Scalesia pedunculata* in the Galápagos Islands after invasive plant species removal. Height of a young sapling is being measured. © Anna Walentowitz

Summary

A common way of mitigating the detrimental effects of invasive species on insular biodiversity is ecosystem restoration (Weidlich *et al.* 2020). On islands, restoration is of utmost importance, due to high numbers of introduced species (Essl *et al.* 2019) and endemism, but also threat rates (Fernández-Palacios *et al.* 2021). Key to successful restoration is the scientific assessment alongside such projects (Higgs 2005), at best for longer periods of times. For this manuscript, I conducted field work in the Galápagos Islands from 2015 to 2021 to assess the natural recruitment of the endemic tree species *Sclalesia pedunculata* after the control of invasive species. Especially the invasive blackberry species *Rubus niveus* is of concern, as it forms dense impenetrable thickets and is a competitor for light. *Sclalesia pedunculata* seeds, seedlings, and saplings, however, depend on high light availabilities to germinate and grow, respectively.



Limited natural regeneration of unique Scalesia forest following invasive plant removal in Galapagos

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Abstract

More than 60% of the flora of the Galapagos Islands is introduced and some of these species have become invasive, severely altering ecosystems. An example of an affected ecosystem is the Scalesia forest, originally dominated by the endemic giant daisy tree *Scalesia pedunculata* (Asteraceae). The remnant patches of this unique forest are increasingly being invaded by introduced plants, mainly by *Rubus niveus* (blackberry, Rosaceae). To help large-scale restoration of this ecologically important forest, we seek to better understand the natural regeneration of *S. pedunculata* after invasive plant control. We monitored naturally recruited *S. pedunculata* saplings and young trees over five years in an area where invasive plant species are continuously being removed by manual means. We measured survival, height and growth of *S. pedunculata* saplings and young trees along permanent transects. Percent cover of surrounding plant species and of canopy shade directly above each *S. pedunculata* individual were determined, as well as distance to the next mature *S. pedunculata* tree. We identified potential factors influencing initial sapling survival and growth by applying generalized linear models. Results showed a rapid growth of saplings and young trees of up to 0.45 cm per day and a high mortality rate, as is typical for pioneer species like *S. pedunculata*. Sapling survival, growth and mortality seemed to be influenced by light availability, surrounding vegetation and distance to the next adult *S. pedunculata* tree. We concluded that natural regeneration of *S. pedunculata* was high only five months after the last herbicide application but that 95% of these recruits had died over the 5-year period. Further studies are needed to corroborate whether the number of surviving trees is sufficient to replace the aging adult trees and this way maintain remnants of the Scalesia forest. Urgent action is needed to help improve future restoration strategies to prevent further degradation of this rapidly shrinking threatened forest ecosystem.

1 | Introduction

As a direct consequence of human activity, island ecosystems worldwide are being transformed by invasive plant and animal species [1]. Many efforts are underway to control and eradicate invasives and restore island ecosystems, intending to conserve native and endemic species diversity [2]. Evaluating the success of these restoration projects is often constrained by a paucity of long-term ecological monitoring data [3,4]. For example, the rate at which tropical forests recover from disturbance (e.g., deforestation, control of invasive species) can vary strongly, and understanding the factors driving the rate of recovery is critical to developing effective restoration measures [5]. Long-term observations of biotic and abiotic conditions within the area under restoration are indispensable to assessing project success [6,7]. Several long-term restoration projects have been undertaken in the Galapagos Islands (e.g., mammal eradication [8]; plant eradication [9]), demonstrating that even in archipelagoes with comparatively late onset of human settlement like Galapagos [10], active ecological restoration is necessary to protect native ecosystems and conserve biodiversity.

There are about 810 introduced plant species in Galapagos [11] and some of these have become invasive, severely affecting the composition of plant communities [12]. A unique ecosystem under threat is the Scalesia forest, originally dominated by the endemic daisy tree *Scalesia pedunculata* (henceforth *S. pedunculata*) that occurs on four islands within the archipelago [13]. On Santa Cruz, the forest suffered massive reductions due to a history of deforestation by land use change and grazing and browsing by goats, pigs and donkeys [14,15]. As a consequence, the remnant forest patches now comprise only 1% of the former distribution [16]. Species composition and population structure of *S. pedunculata* in these patches have been severely transformed by invasive plants, especially by *Rubus niveus* (Rosaceae) and *Cestrum auriculatum* (Solanaceae) [17,18]. The high percent of *R. niveus* cover suppresses regeneration of *S. pedunculata* [18] and reduces the native species richness in the invaded areas [17]. On Santa Cruz, the remnant forest is considered a key ecosystem for many endemic bird and insect species, like the Darwin´s finches that forage and breed in the Scalesia forest [19,20].

Scalesia pedunculata is a pioneer species that exhibits soft wood [21], fast growth and a short life cycle of 15-20 years [13, 14, 17, 21]. It used to dominate in a succession of life stages, with few trees of other species associated [14]. However, with shade-casting thickets of *R. niveus* in the understory, there is almost no germination of *S. pedunculata*, resulting in an extremely low natural regeneration of *S. pedunculata* [18]. This, combined with the high mortality rate of recruits, has led to a dramatic decline of the *S. pedunculata* population over the last decade [17,18].

To address the increasing threat posed by *R. niveus*, the Galapagos National Park Directorate (GNPD) has been controlling this invasive species for over 20 years in different areas of the Galapagos National Park. A study by the authors carried out between 2014 and 2016 documented natural regeneration of *S. pedunculata* after invasive species control, but only over a short time period [18]. Therefore, in this study, we measured biotic parameters in 2015 and survival and growth of *S. pedunculata* saplings and trees from 2015 to 2020 in an experimental trial area of 6 ha in the Scalesia forest on Santa Cruz. By doing so, we sought to increase our understanding of the factors influencing regeneration and recruitment of *S. pedunculata*, following the removal of invasive plant species.

We hypothesized, that (1) the initial growth and mortality rates of *S. pedunculata* saplings and young trees in the remnant forest under restoration would be high, (2) the shading by the canopy would lead to higher sapling and young tree mortality and reduced growth rates, (3) sapling and young tree survival and growth rates would increase with distance from the next mature *S. pedunculata* tree, and (4) sapling and young tree survival and growth would decrease with higher cover of surrounding vegetation.

2 | Methods

2.1 | Study site

The study was carried out in the Scalesia forest remnant in the highlands of Santa Cruz (Galapagos) at an altitude of about 400 – 550 m a.s.l. [13], near the twin volcanic sinkholes “Los Gemelos” (Fig 1). Mean annual precipitation during the five-year study period ranged from 736 mm in 2019 to 1244 mm in 2017, but the mean for all study years was lower than the long-term yearly average of 1380 mm (based on data from 1987 to 2019) (S1 Fig). Average daily temperature in the study area was 22.2°C [22]. The forest was composed of the endemic tree *Scalesia pedunculata* (Asteraceae, about 33% cover), accompanied by the shrubs *Tournefortia rufo-sericea* (Boraginaceae, endemic, about 6% cover), *Chiococca alba* (Rubiaceae, native, about 8% cover), *Psychotria rufipes* (Rubiaceae, endemic, about 3% cover) and *Zanthoxylum fagara* (Rutaceae, native, about 5% cover) [23, percent cover data Jäger, unpubl. data]. Invasive *R. niveus* formed dense thickets in the forest’s understory (about 64% cover) and other introduced and invasive shrubs, like *C. auriculatum* (about 18% cover) and *Psidium guajava* (Myrtaceae, 2% cover) co-occurred [17,18]. These species, as well as the introduced and invasive herb *Tradescantia fluminensis* (Commelinaceae, about 36% cover), had been controlled by the GNPD in an experimental trial area of 6 ha since 2014. Initial control consisted of cutting the *R. niveus* and *C. auriculatum* bush to about 5 cm off the ground with a machete and spraying the regrowth with a combination of the herbicides Combo© and glyphosate after a month. This was repeated monthly two more times, with the last herbicide application occurring five months before the onset of our study in April 2015. Over the following five years, only manual control was carried out every three months (machete, weed trimmer, and hand-pulling) to prevent regrowth of invasive species, mainly of *R. niveus*.

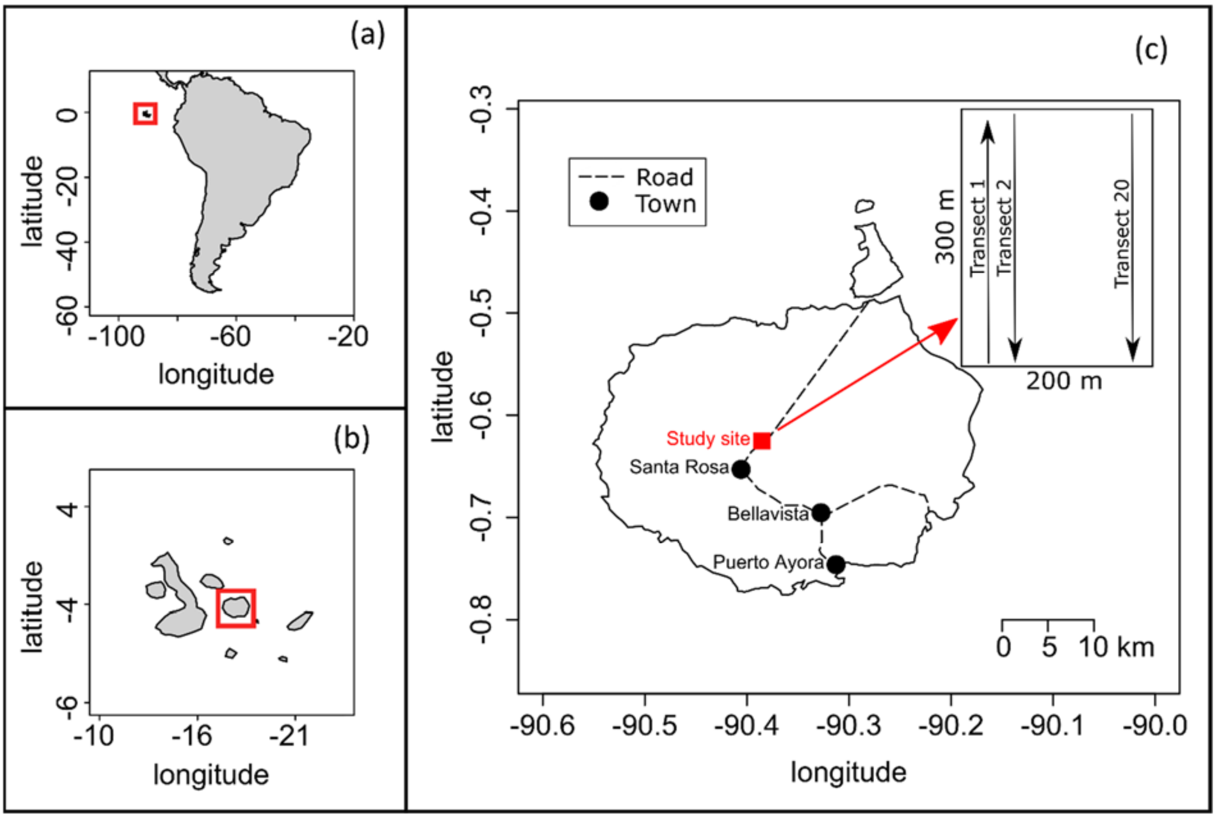

Fig 1: Location of the study site. (a) South America and the Galapagos Islands (red square). (b) Galapagos Islands with Santa Cruz (red square). (c) Santa Cruz with study site indicated in red and sketch of the sampling design. Projection: WGS 84 EPSG 4326.

2.2 | Data sampling and analysis

Field work in the Scalesia forest was conducted under permits issued by the Galapagos National Park Directorate (PC-19-15, PC-50-16, PC-42-17, PC-50-18, PC-55-19 and PC-26-20). Natural regeneration of *S. pedunculata* was determined by establishing 20 parallel permanent transects of 300 m, 10 m apart, in a S-SE to N-NW direction within the study area (Fig 1c). All *S. pedunculata* saplings of a height up to 100 cm (assuming that these had emerged after the last herbicide application 5 months prior to the onset of this study), growing within 1 m to both sides of these transects, were marked with aluminum tags and the exact location was measured with a handheld GPS device (Garmin GPSMAP 65 Series). Measurements were first recorded in April 2015 and then repeated seven times over the course of five years, according to time availability: in June 2015, February 2016, August 2016, March 2017, January 2018, April 2019 and March 2020. At each monitoring event, we documented survival of the marked individuals and calculated mortality rates. Saplings were determined as dead if they were entirely brown and mostly detached from the ground or partly decomposed. We also measured the height of saplings and young trees and calculated mean and maximum growth (defined as the change in height). Daily growth was calculated at the end of the study period by dividing total growth over the five years by the number of days between the first and last monitoring event. Data were processed and descriptive and inferential statistics applied in R Version 4.0.0 [24].

Percent shading by canopy, distance to the next mature S*. pedunculata* tree and percent surrounding vegetation were only measured once at project start in April 2015 and were not repeated over the study period due to time constraints. For this, a photo of the forest canopy parallel to the ground over the top of each *S. pedunculata* individual, with a Nikon D3200 camera (Settings: 300 dpi; aperture value F/7.1; shutter speed 1/2000 sec.). The photos were converted into black and white images by maximizing the contrast in GIMP 2.8.22 [25]. Percent canopy cover (= shade) was calculated for each *S. pedunculata* sapling as the ratio between black and white pixels. Mean percent canopy shade and standard deviation were calculated for the total of all surviving and dead saplings. Distance of each sapling to the nearest mature *S. pedunculata* tree was measured in m. To determine percent cover of individual ground-covering plant species, the area of the saplings' crown was projected onto the ground and defined as 100% cover, and cover of each species within this area was estimated as a fraction. For model building, the surrounding vegetation ground cover underneath each *S. pedunculata* sapling was calculated as the sum of the cover of all species. To determine factors influencing *S. pedunculata* sapling survival and growth during the first year, we implemented general linearized models (GLM) with binomial distribution and logit link function (for survival) and Gaussian distribution (for growth), with fitted curves at a 95% confidence interval. We conducted a correlation analysis of all biotic parameters (S2 Fig) with the package "corrplot" [26], using Pearson's correlation coefficient. The GLMs for *S. pedunculata* sapling survival and growth were built considering the total percent surrounding vegetation cover.

3 | Results

3.1 | Survival

Five months after the last herbicide application, there was an abundant regeneration of *Scalesia pedunculata* in the study area of the Scalesia forest, but only very few were still alive towards the end of the study period (Fig 2).

Fig 2: Mature *Scalesia pedunculata* trees in 2019 with saplings and young trees in the understory in a 6 ha study area in which invasive plant species, especially *Rubus niveus,* had continuously been removed by the Galapagos National Park Directory since 2014. The plant cover on the forest floor mainly consisted of the invasive carpet-forming *Tradescantia fluminensis*.

Of the initial 259 saplings recorded in April 2015, only 13 individuals (5%) were found alive in 2020 (Fig 3a). The largest loss of individuals was recorded after the first year, with only 66 saplings still alive (21%, taking only those individuals into account that could be relocated) in February 2016. In another study in the same area, a similar high mortality rate of *S. pedunculata* recruits was observed (Jäger, unpubl. data). A total of 55 individuals could not be re-located, despite the fact that they were marked with an aluminum tag and their GPS location was known. These had most likely died or were trampled by the ongoing manual invasive plant control actions. Due to the rapid turn-over of organic material in the study area, aluminum tags were probably covered by this and therefore could not be found.

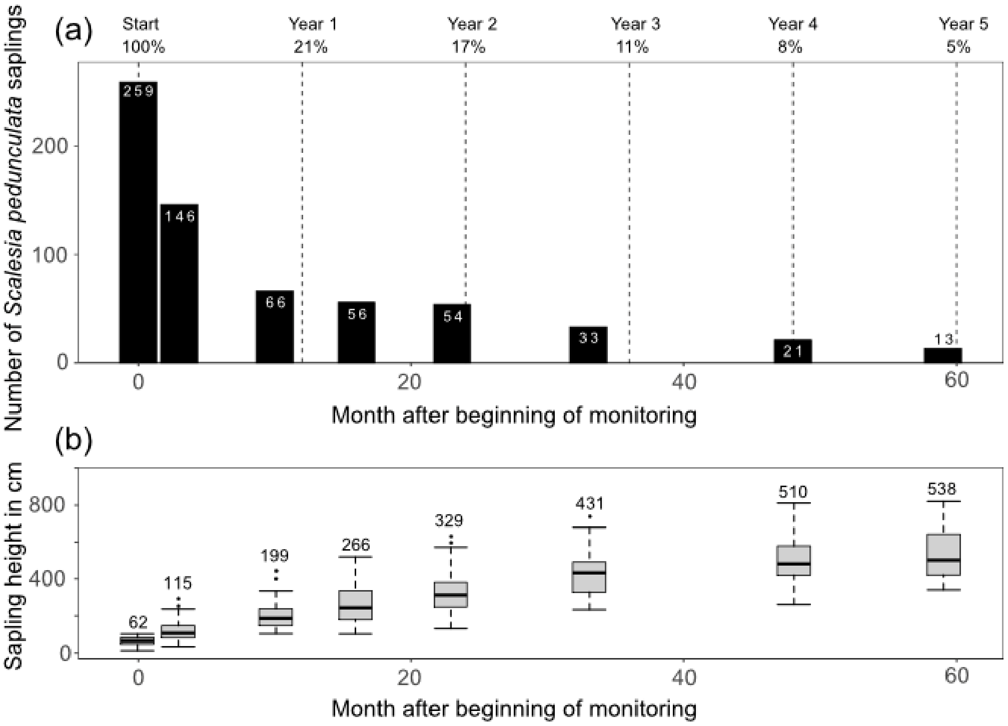

Fig 3: (a) Number (within bars) and percent (top row) of surviving *S. pedunculata* saplings and young trees over 5 years. The mortality rate over five years was 95%. (b) Height of the *S. pedunculata* saplings and young trees over time. The boxplots display the median and the interquartile range (25th to 75th percentile), whiskers indicate the variability outside upper and lower quartiles and outliers are displayed. Mean height is given on top of the boxplots.

Percent canopy shade had the highest explanatory power for sapling survival ($p < 0.001$) based on GLMs (Table 1, Fig 4a). Saplings that were dead after the first year had been exposed to a higher percent total canopy shade than the ones that survived (72.2% ± 13 vs. 56.7% ± 21). The most dominant species in the canopy shade for both groups was *S. pedunculata*, followed by *C. auriculatum*. The distance of saplings to the next mature *S. pedunculata* was significantly larger for surviving saplings compared to dead saplings ($p = 0.05$, 2.13 m ± 1.05 vs 1.58 m, ± 0.81). Percent cover of the surrounding vegetation was higher for surviving saplings compared to dead saplings after the first year (52.8%, ± 35 vs. 41.7%, ± 29), but not significantly so ($p = 0.09$). This vegetation consisted mainly of *R. niveus* (5%) and *T. fluminensis* (25.9%). About 28.9% of the surviving saplings were shaded by *C. auriculatum* (presence/absence, not cover) at first monitoring in April 2015. Percent cover of all species is shown in Table S1.

Table 1: *Scalesia pedunculata* sapling and young tree mortality was significantly correlated with percent canopy shade and distance to the next *S. pedunculata* tree, while percent cover of surrounding vegetation did not have a significant explanatory power. Means are given for alive and dead saplings after the first year (standard deviation in parenthesis). P-values are based on a GLM (binomial distribution, logit function) with the three parameters 'canopy shade', 'distance to the next *S. pedunculata*' and 'cover of surrounding vegetation' included as explanatory variables.

Dependent: Sapling survival	Surviving saplings	Dead saplings	p
Canopy shade (%)	56.7 (21)	71.2 (13)	< 0.001
Distance to next *S. pedunculata* tree (m)	2.13 (1.05)	1.58 (0.81)	0.05
Cover of surrounding vegetation (%)	52.8 (35)	41.7 (29)	n.s.

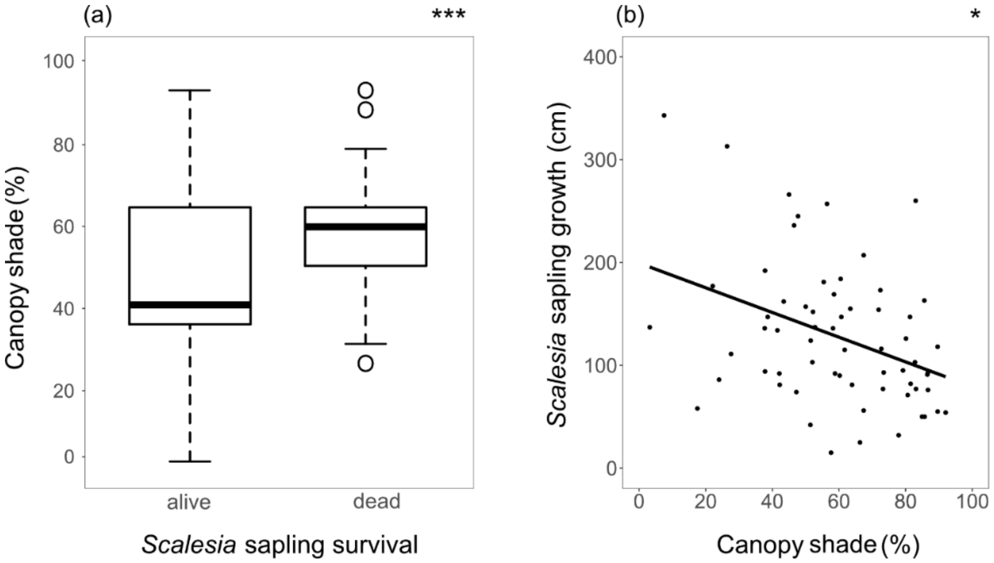

Fig 4: Percent canopy shade was significant in explaining *S. pedunculata* saplings mortality (a, GLM with binomial distribution and logit link function) and growth (b, GLM with a Gaussian distribution) after the first year. Boxplots (a) display the median, interquartile range (25th to 75th percentile), variability outside upper and lower quartiles (whiskers) and outliers. Significance levels are reported as: [*] $p < 0.05$; [***] $p < 0.001$.

3.2 | Height and growth

Average sapling height increased from 62 cm (±23) in 2015 to an average tree height of 538 cm (±170) in 2020 (Fig 3b), which amounts to a yearly average growth of 95 cm, with growth rates differing between years and individuals (S2 Table). Average daily growth over five years was 0.25 cm, but we also measured an average of 0.45 cm a day for the largest plant that reached a height of 820 cm in 2020.

Percent canopy shade was significantly negatively correlated with sapling growth ($p < 0.05$). Distance to the next mature *S. pedunculata* tree and percent surrounding vegetation cover were not correlated with sapling height ($p < 0.05$).

4 | Discussion

Our results showed that while control of *Rubus niveus* in the Scalesia forest on Santa Cruz facilitated an abundant natural regeneration of *Scalesia pedunculata*, only 5% of these new plants survived the 5-year study period (13 out of 259 individuals). A previous publication from the same study area reported a spectacular regeneration of *S. pedunculata* in 2016, but this was about 14 months after the last herbicide application, and no follow-up survey of the population was included [18]. The observed mortality rate of *S. pedunculata* saplings in our study might have been influenced by the last glyphosate application five months prior to the onset of the study, but it is not clear whether glyphosate residuals in the soil affect emerging seedlings [27]. Independently of this, high mortality rates had been observed in other studies addressing the life cycle of *S. pedunculata* and is typical for a pioneer species like *S. pedunculata* [13,16,21,28]. Self-thinning could be a potential explanation since dead stems of *S. pedunculata* were found to be smaller than those of live individuals [29]. Although survival rates of *S. pedunculata* were low, it should be consider that this study followed only one cohort of trees that had emerged after the initial invasive plant species control. Recruits from the seed bank from subsequent years could have substituted those individuals from the first cohort monitored that had died off, as was observed by a study in the same area (Jäger, unpubl. data).

The *S. pedunculata* saplings in our study quickly grew into young trees, reaching a maximum height of 820 cm after five years, growing an average 0.45 cm a day. This finding is consistent with a study carried out in the 1970s, where trees reached 7-8 m in height after 3.5 to 5.5 years, but this was before invasive plants became a problem [28]. Percent shade and proximity to the next mature *S. pedunculata* tree had the highest explanatory power for initial sapling mortality and percent shade for a reduced sapling growth.

Besides the pioneer character and control actions, biotic factors influencing the initial mortality rate and growth of *S. pedunculata* saplings are important for Scalesia forest restoration. As hypothesized, we found that survivorship and height of *S. pedunculata* saplings correlated strongly with light availability. Overall, surviving saplings received less shade, which mainly stemmed from mature *S. pedunculata* trees or the invasive shrub *C. auriculatum*. We, therefore, confirmed the results of previous studies that reported a high light dependency of *S. pedunculata* [13,14,21]. In our study, invasive plant removal caused higher light availability, which in turn facilitated *S. pedunculata* regeneration. Previous studies reported massive dieback of mature *S. pedunculata* trees after the extreme 1982/83 El Niño event that created suitable conditions for natural *S. pedunculata* regeneration from seeds [13,21]. In contrast to these studies, mature *S. pedunculata* trees were still present in our study area and the proximity to the nearest mature *S. pedunculata* tree was negatively associated with the survival of saplings. As *S. pedunculata* is the dominant tree species within this forest type [13], canopy shading is logically reduced at greater distances from mature trees. This aligns with the Janzen Connell hypothesis, which states that propagule survival is dependent on the distance to its parent tree [30,31]. The distribution and survival of *S. pedunculata* seedlings thus seem to be partly the result of a trade-off between light availability, caused by distance to the shading canopy of the parent tree [32], and a short dispersal distance reported for this species [33].

Contrary to our hypothesis, higher vegetation cover surrounding *S. pedunculata* individuals did not significantly affect survival and growth rates of saplings. About 25.9% of this surrounding vegetation was composed of the invasive ground-covering plant *Tradescantia fluminensis* ,and cover of this species increased significantly after control of *R. niveus* in the study area [18]. *Tradescantia fluminensis* is known to be a severe invader elsewhere [34] and has been shown to alter nutrient availability in temperate forests and to hinder native forest regeneration [35,36]. Our study was carried out during an exceptionally dry period [22], which could have affected the natural *S. pedunculata* regeneration but our data do not allow us to determine whether co-occurrence of *T. fluminensis* and *S. pedunculata* is due to favorable microclimate or to facilitation or competition [37]. Thus, future research is needed to disentangle the influence of biotic factors from weather conditions on *S. pedunculata* regeneration over a longer study period. With an anticipated increase in frequency of El Niño (ENSO) events [38,39], regeneration of *S. pedunculata* might differ significantly between years. The twofold pressure from unknown impacts caused by climate change (e.g., increasing temperatures, increasing precipitation and weather extremes) and the anticipated increase of species' invasions, should be taken into account for future restoration actions in the Scalesia forest remnants [40].

In conclusion, invasive plant species have severely altered the Scalesia forest on Santa Cruz to a high degree [18,41]. In combination with its historically reduced range (only 1% of the original forest distribution remains) [16], urgent restoration actions are needed. Our results indicate that natural regeneration of *S. pedunculata* is facilitated by invasive plant species removal. Due to the high mortality rate of recruited *S. pedunculata* saplings (95%), future restoration actions should include the planting of nursery-grown *S. pedunculata* seedlings and young trees, which has proven successful elsewhere [42]. The Scalesia forest is not only unique due to the endemic *S. pedunculata*, it is also an important ecosystem for associated (and endemic) invertebrate and bird species, like the Darwin's finches (19,20). Although the *R. niveus* control had a temporary negative effect on the microhabitat use and feeding behavior of *Certhidea olivacea* (green warbler finch) and *Camarhynchus parvulus* (small tree finch), we call for urgent actions to remove *R. niveus* at a large scale to preserve the last Scalesia forest remnants on Santa Cruz [18, 20].

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Data Availability Statement

All relevant data are within the paper and its Supporting information files.

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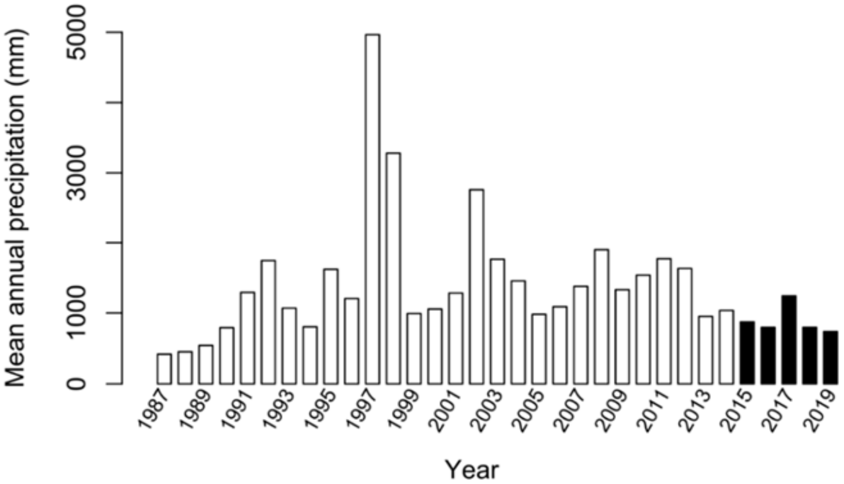
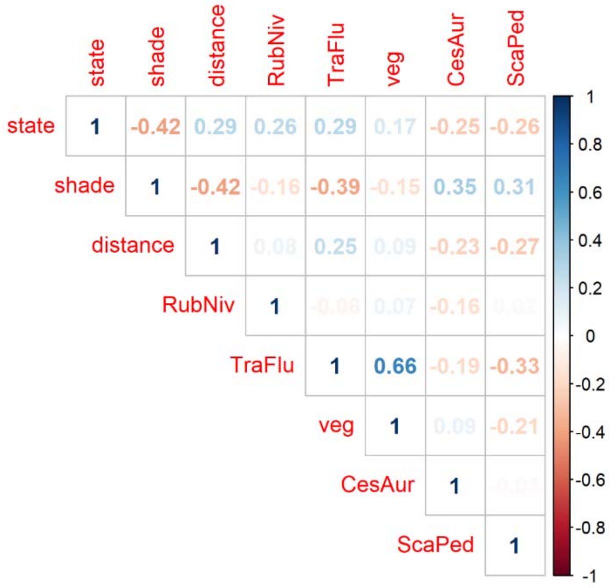
Supporting Information



S1 Fig: Annual precipitation in the highlands of Santa Cruz Island before from 1989 to 2019 and during the study period indicated by black bars.



S2 Fig: Correlation plot of biotic factors of *S. pedunculata* sapling survival and growth based on Pearson's correlation coefficient. Species names are abbreviated by taking the first three letters of their genus and epithet. RubNiv, TraFlu and veg refer to sapling's surrounding vegetation while CesAur and ScaPed belong to the shading canopy.

S1 Table: Initial surrounding vegetation (% cover of single species) of *S. pedunculata* saplings dead or alive after one year with standard deviation in parenthesis (SD).

Species	% cover surrounding alive seedlings (SD)	% cover surrounding dead seedlings (SD)
Asplenium auritum Sw.	0.6 (2.9)	0.5 (4.1)
Asplenium cristatum Lam.	0.1 (1.1)	0
Blechnum occidentale L.	0.6 (3.3)	0.2 (1.3)
Blechnum polypodioides Raddi	0.4 (2.4)	0
Campyloneurum phyllitidis (L.) C. Presl	1.3 (5.6)	0.8 (5.3)
Cestrum auriculatum L'Hér.	3.3 (8.7)	11.3 (15.6)
Chiococca alba (L.) Hitchc.	0.5 (3.5)	0
Commelina diffusa Burm. f.	0.7 (4.6)	0.2 (1.8)
Conyza bonariensis (L.) Cronquist	0.1 (1.1)	0.4 (4.6)
Doryopteris pedata var. palmata (Willd) Hicken	0.2 (1.5)	0.1 (0.9)
Galium galapagoense Wiggins	0	0.4 (3.8)
Ichnanthus nemorosus (Sw.) Döll	1.2 (5.7)	0.9 (3.9)
Paspalum conjugatum Bergius	1.1 (6.8)	0.1 (0.9)
Passiflora colinvauxii Wiggins	0	0.7 (7.3)
Peperomia inaequalifolia Ruiz & Pav.	0.4 (2.4)	0.2 (2.0)
Pilea baurii Robinson	3.6 (10.3)	3.7 (8.9)
Psidium guajava L.	0.4 (3.3)	0
Psychotria rufipes Hook. f.	0	0.2 (1.3)
Pteris quadriauriata Retz.	0.1 (1.1)	0.1 (0.9)
Rubus niveus Thunb.	5.1 (11.7)	0.5 (2.5)
Scalesia pedunculata Hook. f.	1.2 (4.2)	0
Sida rhombifolia L.	0	0.1 (0.9)
Solanum americanum Mill.	0.6 (2.9)	0.8 (4.9)

Tetramerium nervosum Nees	2.9 (9)	10.9 (14.8)
Thelypteris conspersa (Schrad.) A.R.Sm.	0.2 (2.2)	0
Thelypteris hispidula (Decne.) C.F. Reed	0	0.1 (0.9)
Thelypteris tetragona (Sw.) Small	0.6 (2.4)	0
Tournefortia rufo-sericea Hook. f.	0.4 (3.3)	0
Tradescantia fluminensis Vell.	25.9 (37.7)	8.6 (24.3)
Tradescantia zebrine hort. ex Bosse	0	0.2 (1.3)
Vallesia glabra (Cav.) Link	0.2 (2.2)	0

S2 Table: Average and maximum growth of *S. pedunculata* saplings and young trees over time.

Observation period	Average growth (cm)	SD average growth	Max. growth (cm)	Daily average growth (cm)	Sample size (n)
Apr 2015 – Jul 2015	46.7	36.2	220	0.51	146
Jul 2015 – Feb 2016	62.5	41.3	206	0.29	60
Feb 2016 – Aug 2016	66.6	56.2	239	0.35	46
Aug 2016 – Mar 2017	30.5	38.3	111	0.14	45
Mar 2017 – Jan 2018	49.4	49.1	119	0.18	30
Jan 2018 – Apr 2019	33.0	62.9	165	0.07	21
Apr 2019 – Mar 2020	32.6	56.0	110	0.10	13
Apr 2015 – Mar 2020	457.6	161.2	733	0.25	13

Manuscript 6

Castanea sativa tree and fruit amidst ash and tephra depositions in the vicinity of the new volcano *Tajogaite* on La Palma, Canary Islands. © Anna Walentowitz

Summary

The emergence of novel ecosystems is a phenomenon of the Anthropocene (Hobbs *et al.* 2009, 2013; Morse *et al.* 2014; Collier & Devitt 2016). On La Palma (Canary Islands), non-native sweet chestnut (*Castanea sativa*) forest patches are partly replacing the unique laurel forest, that comprises high numbers of endemic species. The deciduous phenology of sweet chestnut trees in contrast to an evergreen island flora make the species highly suitable for detection via remote sensing. We model the potential distribution of sweet chestnut based on occurrence data from remote sensing and field work within the island of La Palma and assess potential consequences for the native flora.

Assessing the Potential Replacement of Laurel Forest by a Novel Ecosystem in the Steep Terrain of an Oceanic Island

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Remote Sensing (2020) 12, 4013

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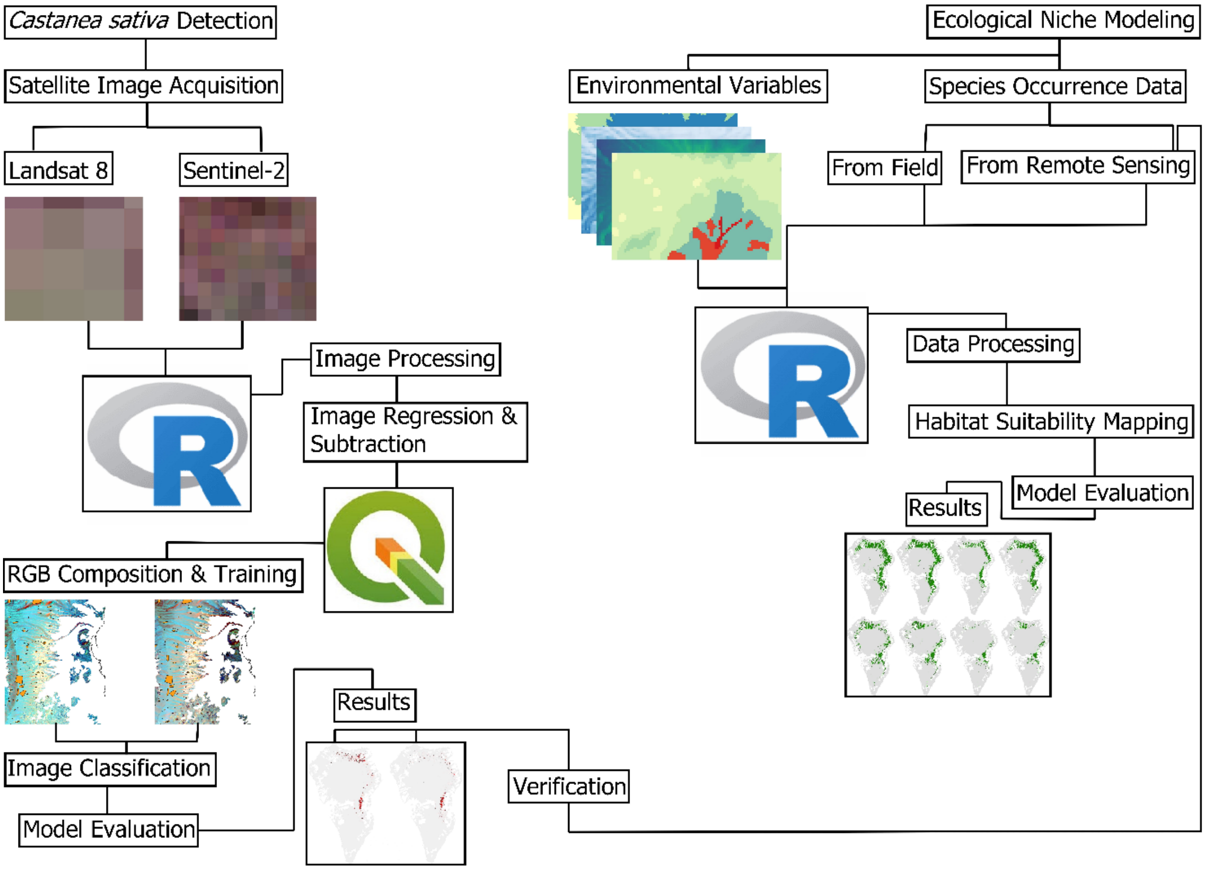
Graphical abstract



Abstract

Biological invasions are a major global threat to biodiversity and often affect ecosystem services negatively. They are particularly problematic on oceanic islands where there are many narrow-ranged endemic species, and the biota may be very susceptible to invasion. Quantifying and mapping invasion processes are important steps for management and control but are challenging with the limited resources typically available and particularly difficult to implement on oceanic islands with very steep terrain. Remote sensing may provide an excellent solution in circumstances where the invading species can be reliably detected from imagery. We here develop a method to map the distribution of the alien chestnut (*Castanea sativa* Mill.) on the island of La Palma (Canary Islands, Spain), using freely available satellite images. On La Palma, the chestnut invasion threatens the iconic laurel forest, which has survived since the Tertiary period in the favourable climatic conditions of mountainous islands in the trade wind zone. We detect chestnut presence by taking advantage of the distinctive phenology of this alien tree, which retains its deciduousness while the native vegetation is evergreen. Using both Landsat 8 and Sentinel-2 (parallel analyses), we obtained images in two seasons (chestnuts leafless and in-leaf, respectively) and performed image regression to detect pixels changing from leafless to in-leaf chestnuts. We then applied supervised classification using Random Forest to map the present-day occurrence of the chestnut. Finally, we performed species distribution modelling to map the habitat suitability for chestnut on La Palma, to estimate which areas are prone to further invasion. Our results indicate that chestnuts occupy 1.2% of the total area of natural ecosystems on La Palma, with a further 12–17% representing suitable habitat that is not yet occupied. This enables targeted control measures with potential to successfully manage the invasion, given the relatively long generation time of the chestnut. Our method also enables research on the spread of the species since the earliest Landsat images.

Keywords: invasive species; island ecology; assisted migration; laurel forest; plant functional type; deciduous trees; species distribution models; Landsat 8; Sentinel-2; *Castanea sativa*

1 | Introduction

Oceanic islands play an eminent role in speciation and endemism [1], and they contribute disproportionately to global biodiversity relative to their small area [2]. Their isolation, aggregation in archipelagos, island life cycles, relief dynamics, climate, topography, and natural and anthropogenic disturbance regimes produce and maintain a high diversity of biota and the respective ecosystems formed by those species [3]. Oceanic islands are often seen as evolutionary showcases [4] prone to pulse dynamics [5] or as evolutionary arenas [6], where speciation can be studied. However, the uniqueness of their flora, fauna, and ecosystems is also related to the fact that they host relict species and ecosystems, such as the evergreen laurel forest in the Canary Islands including our study region: the entire island of La Palma [7].

Endemic ecosystems (i.e., specific ecosystems that are characterized and dominated by species with a very limited spatial distribution) are particularly threatened by species invasion [8–11]. Invasive species are species that establish in new, non-historical ranges and are harmful to their environment [12]. They can decrease native species abundances via competition, predation, parasitism, and alteration of habitat conditions, causing a loss of biodiversity, ecosystem functioning, and services [13]. Invasive species often cause huge economic costs for society [14]. The abundance of invasive species was recently found to have increased by up to 70% across 21 countries since 1970 [15]. The focus of invasion research is mostly on prominent single species of well-known invasion potential, such as *Lantana camara* or *Ailanthus altissima* [16,17]. Non-native woody species are disproportionately represented among the most severe invaders around the world [18], and escapes of tree species from plantations have been highlighted as a particular problem [19]. Chestnut (*Castanea sativa* Mill.) (Fagaceae) is a widespread deciduous tree species across Europe, often managed for fruit and wood production. It is also an important species for apiculture and historically has had other uses such as in tanning and pig farming [20]. The species was introduced to La Palma as early as 1493 [21] and managed in orchards, most of which are abandoned today. Observations of local authorities suggest that the species is increasingly establishing in natural, evergreen forest ecosystems—*C. sativa* is the agent of change in the ongoing replacement of a native ecosystem by an ecosystem that did not previously exist on La Palma. Such a deciduous broadleaved forest, with pronounced seasonal leaf phenology, is a novel ecosystem in the context of the Canary Islands.

Remote sensing (hereafter abbreviated to RS) has been used for almost 65 years in vegetation science [22]. However, ecological studies from space only began after the launch of Landsat 1 in 1972 [23]. In many cases, RS is the only feasible method for measuring the characteristics of habitats across broad areas and for detecting environmental changes that occur as a result of human or natural processes [24]. It is becoming increasingly popular among conservationists and ecologists. Satellite-based data have a wide range of applications in ecological studies, including mapping of plant communities and also single plant species [25]. A recent study on La Palma used a time series of Sentinel-2 images to identify plant communities and measure beta-diversity [26].

Remote sensing is advancing invasion research and management by detecting and mapping invasive species, their drivers, and potential future distributions [27,28]. Differences in structural, biochemical, and physiological characteristics between species can make it possible to distinguish invasive plant species from native co-occurring vegetation by their spectral signatures [29]. However, there are limits to this if invasives and natives share comparable reflection spectra. If phenological differences between species exist, these can play a key role in identifying invasive species within native vegetation by RS [30]. To detect seasonal phenological differences between plant species, multitemporal RS data are required, for instance, provided by spaceborne Landsat and Sentinel sensors. The timing of RS acquisition is crucial for the detection of phenologically differentiated species. Accordingly, Evangelista et al. [31] used six Landsat 7 ETM+ satellite scenes across the growing season to remotely sense the evergreen *Tamarix* species invading native deciduous vegetation along the Arkansas River in Colorado, USA.

Slight differences in seasonal phenology can be sufficient to monitor invasive plant species but may require hyperspectral airborne sensors to detect them, with the trade-off of high costs [32]. Such hyperspectral approaches and time series can help to identify invasive plant species even in non-seasonal climate and ecosystems, as demonstrated by Asner et al. [33], who detected the invasive evergreen shrub *Myrica faya* Dryand. (syn. *Morella faya* Aiton) in Hawaiian rainforests. However, that study used EO-1 Hyperion satellite data, and this satellite (and sensor) has been decommissioned and is no longer available.

Generally, the potential to detect invasive species remotely increases with finer spectral, spatial, and temporal resolution of RS imagery [34]. Tarantino et al. [17] showed the potential of multi-seasonal panchromatic WorldView-2 satellite imagery for mapping the deciduous tree *Ailanthus altissima* (Mill.) Swingle, invading a protected area in Southern Italy. In this case, the detection of the invasive tree species was enhanced by the contrast with the grass cover of the invaded ecosystems, as well as the multitemporal, multispectral, and very high-resolution satellite imagery. Even if there is a follow-up satellite (WorldView-3) after the soon-expected end of the lifetime ofWorldView-2, the data are not freely accessible, limiting their use for conservation practice and for comparative studies. Free and open-access RS data provide unlimited use but come at the expense of relatively coarse spatial, spectral, and temporal resolution.

Remote sensing also supports invasion research and management indirectly by providing RS data for species distribution and habitat suitability models [27,30]. Vicente et al. [35] were able to map the current and predict the future distribution of the invasive tree species *Acacia dealbata* Link in northern Portugal using remotely sensed predictor variables. In contrast to species distribution models, ecological niche modelling and habitat suitability mapping aim to reveal the potential distribution of a species by applying interpolation between known species occurrences. Such modelling techniques and resulting maps aim to guide conservation management and planning [36]. Andrew and Ustin [37] modelled the habitat suitability of the noxious pepperweed (*Lepidium latifolium* L.) invading San Francisco Bay/Sacramento-San Joaquin River Delta, California, USA. Species presence was derived from airborne HyMap hyperspectral imagery and environmental predictors from LiDAR. Accordingly, RS-based modelling approaches can map and predict rapid range expansions of invasive species by monitoring invasive species' ecological niches [38].

The free availability and global coverage of RS data are beneficial for comparative studies, and for improving the quality of other study outcomes. Result validation and quality control are particularly important for studies of moving targets with enormous impact potential, such as invasive species. Based on the known benefits and limits of RS applications in invasion research, and considering options for compatibility with future studies, we use multitemporal and multispectral Landsat 8 and Sentinel-2 satellite imagery combined with field observations of *C. sativa* to investigate the current and potential future distribution of the species on the Canary island of La Palma. We used linear image regression [39] and random forest classification [40] to detect *C. sativa* and map its current spatial distribution. As the very steep and unstable slopes limit the extent of field surveys on La Palma, we utilized *C. sativa*'s distinctive phenology to map its current spatial distribution through RS. We then conducted and compared ecological niche models (hereafter ENM), also known as habitat suitability models, based on field observations of *C. sativa* and on remotely sensed *C. sativa* occurrences. This study thus aims to detect and map the invasive alien chestnut tree *C. sativa* on the island of La Palma and to assess the risk of the species replacing native and unique ecosystems such as the evergreen laurel forest of the Canary Islands.

We build on previous studies on the detection of invasive plant species through RS, aiming to improve RS-based assessments of invasive plant species not only through comparing the sensitivity of commonly used sensors that offer open RS data (Landsat/Sentinel) but also, and particularly, through linking modelling approaches with RS and with field data. This approach also allows better assessment of existing invasions using long time series. Additionally, we identify new potential for future invasion research. Combining RS and SDMs can provide testable predictions for future invasion processes under climate change. Finally, our study is the first using RS for a better understanding of tree invasion and its consequential impact on the unique laurel forest.

2 | Materials and Methods

2.1 | Study Site and Field Data

La Palma, also known as “la isla verde” or “la isla bonita”, is one of the highest and western-most islands of the Canary Islands archipelago. Large surfaces of the island are still covered by natural and semi-natural vegetation. The steep slopes in the northeast of the island are exposed to constant moisture supply by trade winds. Here, natural laurel forests are found on steep, almost inaccessible slopes (Figure 1). This ecosystem covered large parts of the northern hemisphere during the Tertiary period, as indicated by fossil records of preserved tree leaves in lignite all over Europe [41]. Today, comparable climatic conditions to the zonal climate of the Miocene (i.e., constant moisture supply and warm temperatures) exist on some oceanic islands of sufficient elevation in the trade-wind zone, including La Palma.

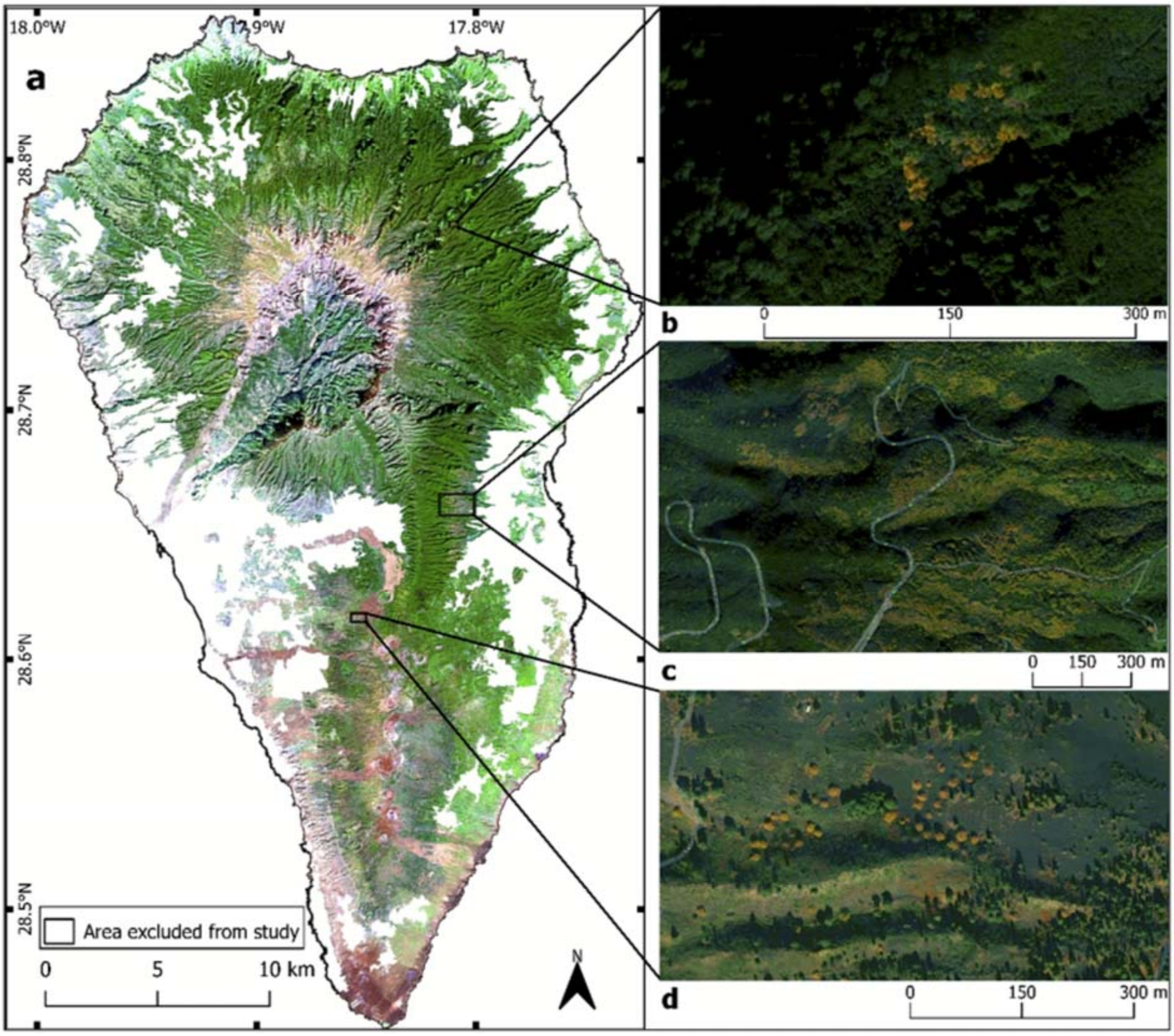


Figure 1: (a) Sentinel-2 true natural colour image of the study area (Red: band 4, Green: band 3, Blue: band 2). (b–d) are Google satellite zooms of characteristic landscape units. Trees with yellow canopy in the boxes (b–d) represent single trees, groups or patches of *C. sativa*.

Despite the strong resemblance in the climate, vegetation structure, and characteristic laurophyllous plant functional types between the present-day Canary Islands and the Tertiary period, the current Canary Island laurel forest is not a simple copy of a Tertiary biome. The current laurel forest species composition of the Canaries that established since the Pliocene is an assemblage of taxa that differ in origin [42]. Very likely, oceanic islands that have since eroded to guyots (seamounts) served as stepping-stones of suitable habitat for species dispersal closer to the European continent [43].

However, the laurel forest of the Canary Islands has been strongly reduced through exploitation since the European colonization [44]. Most remnant areas are on steep slopes, where access for forestry is restricted, if not impossible—but this restriction also applies to scientific field work. In consequence, RS approaches, although themselves not free from limitations associated with steepness and cloudiness, need to be implemented for data collection within and across steep valleys, slopes, and remote ridges.

In situ recording of mature individuals of *C. sativa* in the field was conducted during 10–24 April 2019. We mapped individual trees, recording GPS points for each. The sampling aimed to cover the entire range of the species on the island. This, combined with limited available time in the field and the restricted accessibility to many parts of the range because of very steep and remote terrain, meant that we mostly collected data relatively close to roads. To maximize data collection in these circumstances, we planned the field data acquisition based on previous studies on the island, both by members of our team and through the expertise of the local administration (Cabildo Insular de La Palma).

2.2 | Change Detection

Deciduous tree species have a distinct phenological cycle with synchronous leaf flush in spring and leaf shedding in autumn. In *C. sativa* on La Palma, this rhythm is presumably maintained and triggered by the photoperiod, even though harsh winter temperatures are missing, and the evolutionary driver of leaf shedding is no longer effective. In consequence, *C. sativa* can be mapped in a matrix of evergreen vegetation through digital change detection. Its most distinctive stage is its leaflessness between autumn and spring, making it a unique species in the otherwise evergreen ecosystem. To map *C. sativa*, we can therefore take advantage of the much larger change between seasons, in satellite images, in places where chestnut is (in-leaf vs. leafless) than in places where it is absent (in-leaf throughout)—making change detection through image regression appropriate for this purpose. We use image regression with the Landsat 8 images from 7 March and 29 July 2017, and with the Sentinel-2 images from 8 July 2018, and 13 February 2019 (Appendix A). By applying change detection to a pair of Landsat 8 images and to a pair of Sentinel-2 images, we can compare the detection performance of the two sensors.

Landsat 8 and Sentinel-2 surface reflectance data were obtained from USGS and Copernicus Open Access Hub. The Landsat 8 surface reflectance data are orthorectified data generated at 30 m grid cell resolution. The data are free from any atmospheric artefacts, illumination, and viewing geometry bias [45]. Similarly, the Sentinel-2 data are geometrically, radiometrically corrected, orthorectified, and spatially registered bottom-of-the-atmosphere reflectance products that are generated at 10, 20, and 60 m spatial resolutions [46]. Therefore, no further pre-processing of the images was carried out for those parameters. However, the part of the Landsat 8 image from March 2017 that contained clouds was cropped out with the help of Quality Assessment band shipped with the Landsat 8 surface reflectance product and compensated with an image from 3 February 2017 after histogram matching in R using the package RStoolbox [47]. A few cloud-contaminated pixels were left around the edges. The areas classified as agriculture and settlements by Corine land cover data 2018 were cropped out. Therefore, our study area, as calculated in R using the study area shapefile, covers approximately 545.82 km^2. The Sentinel-2 images used in this study are of 10 m spatial resolution.

Several techniques are used for digital change detection [39,48]; we chose image regression and differentiation for our analysis. Image regression does not need training data and can reduce atmospheric haze and sun angle effect [39]. Change detection, when used on its own, relies on thresholds to discern changed and unchanged pixels. Therefore, we integrated digital change detection with supervised classification, to avoid thresholds. The image regression technique assumes that the pixel values at time t1 are linear functions of the pixel values from time t2. Therefore, an image from one date can be regressed against the image from another date using least-squares regression [39,48].

Here, we used four different bands (blue [B], green [G], red [R], and near-infrared [NIR]) from each sensor, which we refer to as band 1, band 2, band 3, and band 4, respectively. Therefore, $t1_1^n$ is the image from the date 1 with n = 4 spectral bands, and $t2_1^n$ is the image from date 2 with the same number of spectral bands. We considered the image from one date to be a linear function of the image from the other date. Therefore, the image from date 1 was regressed on the image from date 2. We arbitrarily assigned the images from July as date 1.

$$t1_1^n = a + b\, t2_1^n + e \tag{1}$$

where a is intercept, b is slope, and e are the residuals.

If y_1^n is the predicted image on the image $t2_1^n$ from the regression line in the Equation (1), the changed image can be obtained by

$$d_1^n = y_1^n - t1_1^n \tag{2}$$

where d_1^n is the subtracted image from band 1 to *n*.

However, the change in pixels in the images obtained from the Equation (2) were not easily visible and discernible. The NIR band reflects more light from healthy vegetation than from stressed vegetation. Therefore, the NIR bands were subtracted from the red bands in the respective images obtained from the Equation (2).

$$D = d_3 - d_4 \tag{3}$$

where, D is the resulted change image.

Finally, the raster results were created using the band composition of *D*, d_3 and d_2, respectively, to obtain the changed pixels between two dates. Changed pixels gained from the image regression and image differentiation were compared with Google Earth images and field data.

2.3 | Random Forest Classifications

The supervised classification algorithm Random Forest (RF) was applied in this study to extract the *C. sativa* present spatial distribution. RF is a machine learning algorithm that works on bagging approaches: The algorithm grows multiple decision trees from the random subsets of data and gives a final decision based on the majority of votes from the resulting trees [40]. The algorithm has been reported to produce promising results [49].

The changed pixels may not all be associated with *C. sativa*. Therefore, *C. sativa*, forests and natural ecosystems were trained in QGIS based on the field reference data (Appendix B) and Google Earth images were taken as references. For the training data, the raster data obtained in Figures 2 and 3 were used to discern changed pixels (*C. sativa*), and unchanged pixels (forests and other natural ecosystems). The data were split into training and testing data in the ratio of 70% to 30% for each changed image from Landsat 8 and from Sentinel-2. The data used to train the model were cross-validated with ten-fold cross-validation. Supervised classifications were carried out in R with the caret [50] package on the images obtained from the image regression and image subtraction that include five bands as a stack. In the RF models, 650 trees were grown for each supervised classification—the out of bag error in the random forest classification reached a low level at 650 trees and was near-constant with more. The models were validated using the respective testing data (Appendix C).

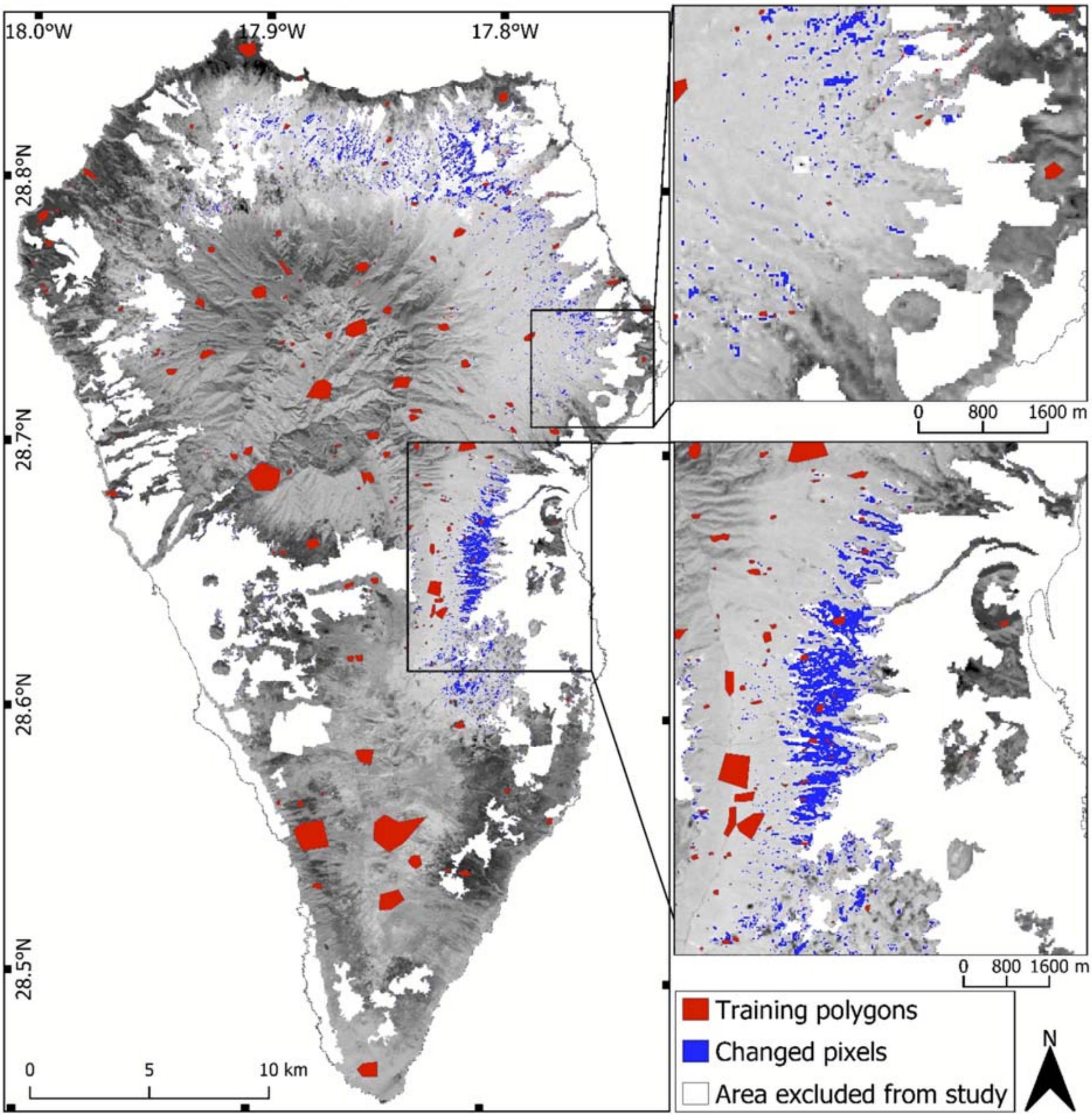


Figure 2: Changed pixels (proxy for leaf on/leaf off) between March 2017 and July 2017 in the Landsat 8 image obtained from the image regression and image differentiation, grayscale raster composite, red-NIR, red, green, each band with 1/3 saturation. Blue colour highlights changed pixels between those dates. Training polygons (red) are the training samples used to discriminate between changed and unchanged pixels. Settlements and other intensive human land-uses were cropped out (shown in white).

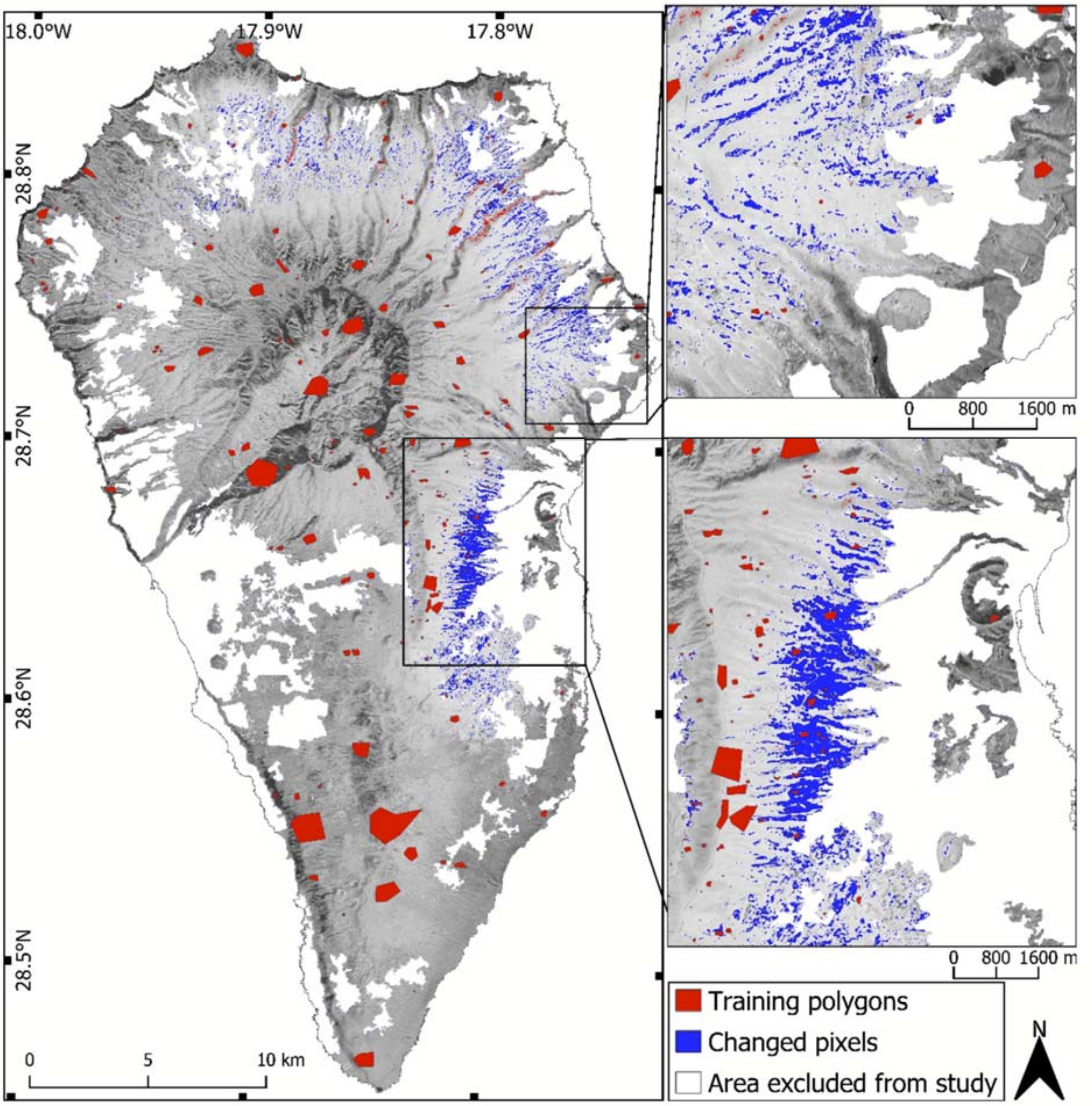


Figure 3: Changed pixels (proxy for leaf on/leaf off) between July 2018 and February 2019 in the Sentinel-2 image obtained from the image regression and image differentiation, grayscale raster composite, red-NIR, red, green, each band with 1/3 saturation. Blue colour highlights changed pixels between those dates. Training polygons (red) are the training samples used to discriminate between changed and unchanged pixels. Settlements and other intensive human land-uses were cropped out (shown in white, excluded from study).

2.4 | Ecological Niche Modelling

Castanea sativa occurrence and coverage were recorded and mapped in the field from 11 April to 23 April 2019, mainly using road access. The sampling was conducted based on expert knowledge, and the change detection map (Figures 2 and 3) as well as through random *C. sativa* observations. The Global Positioning System (GPS) locations were recorded in the field for presence locations (Appendix B) using a WPL-2000 GPS device.

We retrieved a set of biotic and abiotic environmental variables from Cabildo Insular de La Palma, modified from [51]. Topographic information on aspect and slope was calculated in QGIS from the 2 m spatial resolution digital elevation model obtained from [52]. All environmental variables had a spatial resolution of 100 m except elevation, slope, and aspect; we aggregated the resolution of these to 100 m. After performing a correlation analysis on the entire set of environmental variables (r > 0.7, Appendix D), the following explanatory variables for ENMs remained: winter precipitation, summer precipitation, inter–annual precipitation, intra-annual precipitation, vegetation associations, solar radiation, elevation, slope, aspect, and parent materials (Appendix E). The mean annual temperature was highly correlated with elevation (r > 0.7), and mean annual precipitation was highly correlated with mean winter precipitation (r > 0.7) (Appendix D). We excluded mean annual temperature because La Palma possesses a high altitudinal gradient, and thus, the temperature difference is a major function of elevation even if aspect also plays a role due to differences in cloud cover and insolation. Similarly, mean annual precipitation was excluded because the precipitation exhibits a clear seasonal pattern with high amounts during winter and less precipitation in summer. From an ecological perspective, the variation in precipitation was a better choice to characterize habitat suitability of *C. sativa* compared to annual mean precipitation.

For the ENMs, both species occurrence data from the field and from RS were used independently. We used R version 3.6.1 [53] and Quantum GIS (QGIS) version 3.6.3, as well as Google Earth applications. To obtain a habitat suitability map for *C. sativa*, we applied generalized additive models (GAMs), Maximum Entropy (MaxEnt) and Random Forest (RF), combining them into an ensemble model (EM) using biomod2 [54] (see results for each model algorithm in Appendix F). GAMs are data-driven, slightly modified regression models that use non-parametric, data-defined smoothers to fit nonlinear functions. GAMs are capable of modelling complex ecological response shapes [55,56]. MaxEnt is designed to estimate target probability distributions by finding the probability of maximum entropy [57]. The algorithm is extensively used in ENMs [58], but there are limitations when data are missing at the edges of species' distributions. In consequence, we opted for an EM, in order to obtain more robust outcomes than likely to be delivered by an individual modelling technique [59].

We randomly extracted 2500 RS species occurrence points from the area where spatial agreements in the resulting maps between both images were found. Data obtained were thinned with minimum spatial distances of 300 m and 100 m for RS data and field data, respectively, using spThin [60] package in R, to avoid spatial bias. We used 300mfor RS data thinning and 100mfor field data thinning because the RS data were uniformly rasterised, and field data were clumped due to inaccessible field sites. Applying 300 m in field data would result in far fewer species occurrences. The rationale for a 100 m minimum distance is that the environmental raster data that we used has a spatial resolution of 100 m. Hence, we wanted to avoid more than one species occurrence point in a single pixel. Final numbers of 241 and 172 occurrence points of RS and field, respectively, were used for modelling. With the biomod2 [54] package in R, the three different modelling approaches (GAMs, MaxEnt, and RF models) were integrated for the EMs. We generated the same number of pseudo-absence points as presence, taking prevalence into account [61,62] and excluding the area buffered by a 30 m radius from the species' occurrence points. The models were each run four times, with ten sets of pseudo-absence records that resulted in 120 models in total for each data set (field-collected species occurrence data and RS species occurrence data).

For EM projections, only models meeting the quality standards of total true skill statistic (TSS) > 0.7 and area under the receiver operating characteristic curve (AUC) > 0.8 were used. Individual models that did not meet these requirements were excluded from building the EM—including all the GAM and MaxEnt models [Appendix G]. Our resulting EMs were based on 50 and 34 single models for RS and field occurrence data, respectively. Mean of the weighted sum of probabilities, committee average across prediction, and mean probabilities across prediction of the ensemble forecasts were used to generate the suitable habitat map for *C. sativa*.

Receiver operating characteristic curve cut-offs that maximized the sum of specificity and sensitivity were used as the threshold to generate species habitat suitability (binary) maps. The binary maps were used to quantify the suitable habitat for *C. sativa* from each modelling approach and to analyse the variation in those areas with respect to the environmental variables used for the models.

3 | Results

3.1 | Change Detection

C. sativa occurrence locations detected by RS and in the field (Appendix B) had strong spatial agreements with the changed pixels (Figures 2 and 3), and model accuracy was high (Table 1). Additional pixels were also detected as changed pixels. However, they were ambiguous and were not distinguishable from other vegetation or attributes in the Google Earth reference image, and those locations were also not available from field data. Such ambiguities may have resulted from land-cover changes rather than from changes that occurred because of *C. sativa*'s phenological cycle.

Table 1: Statistical evaluation of Random Forest (RF) performance and map accuracy assessment. The overall accuracy and kappa were obtained from the testing data and the out-of-bag error (OOB) generated by RF of each of the model obtained from training data.

Sensors	**Parameters**		
	OOB Error %	Overall Accurary %	Kappa
Landsat 8	1.29	98.8	0.798
Sentinel-2	0.44	99.5	0.879

The different sensors resulted in different areas of spatial coverage of *C. sativa* (Figure 4). The total coverages of *C. sativa* found in 2019 were 5.26 km2 in the Sentinel-2 and 6.72 km2 in the Landsat 8 images, which make 1% and 1.23%, respectively, of the total island area. Most of the detected occurrences of chestnut were from the eastern slopes and northern parts of the island. Only a few occurrences were detected on the southern slopes (Figure 4). Most of the occurrences were close to agricultural land and some were on lapilli fields. No *C. sativa* occurrences were detected in southern parts and coastal areas of the island. The *C. sativa* occurrence pixels in the Sentinel-2 are more scattered than in the Landsat 8 image (Figures 4 and 5). Even in the area where both sensors spatially agree, Landsat 8 was found to have a wider coverage than Sentinel-2 (Figure 5).

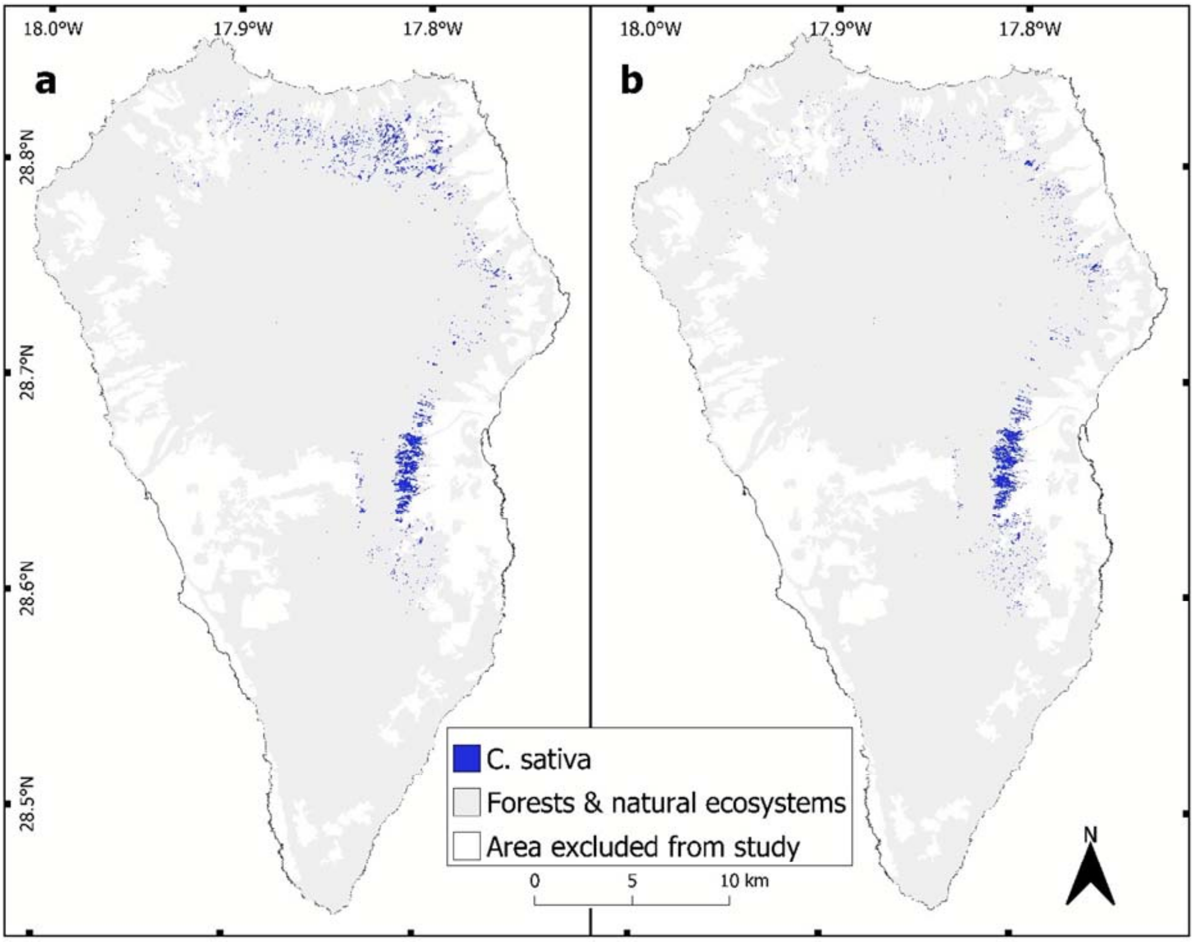


Figure 4: *C. sativa* spatial coverage (blue) detected on (a) the Landsat 8 image and (b) Sentinel-2 image obtained from the Random Forest (RF) classifications. The classifications were carried out on the images obtained from the image regression and differentiation. 'Forests and natural ecosystems' (grey shading) are land cover not related to direct human land use. Settlement and agriculture (areas used for direct human purposes, including roads, buildings, agricultural lands, etc.) were cropped out and not included in the analysis.

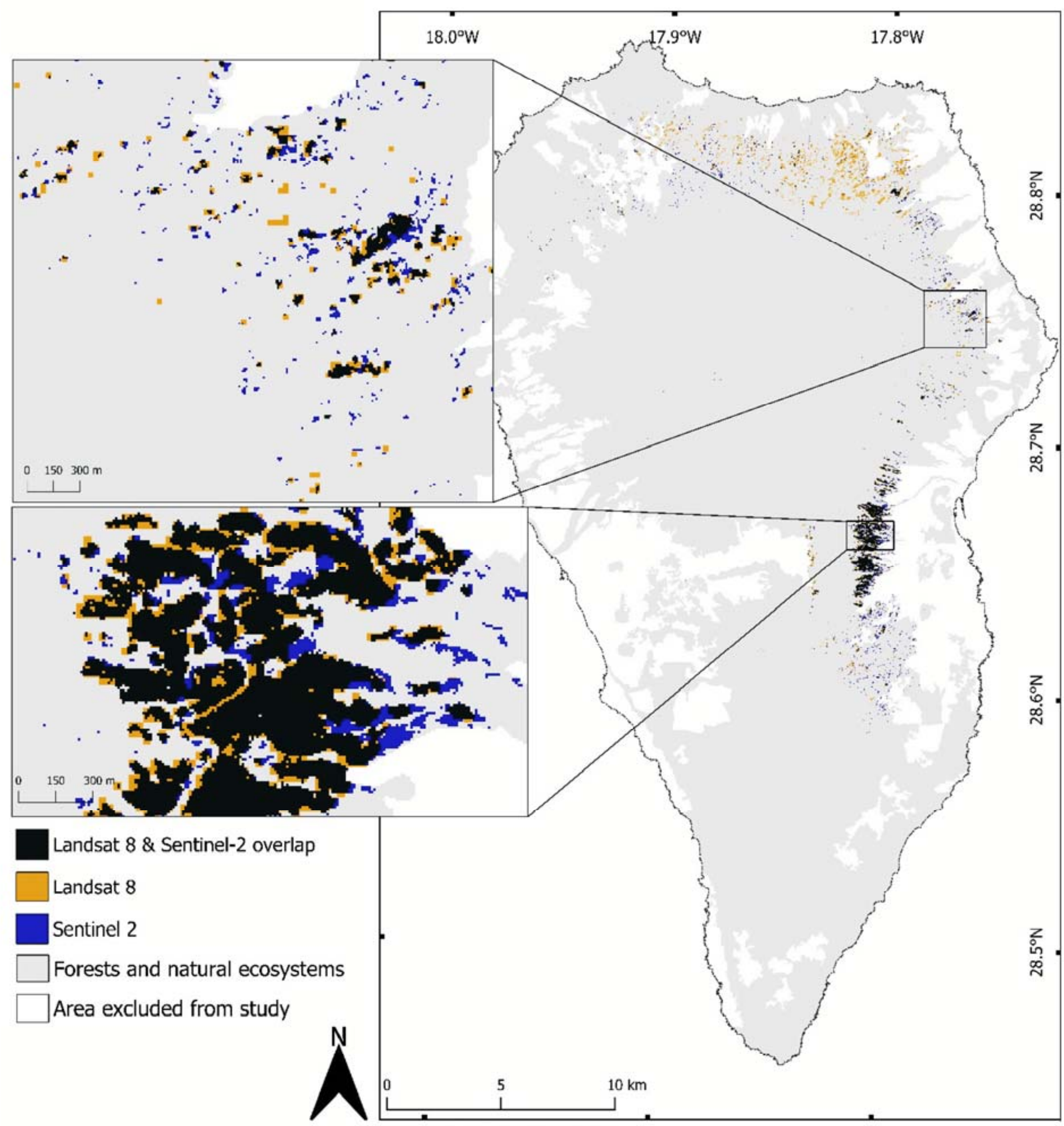


Figure 5: *C. sativa* spatial coverage in the images from the Landsat 8 and Sentinel-2 overlapping, Landsat 8 only, and Sentinel-2 only. Black are pixels where *C. sativa* was detected in both sensors' images; orange are pixels where *C. sativa* was only detected in the Landsat 8 image; blue are pixels where *C. sativa* was only detected in the Sentinel -2 image. The spatial resolution of Landsat 8 is 30 m, and Sentinel-2 is 10 m. 'Forests and natural ecosystems' (grey shading) are areas not directly used for human purposes. Human settlements, infrastructure, and agriculture (white) were cropped out.

Spatial coverage of *C. sativa* increases progressively from 400 m a.s.l. to 700 m a.s.l. and decreases above 700 m a.s.l. in the images from both the sensors (Figure 6).

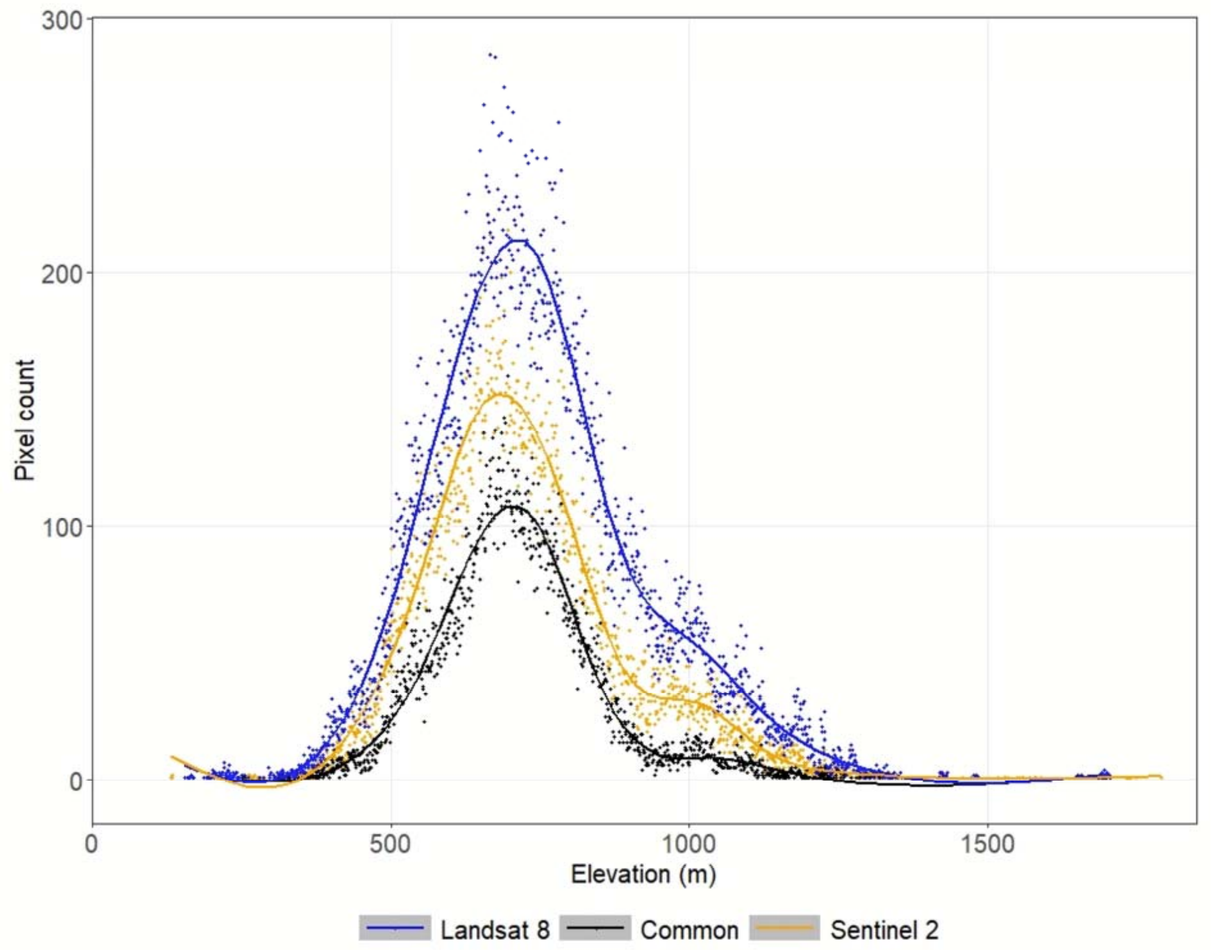


Figure 6: Number of pixels associated with *C. sativa* detected from RS along the altitudinal gradient. Values along the y-axis are the total number of pixels covered by *C. sativa* and values along the x-axis are the elevational gradient of La Palma (in m a.s.l.). Blue: Landsat 8 only; orange: Sentinel 2 only; black: shared pixels of both Landsat 8 and Sentinel-2. The spatial resolution of Landsat 8 was disaggregated to 10 m for comparison purpose.

3.2 | Ecological Niche Modelling

All ENMs showed that habitats in the eastern and northern parts of the island—including the areas of present distribution—were more suitable for *C. sativa* (Figures 7 and 8, Appendices F and H for single model results). The ENMs based on species occurrences from field observation and the ENMs based on species occurrences from RS data were found to have very good AUC and TSS scores (Table 2 and Appendix I). The ENMs based on the RS data (Figures 7b and 8b) predicted larger suitable area for *C. sativa* compared to the prediction made by the models based on the field-collected species occurrence data (Figures 7a and 8a). However, the models based on the field-collected species occurrences seemed to cover more heterogeneous areas, even though the total suitable area for the species was predicted to be less in the field-collected species occurrence-based models.

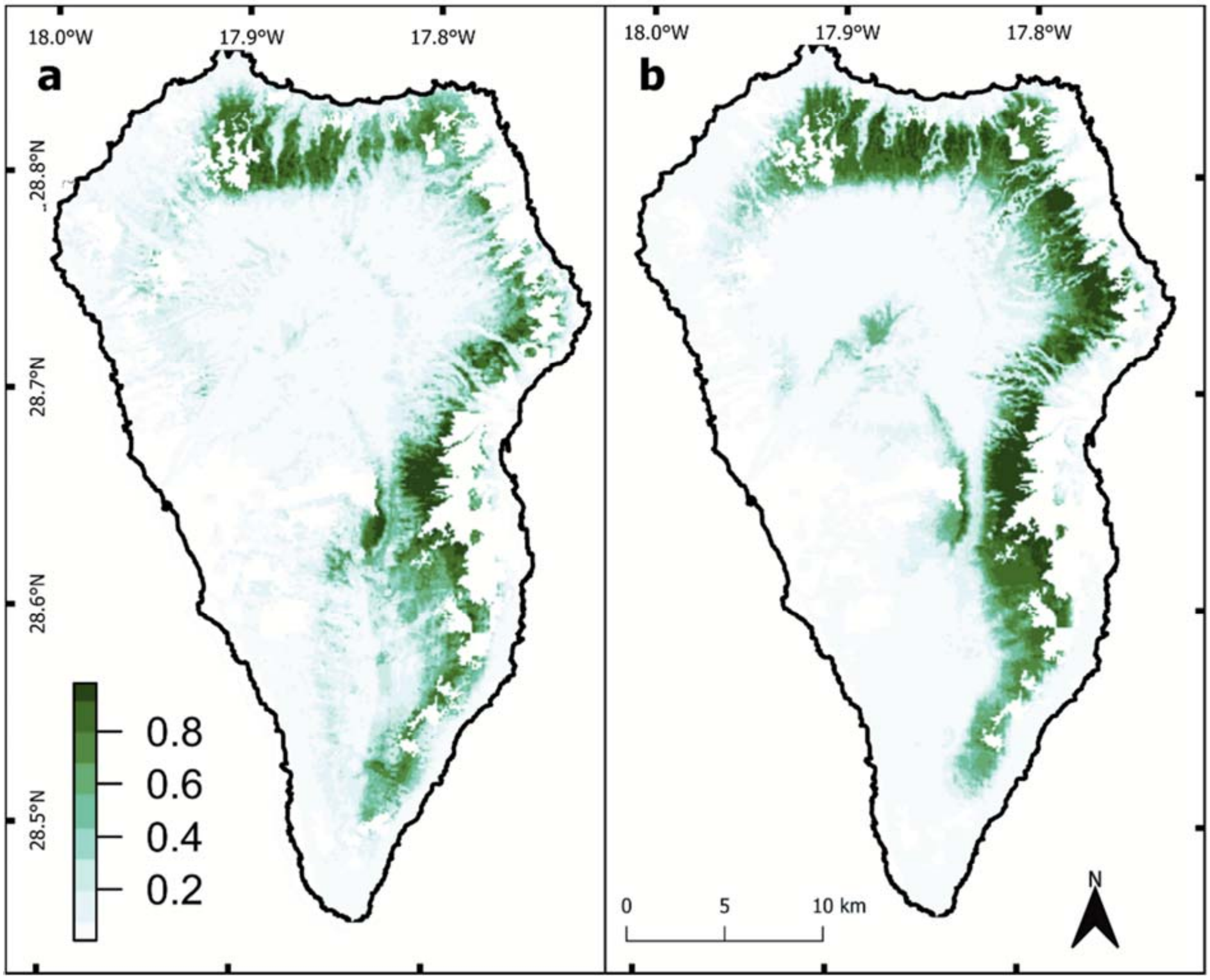


Figure 7: *C. sativa* habitat suitability maps obtained from the ecological niche modelling (ENM) using ensemble models (EM). (a) The map obtained from the model based on field-collected species occurrence data. (b) The map obtained from the model based on the species occurrence data derived from remote sensing. The vertical legend on the bottom-left shows the degree of suitability; values closer to 1 indicate comparatively higher habitat suitability.

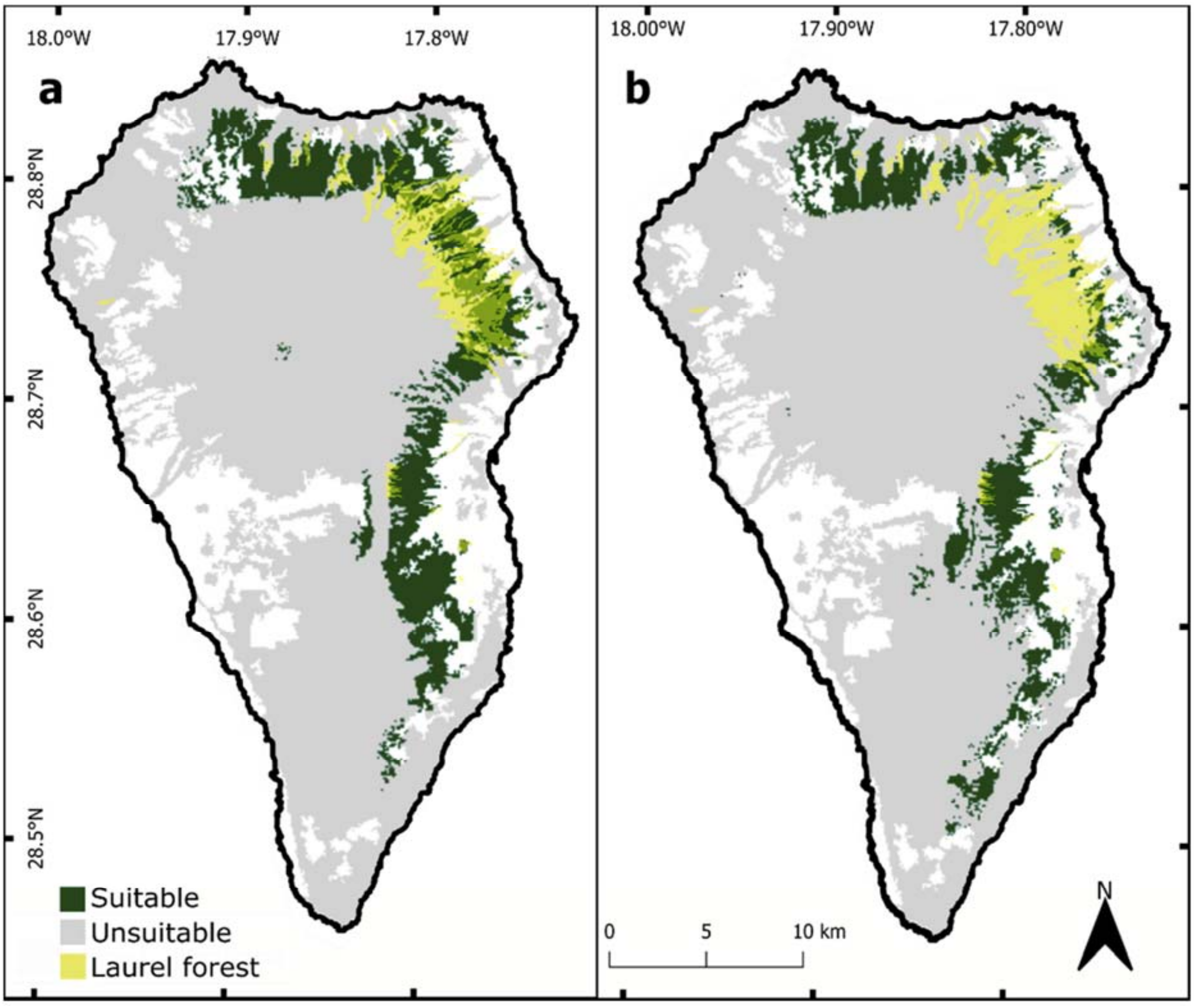


Figure 8: *C. sativa* binary habitat suitability maps from (a) the ensemble model (EM) based on the field-collected species occurrence locations, and from (b) the EM based on RS-derived species occurrence locations. These maps are the outcomes of the binary transformation of the predicted maps from the respective models. The extent of the laurel forest (based on the plant communities defined by Del Arco Aguilar et al. [63]) is indicated as a yellow semi-transparent layer.

Table 2: Statistical parameters of model performances, thresholds applied to convert maps resulted from each modelling approach to binary maps and area suitable for *C. sativa*. All the parameters are means of ensemble model outputs.

Parameters								
Model	AUC		Threshold		TSS		Area (km^2)	
	Field	RS	Field	RS	Field	RS	Field	RS
EM	0.982	0.961	564.83	634.42	0.885	0.805	66.73	90.12

4 | Discussion

This study assesses the current and potential distribution of non-native *C. sativa*, invading the endemic species-rich ecosystems of La Palma. The establishment of deciduous chestnut (*C. sativa*) on La Palma and its spread into the native laurel forest has the potential to initiate a secondary succession that may change the evergreen broadleaved forest towards a different ecosystem in terms of phenology and light regime. *C. sativa* was introduced on the island approximately 500 years ago for agricultural purposes [21]. Extremely steep and unstable slopes restrict access to the sites. Further, only estimating the current distribution of the alien species would be problematic because the current situation is just a snapshot of the potential occupied space and ecological niche on the island [64]. Therefore, it is important to combine in-situ and RS data with modelling approaches.

We found through this combined methodology that deciduous chestnut trees and forest today occupy approximately 1.2% of the total area of natural ecosystems (i.e., non-agricultural and excluding infrastructure and settlements) on La Palma, with a further 12–17% representing suitable habitat that is not yet occupied by this species. This is important because this non-native deciduous tree species can reach high canopy cover and has the potential to strongly modify the species composition of the original evergreen forest ecosystems, as well as the nature of the ecosystem (e.g., leafless in winter) and the services it provides. Comparing the current spatial distribution of *C. sativa* in La Palma obtained from RS and the results obtained from ENMs, we can see that *C. sativa* has not yet reached its full potential distribution on La Palma. Our results show varying areas of available suitable habitats for *C. sativa* that could be occupied in the future, depending on the reference data and modelling algorithm. However, in all cases, there is a considerable overlap of the species' niche with the distribution of the native laurel forest ecosystem in the eastern and northern slopes of the island.

Despite their southern location, the Canary Islands are clearly part of the Holarctic realm. Most of the plant families native to the islands are very abundant across the Mediterranean. In addition, the ecosystems of the archipelago are strongly linked to Mediterranean climate and ecosystems through their evolutionary history and phylogenetic relations. Although the Macaronesian islands have many endemic species, the perennial and woody taxa that shape the islands' forest and shrubland ecosystems are either shared with the Mediterranean region of Europe (native non-endemics on the Canaries) or in the case of endemic species have their closest relatives there, and not in the Palaeotropcis (e.g., *Laurus*, *Viburnum*, *Prunus*, *Pistacia*, *Olea*, *Arbutus*, *Asparagus*, *Cistus*, *Echium*, *Carlina*, *Genista*, *Helianthemum*, *Hypericum*, *Lavandula*, *Micromeria*, *Ononis*, *Rhamnus*, *Rubia*, *Ruscus*, *Salvia*, *Sideritis*, *Smilax*, *Sonchus*, *Thesium*). Several native ferns of the laurel forest are also abundant in moist forests of the Mediterranean (e.g., *Asplenium hemionitis*, *Selaginella denticulata*, *Adiantum capillus-veneris*, *Polystichum setiferum*, *Woodwardia radicans*). Sub-Mediterranean species such as *C. sativa* find adequate climatic conditions mainly at mid-elevation of the volcanic mountains on those islands that exhibit a pronounced topography.

Habitat suitability is calculated by models that are based either on in situ data or on RS data. Our study combines a slightly modified change detection technique with machine learning supervised classification algorithms. The change detection technique is especially suitable for invasive plant species detection if the species exhibits clear phenological changes compared to native vegetation through time, as shown by the detection of glossy buckthorn (*Frangula alnus* Mill.) spreading into forests of southern Quebec, Canada, by applying a linear temporal unmixing model to a time series of the normalized difference vegetation index (NDVI) derived from Landsat 8 Operational Land Imager (OLI) [65]. The RS-based *C. sativa* spatial distribution assessments yielded differences in spatial coverage, with the area estimated by Landsat 8 slightly higher than that estimated by Sentinel-2. The variation in the image resolutions between two sensors may be one of the reasons for greater spatial coverage estimated from the Landsat imagery. As Landsat 8 images have a spatial resolution of 30 m and Sentinel-2 images (used in this study) have a spatial resolution of 10 m, one pixel of Landsat 8 is equivalent to 9 pixels of Sentinel-2.

Smaller spatial extent of *C. sativa* area extracted from Sentinel-2 compared to Landsat 8 translated into less modelled spatial coverage based on Sentinel-2 compared to Landsat 8. Both sensitivity and grain size in spatial resolution can lead to such findings. Image quality, especially in a heterogeneous environment where plant species cannot easily be discerned, may result in spectral mixing [66], which is poorly represented by a low-spatial-resolution image. Thus, with lower spatial resolution, classification accuracy tends to decrease [67]. However, this relationship can reverse when using very high spatial resolution imagery [68]. Furthermore, residual yet marginal cloud coverage on the image from 7 March 2017, could have influenced the performance of the Landsat 8 scene.

The survival of *C. sativa* across the heterogeneous environment in La Palma suggests that the species shows high adaptive ability. We find that the moist and humid regions with broad-leaved trees, shrubs, and herbs are most suitable for the species. Similarly, Ríos-Mesa et al. [21] stated that on Tenerife, *C. sativa* is more dominant in the regions where trade winds humidify the area.

Ecological theory suggests that species-rich ecosystems can be more resistant to invasion [69–71]. Since many niches are not occupied on islands, it is expected that more species will naturalize in the future [72]. Such an increasing saturation of species richness could enhance the functioning of ecosystems [73]. However, individual alien species may also modify important ecosystem functions, causing negative effects even centuries after their establishment when replacing other key species such as dominant plant functional types [13].

The replacement of one dominating plant functional type by another can particularly affect sensitive ecosystems on very steep slopes in a humid zone. The natural stability of the laurel forest on these slopes is astounding and results from its species diversity and the clonal root systems of the contributing tree species in combination with their evergreen foliage [44]. A regime shift away from long-lived, clonal evergreen trees can create new risks for the human population downslope through altered run-off, erosion and landslide potential. The respective loss of diversity caused by an invading species also affects ecosystem stability [70].

The development of a forest with deciduous canopy in contrast to the native evergreen forest is creating a novel ecosystem in the Canary Islands, where such ecosystems did not exist before. The emergence of novel ecosystems with altered species composition, structure, and functioning [74] is a common phenomenon worldwide. Such substantial changes are in the first instance linked with uncertainty because expert knowledge on such novel systems does not exist. The lost system may also matter. Functional traits, structures, phenology, and biodiversity can be assessed for newly emerging ecosystems and compared to the replaced ones. In the case of the alien deciduous chestnut forest on the Canary Islands, a highly diverse and evergreen forest is replaced by monodominant stands with seasonal foliage. Consequences for species loss, erosion control, landslide threat, and carbon sequestration are to be expected and require further monitoring [13].

Here we used open-access RS data, which come at the expense of relatively coarse spatial and spectral resolutions. We could, nevertheless, achieve a very high detection accuracy because the application of multi-date RS data made it possible to effectively resolve the phenological differences of deciduous *C. sativa* in this particular study system. When such clear spectral differences are known, expensive very-high-resolution RS data are not required to detect invasive species, even though most studies recommend such RS data for high accuracy. For example, multispectral Quickbird data including 4 bands and a spatial resolution of 2.4 m were used to map invasive *Tamarix* species along the Colorado River [75]. However, commission errors were still high due to the relatively coarse spectral resolution. Another comparison revealed that AISA hyperspectral imagery is more effective than Quickbird in identifying invasive individuals [76]. Müllerová et al. [77] investigated the effectiveness of panchromatic, multispectral, and colour very high spatial resolution aerial photography (resolution 0.5 m) and medium spatial resolution satellite data (Rapid Eye, resolution 5 m) in monitoring the noxious invasive giant hogweed (*Heracleum mantegazzianum* Sommer & Levier) using pixel- and object-based image analysis. The authors found that object-based analysis of aerial 0.5 m resolution data during the flowering period resulted in high detection accuracy, while pixel-based analysis of 5 m resolution satellite data achieved moderate accuracy. Underwood et al. [78] detected iceplant (*Carpobrotus edulis* L.) and jubata grass (*Cortaderia jubata* Lemoine ex Carriere) in Mediterranean-type ecosystems of California using Airborne Visible and Infrared Imaging Spectrometer (AVIRIS) imagery with 4 m resolution. These RS data were particularly useful because both invasive species could be distinguished from co-occurring species by leaf water content. Downy brome (*Bromus tectorum* L.) was mapped in semi-arid rangeland ecosystems of Washington state, USA, using AVIRIS imagery with 4 m [79]. The authors compared the detection accuracy from single-date and multi-date AVIRIS data applying a filtering algorithm for image classification. The accuracy was higher for multitemporal RS data that could resolve phenological differences through time. In terms of the effectiveness of multitemporal RS data, Hestir et al. [80] and Evangelista et al. [31] show that omission errors for mapping phenologically different and invasive plant species depend strongly on acquisition dates of RS images. Interestingly, in the Great Basin, *B. tectorum* could only be detected with very low accuracy (35%) using multitemporal data from Landsat MSS, TM, and ETM+, which are spaceborne sensors with relatively low spectral and spatial resolution [81]. However, the invasive shrubs *Frangula alnus* Mill. and *Rhamnus cathartica* L. were sufficiently mapped in Ohio and Michigan States, USA, by applying multitemporal Landsat TM and ETM+ satellite images [82]. In addition, airborne LiDAR and hyperspectral sensors are commonly used in precision agriculture and forestry to map crop quality, weeds, and pests [83], and thermal spectrometers have also proven to be very advantageous for detecting invasive plant species [84]. In view of all these examples, it remains challenging to select the appropriate RS data, particularly concerning the temporal, spatial and spectral resolution, to efficiently detect invasive plant species among native vegetation [30]. However, given the inaccessibility and high costs of very-high-resolution RS data, free and open-access RS data should be promoted in research and conservation when they are appropriate. Here we prove the effectiveness of open-access RS data for invasion science and management despite relatively coarse spatial, temporal, and spectral resolution of RS data.

Ensemble models perform better than single models in predicting invasive plant species' habitat suitability [85]. Nevertheless, using correlative models such as ENMs to predict the potential distribution of invasive species can be problematic because invasive species can establish in environmental niches that are new or very restricted compared to their native range [86]. Moreover, our models do not address the question of community saturation, i.e., to what degree environmental drivers limit species richness, composition and invasion of communities [73]. Moreover, the choice of environmental predictors drives the explanation of distributions [30]. The prediction success additionally depends on the frequency of test occurrences that makes prediction success a potentially biased estimator of model performance [61]. Hence, invasives' distributions in non-native ranges may be severely under- or overestimated by ENMs. However, such predictions are often the only reasonable way to guide conservationists to potential areas of invasion [87,88]. Range expansions of invasive species can happen rapidly due to changes in the species' invasibility or environmental factors such as land use and climate change [89]. Consequently, models based on species occurrence points should be interpreted as risk of species establishment, not species abundance, or impact [90].

Correlative model predictions involving abiotic factors only are also criticized because real invasion processes such as interspecific competition are ignored [91]. Mechanistic or process-based models may thus perform better than correlative models. However, process-based models require greater understanding of the invasion process than is usually available. Notably, biological mechanisms can be revealed by RS approaches. Asner et al. [33] revealed climate interactions promoting the invasive evergreen tree *M. faya* spreading into Hawaiian rainforest by analysing a time series of EO-1 Hyperion satellite data only. Once mechanistic models are applied, their performance can be validated by species distribution data directly derived from RS [30].

Detection accuracy depends not only on RS data and modelling approaches but also on algorithms applied for image classification. In Mediterranean forests, spaceborne QuickBird and airborne ADS40-SH52 imagery was combined to identify individual trees of the Iberian wild pear (*Pyrus bourgaeana* Decne.) [67]. Applying maximum likelihood approach and support vector machines on a pixel-by-pixel basis yielded different results depending on the combination of RS data and classification algorithms. Müllerová et al. [77] conclude that object-based analysis of aerial photography with 0.5 m resolution taken during the flowering period resulted in high detection accuracy, while pixel-based analysis of 5 m resolution Rapid Eye data achieved moderate accuracy in monitoring the noxious invasive giant hogweed (*H. mantegazzianum*).

The spectral signatures of species change through time due to biochemical, physiological, phenological, and environmental factors [92]. This variation of spectra limits the transferability of the relationships between spectral signatures, species, and environments to other study systems. Consequently, we recommend adapting our methodological approach individually to other systems.

5 | Conclusions

This study identifies the probability of invasion of the introduced *C. sativa*, with particular focus on the laurel forest ecosystems of the island of La Palma, Canary Islands, Spain. Even if the spread of this deciduous tree species has been slow until now, major uncertainties arise from the fact that represents a plant functional type different from the zonal vegetation. Only two, rare native deciduous tree species can be found naturally (*Salix pedicellata* subsp. *canariensis* (C. Sm. ex Link) A. K. Skvortsov; *Sambucus palmensis* Link), along semi-permanent brooks and streams. However, these native deciduous species play no role in the natural evergreen forest ecosystems of the island.

The projected potential for the replacement of an evergreen broadleaved laurel forest rich in endemic tree species by a deciduous broadleaved forest formed by one introduced tree species does not inform about the speed of such processes. Inertia in long-lived tree species that can sprout from their rootstock is likely to avoid a rapid transition. However, a very resilient and stable ecosystem could be replaced by a less resilient and less stable one with only seasonal leaf cover and low species diversity. The steep and moist slopes of the island limit the accessibility in the field. We therefore recommend monitoring the future spread of *C. sativa* using RS approaches, as herein.

Our findings can be applied to other islands of the archipelago, where comparable climatic conditions are found and the characteristic laurel forest occurs, i.e., El Hierro, La Gomera, Tenerife, and Gran Canaria. For these islands, our findings provide an early warning to generate awareness of possible invasion processes and to start proactive measures to avoid invasion into unique, valuable, and remnant laurel forests. Our results can also be transferred to the islands of Madeira and the Azores, where climatic conditions are very likely even more appropriate for *C. sativa*. In the case of the Azores, the laurel forest is almost completely replaced by conifer plantations and other invasive species (e.g., *Pittosporum undulatum* Vent., *Hedychium gardnerianum* Sheppard ex Ker Gawl.) This makes the preservation of the Canary Island laurel forest an even more important priority in the international context.

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Appendix A

Table A1: Satellite images used in the study.

Sensor	Scene ID
Landsat 8	LC08208040201707290 1T1-SC20190612132658
Landsat 8	LC082080402017030701T1-SC20190128221754
Landsat 8	LC082080402017020301T1-SC20190612132509
Sentinel-2	S2A_MSIL2A_20180708T120331_N0208_R023_T28RBS_20180708T141805
Sentinel-2	2A_MSIL2A_20190213T120321_N0211_R023_T28RBS_20190213T172742

Appendix B

Table A2: Total number of training and testing data used in Random Forest classification.

Sensor	Data	
	Training	Testing
Sentinel-2	101501	43499
Landsat 8	11557	4952

Appendix C

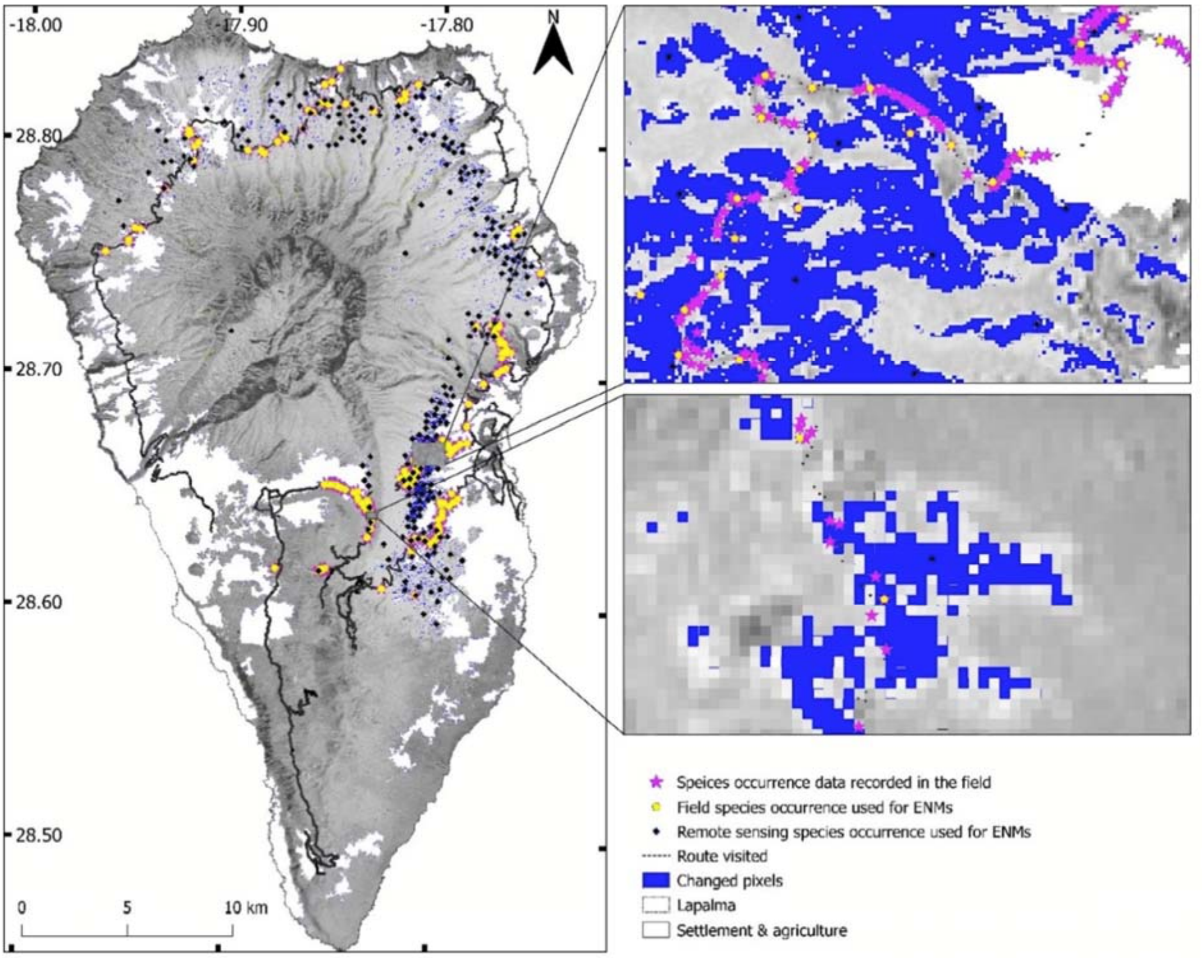
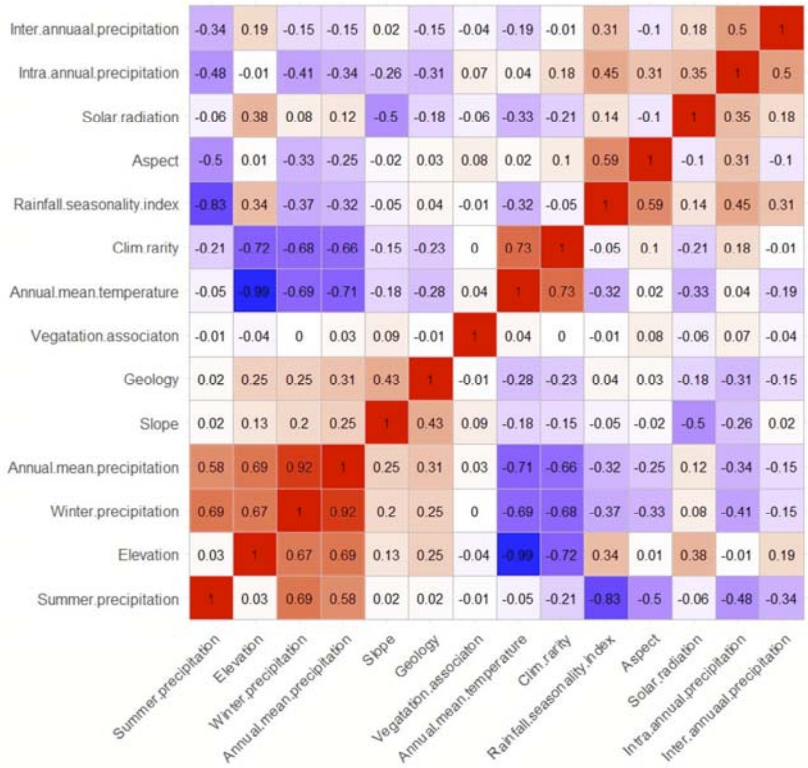


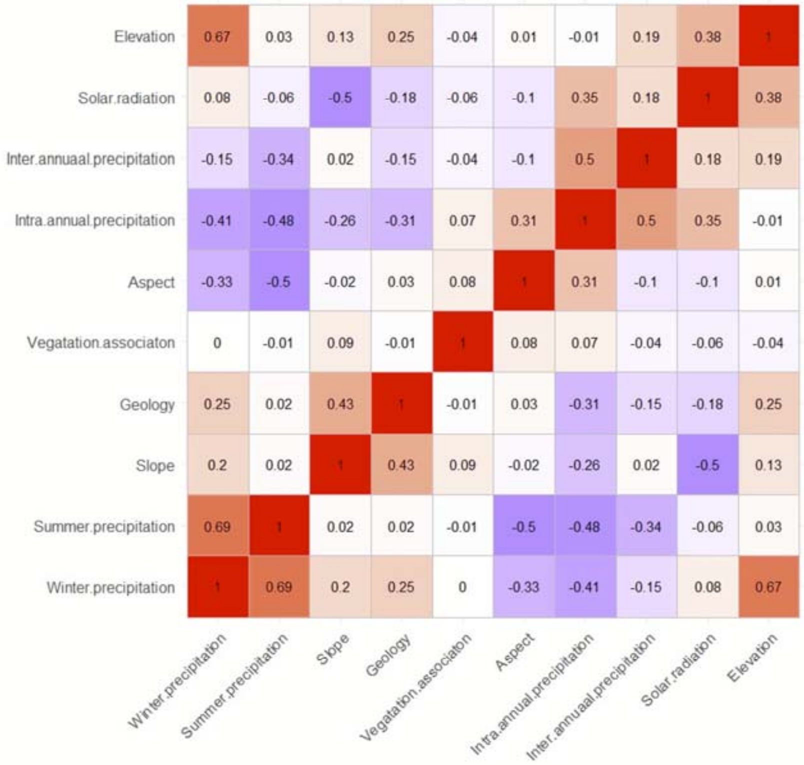
Figure A1: Species occurrence locations recorded from field and species occurrence locations used in Ecological niche modellings (ENMs) with two cut-out sections for details.

Appendix D



	Summer.precipitation	Elevation	Winter.precipitation	Annual.mean.precipitation	Slope	Geology	Vegatation.associaton	Annual.mean.temperature	Clim.rarity	Rainfall.seasonality.index	Aspect	Solar.radiation	Intra.annual.precipitation	Inter.annuaal.precipitation
Inter.annuaal.precipitation	-0.34	0.19	-0.15	-0.15	0.02	-0.15	-0.04	-0.19	-0.01	0.31	-0.1	0.18	0.5	1
Intra.annual.precipitation	-0.48	-0.01	-0.41	-0.34	-0.26	-0.31	0.07	0.04	0.18	0.45	0.31	0.35	1	0.5
Solar.radiation	-0.06	0.38	0.08	0.12	-0.5	-0.18	-0.06	-0.33	-0.21	0.14	-0.1	1	0.35	0.18
Aspect	-0.5	0.01	-0.33	-0.25	-0.02	0.03	0.08	0.02	0.1	0.59	1	-0.1	0.31	-0.1
Rainfall.seasonality.index	-0.83	0.34	-0.37	-0.32	-0.05	0.04	-0.01	-0.32	-0.05	1	0.59	0.14	0.45	0.31
Clim.rarity	-0.21	-0.72	-0.68	-0.66	-0.15	-0.23	0	0.73	1	-0.05	0.1	-0.21	0.18	-0.01
Annual.mean.temperature	-0.05	-0.99	-0.69	-0.71	-0.18	-0.28	0.04	1	0.73	-0.32	0.02	-0.33	0.04	-0.19
Vegatation.associaton	-0.01	-0.04	0	0.03	0.09	-0.01	1	0.04	0	-0.01	0.08	-0.06	0.07	-0.04
Geology	0.02	0.25	0.25	0.31	0.43	1	-0.01	-0.28	-0.23	0.04	0.03	-0.18	-0.31	-0.15
Slope	0.02	0.13	0.2	0.25	1	0.43	0.09	-0.18	-0.15	-0.05	-0.02	-0.5	-0.26	0.02
Annual.mean.precipitation	0.58	0.69	0.92	1	0.25	0.31	0.03	-0.71	-0.66	-0.32	-0.25	0.12	-0.34	-0.15
Winter.precipitation	0.69	0.67	1	0.92	0.2	0.25	0	-0.69	-0.68	-0.37	-0.33	0.08	-0.41	-0.15
Elevation	0.03	1	0.67	0.69	0.13	0.25	-0.04	-0.99	-0.72	0.34	0.01	0.38	-0.01	0.19
Summer.precipitation	1	0.03	0.69	0.58	0.02	0.02	-0.01	-0.05	-0.21	-0.83	-0.5	-0.06	-0.48	-0.34

Figure A2: Pearson correlation coefficients of environmental raster used in ecological niche modelling (ENM).



	Winter.precipitation	Summer.precipitation	Slope	Geology	Vegatation.associaton	Aspect	Intra.annual.precipitation	Inter.annuaal.precipitation	Solar.radiation	Elevation
Elevation	0.67	0.03	0.13	0.25	-0.04	0.01	-0.01	0.19	0.38	1
Solar.radiation	0.08	-0.06	-0.5	-0.18	-0.06	-0.1	0.35	0.18	1	0.38
Inter.annuaal.precipitation	-0.15	-0.34	0.02	-0.15	-0.04	-0.1	0.5	1	0.18	0.19
Intra.annual.precipitation	-0.41	-0.48	-0.26	-0.31	0.07	0.31	1	0.5	0.35	-0.01
Aspect	-0.33	-0.5	-0.02	0.03	0.08	1	0.31	-0.1	-0.1	0.01
Vegatation.associaton	0	-0.01	0.09	-0.01	1	0.08	0.07	-0.04	-0.06	-0.04
Geology	0.25	0.02	0.43	1	-0.01	0.03	-0.31	-0.15	-0.18	0.25
Slope	0.2	0.02	1	0.43	0.09	-0.02	-0.26	0.02	-0.5	0.13
Summer.precipitation	0.69	1	0.02	0.02	-0.01	-0.5	-0.48	-0.34	-0.06	0.03
Winter.precipitation	1	0.69	0.2	0.25	0	-0.33	-0.41	-0.15	0.08	0.67

Figure A3: Pearson correlation coefficients of environmental raster used in ecological niche modelling (ENM).

Appendix E

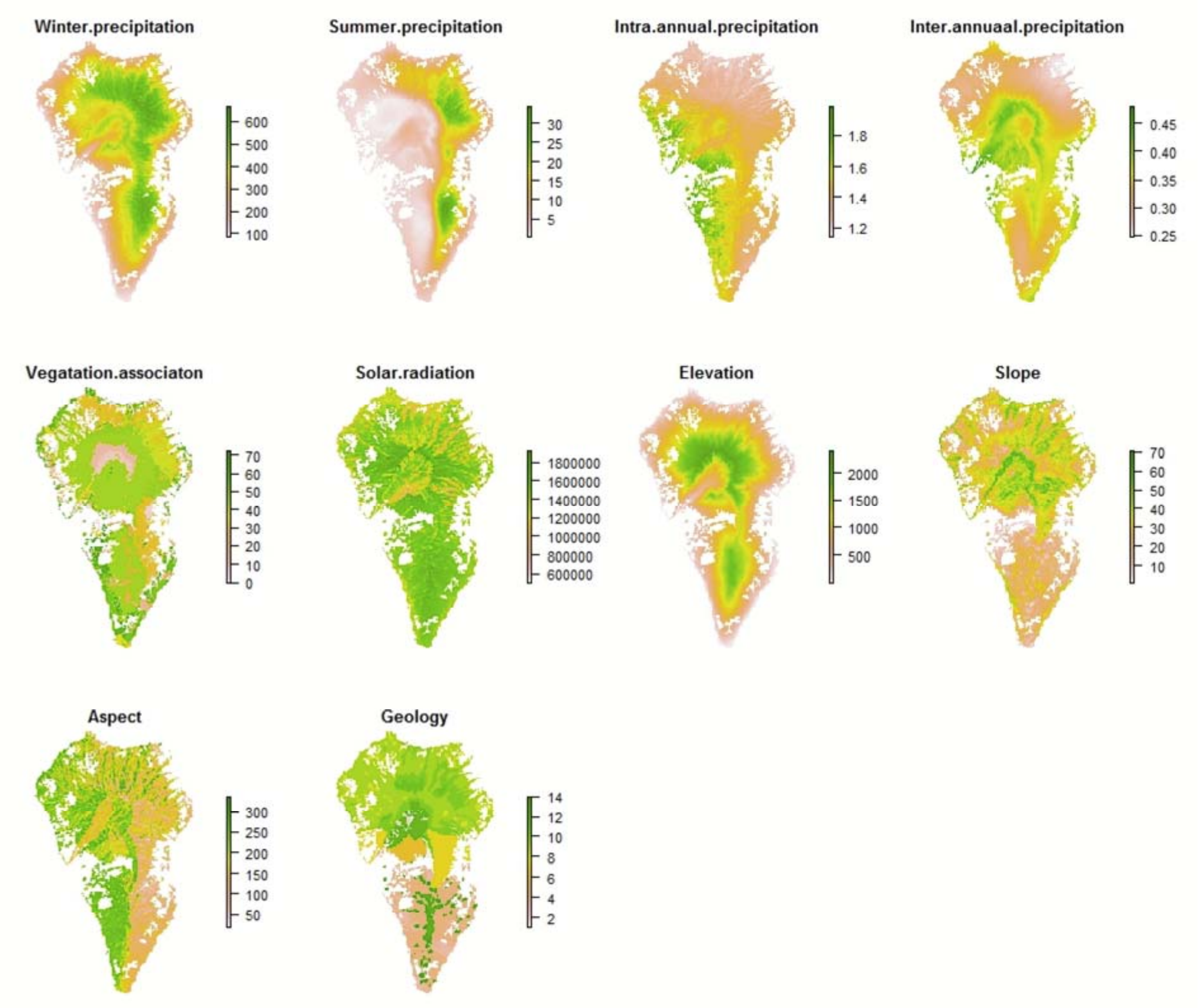


Figure A4: Environmental raster used in ecological niche modelling (ENM); Data surfaces are modified from data published in Irl et al., 2015.

Appendix F

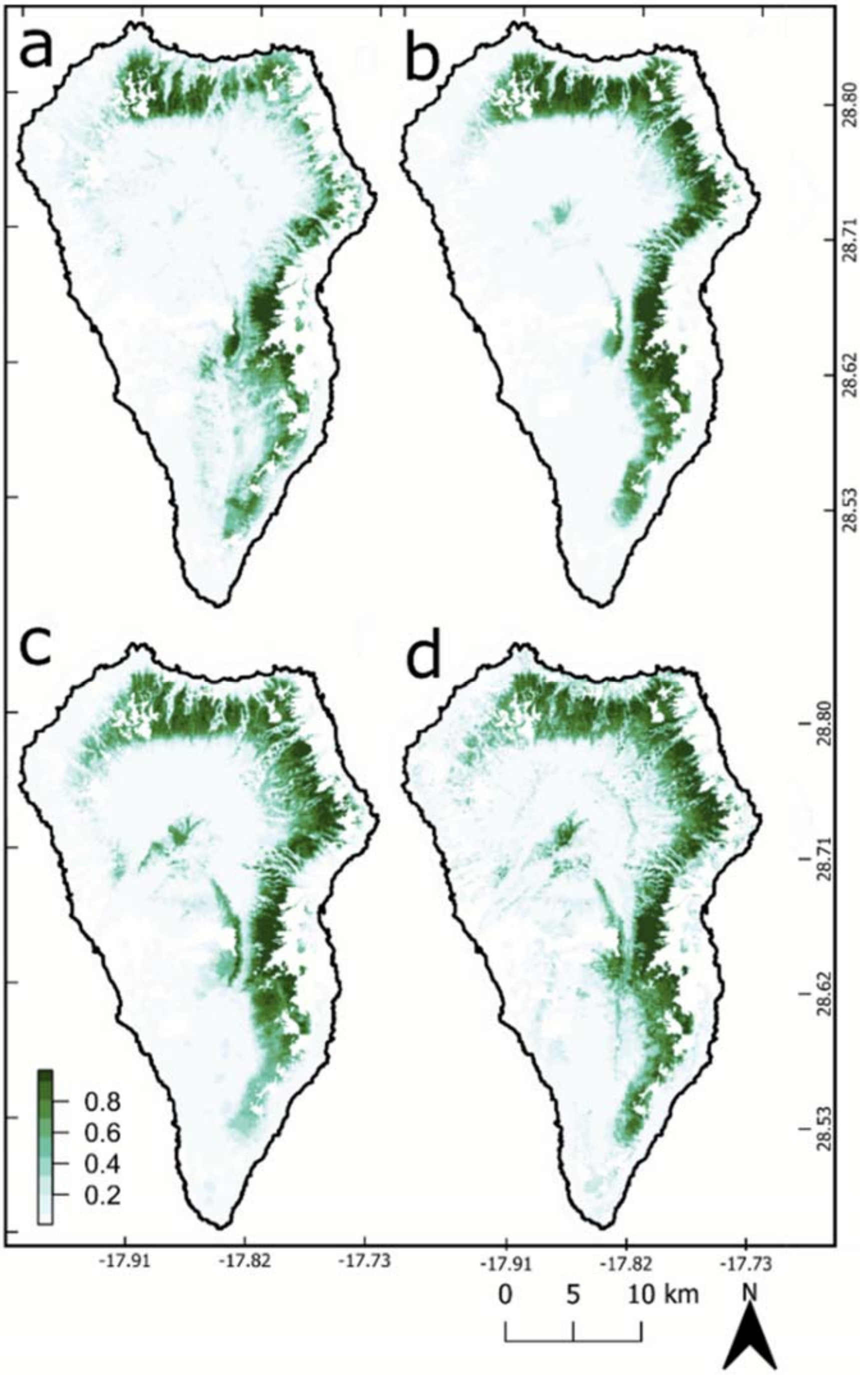


Figure A5: *C. sativa* habitat suitability maps (a) from the Random Forest (RF) field-collected species occurrence locations, (b) from the (RF) based on the remote sensing (RS) species occurrence locations, (c) from the Generalized Additive Linear Model (GAM) based on the RS species occurrence locations and (d) from the Maximum Entropy (MaxEnt) Model based on the RS species occurrence locations.

Appendix G

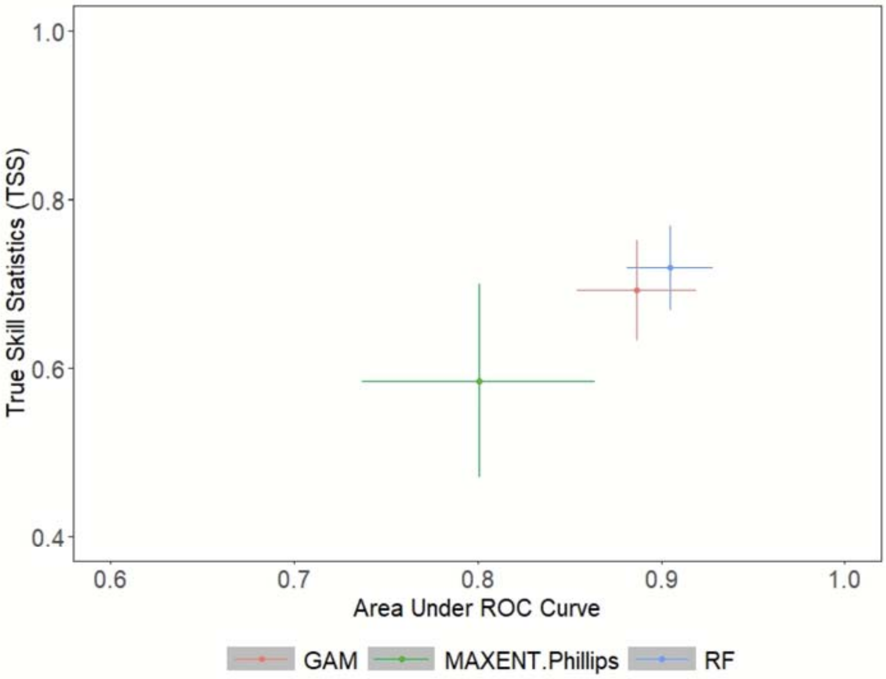


Figure A6: The initial model evaluation for the models from the RS data. Among the 120 models, the models which have True Skill Statistics and Area Under ROC scores greater than 0.7 and 0.8 respectively were only considered in habitat suitability modelling.

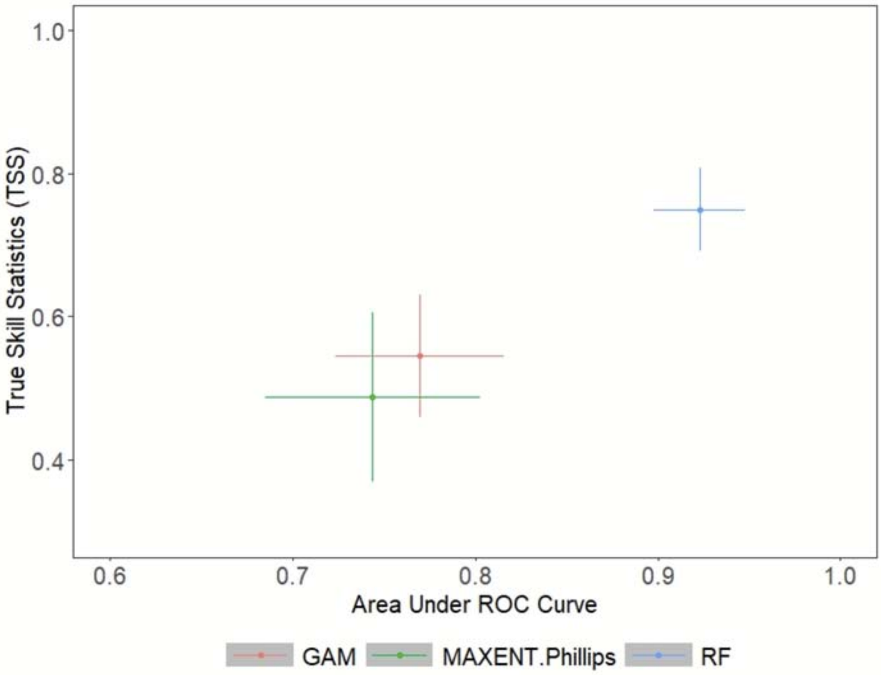


Figure A7: The initial model evaluation for the models from the Field data. Among the 120 models, the models which have True Skill Statistics and Area Under ROC scores greater than 0.7 and 0.8 respectively were only considered in habitat suitability modelling.

Appendix H

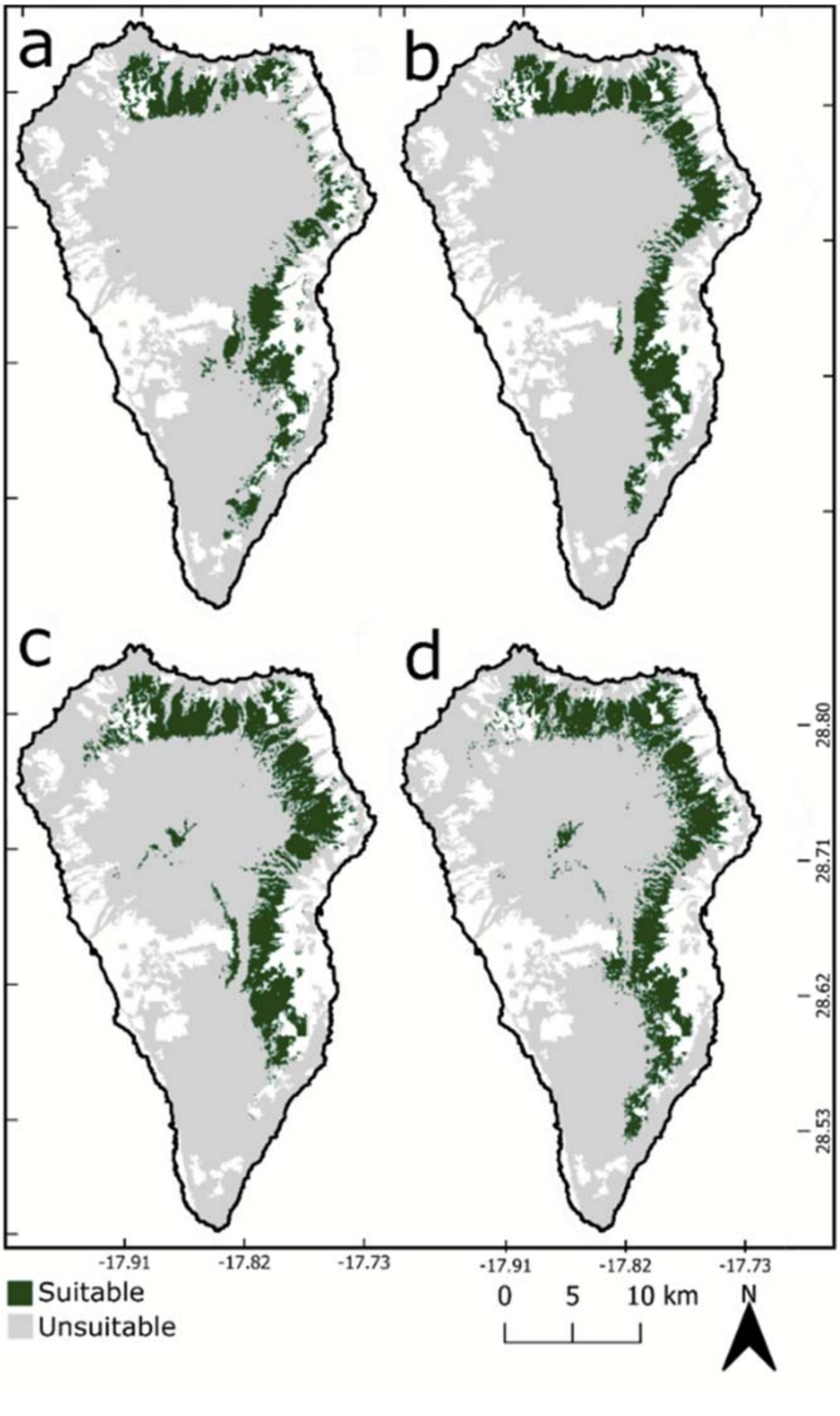


Figure A8: *C. sativa* presence absence maps (a) from the Random Forest (RF) field-collected species occurrence locations, (b) from the Random Forest (RF) based on the RS species occurrence locations, (c) from the Generalized Additive Linear Model (GAM) based on the remote sensing (RS) species occurrence locations and (d) from the Maximum (MaxEnt) Model based on the RS species occurrence locations.

Appendix I

Table A3: Ecological niche modelling performances. The GAM and MaxEnt rows for the Field columns are NA because the TSS and AUC from these were less than 0.7 and 0.8 so we excluded these models from the analysis.

Parameters						
Model	AUC		Threshold		TSS	
	Field	RS	Field	RS	Field	RS
EM	0.982	0.961	564.833	634.417	0.885	0.805
GAM	NA	0.943	NA	572.540	NA	0.789
RF	0.982	0.968	570.875	675.625	0.881	0.811
MaxEnt	NA	0.928	NA	634.167	NA	0.730

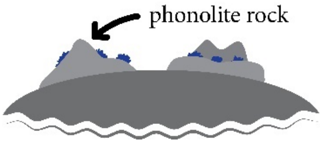
Manuscript 7

Light-coloured phonolite rock amidst a matrix of black basalt. © Anna Walentowitz

Summary

Arks of natural biodiversity gain importance as reference sites for research and conservation during times of immense environmental change caused by humans. On the island of La Palma, light-coloured phonolite rocks distributed within field of black lava are such sites that even today exhibit mostly native including numerous endemic plant species (Walentowitz *et al.* 2021a; Kienle *et al.* 2022). Non-native plant species are largely absent. At the example of plant species growing

on phonolite rocks and adjacent basalt, we assess the importance of geodiversity for the emergence of biodiversity patterns (Alahuhta *et al.* 2020; Ren *et al.* 2021).



Geodiversity and biodiversity on a volcanic island: the role of scattered phonolites for plant diversity and performance

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Abstract

Oceanic islands are cradles of endemism, contributing substantially to global biodiversity. A similarity in magmatic origin translates into high global comparability of substrates of volcanic islands on the oceanic crust with, however, slightly chemically or physically differentiated petrography in some places. Phonolites are examples of rare localities with intermediate chemical characteristics between felsic and mafic and with diverse textures. They contribute to habitat heterogeneity and offer specific growth conditions in a significantly different matrix of basaltic substrates. The explicit contribution of geodiversity to island biodiversity has been little studied, despite growing evidence of its importance on continents. On the island of La Palma, Canary Islands, isolated phonolitic rocks are conspicuous due to their light colour and specific shape. Although these outcrops only cover small areas, their unique form and composition increase within-island geodiversity. To investigate how this affects biodiversity on La Palma, we sampled all vascular plant species in 120 plots on four sets of paired sites in order to test if plant diversity and performance is enhanced on phonolitic rocks compared to basaltic rocks. We recorded species number and abundance as well as individual plant height and diameter as proxies for aboveground resource allocation and tested for differences in vegetation cover and species composition between the bedrock types. We found higher species richness and abundance on phonolites than neighbouring basaltic substrates, and individuals of the same species were larger (in height and diameter) on phonolites compared to neighbouring basalt. An endemic woody species with two distinct varieties even appears almost exclusively on the small surfaces of phonolitic rock. Despite extremely limited spatial extent, phonolitic rocks can play an important role in plant biodiversity on islands.

1 | Introduction

Biodiversity is known to depend mainly on abiotic drivers, such as climate and topography (Field et al., 2009). However, the importance and explicit impacts of geodiversity on biodiversity have long been insufficiently researched and partly ignored. Only recently has the topic started to receive more attention (e.g. Gray, 2004; Lawler et al., 2015; Bailey et al., 2017; Alahuhta et al., 2020; Barajas-Barbosa et al., 2020). Geodiversity is in many respects an abiotic equivalent to biodiversity (Gray, 2011) and represents the variability of chemical components, surface structure, and edaphic and hydrological features (Gray, 2004; Bailey et al., 2017). This variability contributes to habitat diversity and thus affects biodiversity patterns via the provisioning of ecological niches (Liu et al., 2013; Gillespie and Roderick, 2014; Bailey et al., 2017). Geological elements provide unique or distinctive habitats for plants and insects, deliver initial growth conditions for vegetation or fungi formation, and are part of nutrient cycling and soil–atmosphere interactions (Tukiainen et al., 2016).

Biodiversity is distributed unevenly throughout the world (Gaston, 2000), with a disproportionately large contribution from oceanic islands due to their high endemic richness (Kier et al., 2009). Substrates that differ in geochemistry and petrography are likely to be relevant for biodiversity on oceanic islands, where most rocks commonly share similar volcanic genesis, resulting in only slight differences in the parent material. Distinct substrates with limited extent, such as individual rock types, may function as a second isolating abiotic filter for populations in addition to the spatial isolation of oceanic islands that are known to be of outstanding importance for speciation at the global scale (Kier et al., 2009). Specific rock habitats, particularly rocks that exhibit petrographic and geochemical substrates such as serpentinites, are known to be rich in habitat-specific endemics (e.g. Harrison et al., 2006; Kazakou et al., 2010). Those species evolved specific adaptations to the unique nutrient contents and soil conditions and the presence of heavy metals that cannot be tolerated by other plant species (Harrison and

Rajakaruna, 2011). This phenomenon is known as well on continents, where substrates such as serpentinite and gypsum outcrops host specialised floras and contribute to broad-scale diversity (see, e.g. Chiarucci et al., 1998; Pausas et al., 2003). It underlines the relevance of understanding the importance of geodiversity for insular biodiversity, which is particularly vulnerable to extinction due to highly restricted ranges and small population sizes of insular endemic species (Paulay, 1994). Phonolites are rocks that occur at volcanic intraplate settings in insular and continental contexts worldwide (Garcia et al., 1986; Ackerman et al., 2015; Hagos et al., 2017). They exist in a variety of geologic outcrops formed by volcanic activity. Such outcrops mainly exist on continents, where they are often linked to faults and tectonic activity. Major components of these extrusive igneous rocks (formed from lava with low silica content) are alkaline feldspars together with foid minerals, nepheline, and pyroxene (Abratis et al., 2015; Ackerman et al., 2015) or their conversion products.

On the island of La Palma (Canary Islands, Spain), several phonolitic rock outcrops are embedded into a matrix of basaltic origin (Middlemost, 1972). The dominant rock type found on La Palma is olivine and augite–titanaugite porphyric basalt, resulting from rapidly rising magma from the upper mantle (Middlemost, 1970). In contrast, there were times when a sizeable magmatic chamber below the island enabled differentiation of magma and the removal of silica, thus yielding ultramafic, trachytic, and phonolitic rocks (Middlemost, 1970). Phonolite trachytes (showing the exhalation of gases during eruptions) occur on various volcanic islands such as La Palma, St Helena, Fernando de Noronha, Trinidade and Sal (Cabo Verde). On La Palma, their distribution is focused on the southern (young) part of the island. The major chemistry of phonolites on La Palma is comparable to that of “average phonolites”, as described by Nockolds (1954). The current volcanic activity and lava flow deriving from the Cumbre Vieja volcano (Pankhurst et al., 2021) are a demonstration of how phonolitic rocks became isolated by younger lava solidifying around the peaks of phonolitic rock. This event illustrates that the isolation of the investigated phonolitic habitats (e.g. Roque Teneguía) is far from being a singularity but rather a process that is highly likely to have happened repeatedly on oceanic islands in general.

Volcanic activity with production of tephra and lava flows is a noticeably young phenomenon in the southern part of La Palma, with even present-day eruptions (Pankhurst et al., 2021). Thus, the remnant phonolitic rocks are the tips of a former land surface that are today embedded in a basaltic matrix of noticeably immature age (Garantje et al., 1998). As a consequence, weathering processes on phonolites were active on longer timescales compared to other surrounding rocks. In addition to petrography, differences in weathering between the rock types and resulting nutrient availability also infer different timescales of exposure.

A higher nutrient availability enables higher plant abundances and larger plant size. Porder et al. (2004) found comparable conditions at a catena of different rock ages on the Hawaiian Islands. Compared to basaltic lava outcrops, phonolites differ in their chemical composition and additionally in colour, texture, density, weathering, and formation fracturing (von Fragstein et al., 1988). Tafoni-weathering (Formoso et al., 1989) can be observed on phonolitic surfaces, indicating temperature and moisture gradients between the surface and the solid body of rocks (Brandmeier et al., 2011) that appear in combination with wind exposure. Circulating leachate reaches the rock's surface and evaporates, exposing its dissolved mineral content and enabling the development of secondary mineral assemblages (Spürgin et al., 2019). These can contribute to plant nutrient supply, which is also why ground phonolite rock powder is used as an effective fertiliser (Faccini et al., 2015). For phonolites, increased release of nutrients can be mediated by bio-weathering actions and plants receiving this fertiliser showed higher productivity, and increased accumulation of the macronutrient potassium in plants could be detected when applying phonolite rock powder (Tavares et al., 2018; Nogueira et al., 2021). Phonolites and the related larger-grained nepheline syenites contain significantly larger amounts of the essential nutrient potassium (see Table A1 in the Appendix for a literature overview). Even if quantitatively small, such processes are of particular importance at nutrient-poor sites. In contrast, the young basalts in the southern part of La Palma are barely weathered (Carracedo et al., 1999), appearing rough and friable with sharp spikes. We expect these petrographic and geochemical differences of parent material to affect vegetation cover and species occurrence.

Geologic outcrops, such as phonolites, increase microenvironmental heterogeneity, enhancing species richness at a landscape scale (Hjort et al., 2015). Increased speciation rates on isolated outcrops of scarce rocks are thought to lead to a higher percentage of endemic species than the surrounding matrix (Ricketts, 2001). Geodiversity may thus promote both species richness and endemism. However, relatively little is known about the extent to which phonolites promote species diversity in general and particularly endemism. To approach this topic theoretically, phonolitic outcrops could be considered as small habitat islands within a basaltic matrix (Fig. 1b). The established species–area relationship (SAR) and the species–isolation relationship (SIR; MacArthur and Wilson, 1967; Rosenzweig, 1995; Giladi et al., 2014) predict a smaller number of species on these small and isolated phonolitic rocks in comparison with basaltic rock outcrops in their surroundings. From the beginning of these concepts (MacArthur and Wilson, 1967), they were not only meant for real islands but instead took "islands" as examples of isolated habitats (or habitat islands) within a terrestrial landscape matrix. However, the expected higher availability of nutrients would give such habitats more favourable conditions for plant growth. In addition, it is by no means certain that the phonolitic rocks were permanently separated from each other in southern La Palma's geological evolution. Possibly, a historically much larger phonolitic rock is today largely buried by basaltic eruptions (Garantje et al., 1998). Thus, a few phonolite outcrops may serve as refugia for remnant populations (Eriksson, 1996) of species specialised to phonolitic rocks.

Figure 1: The endemic *Cheirolophus junonianus* (a, bottom left) and further plant species on a phonolite rock (© Severin Irl). Aerial image of rocks of phonolites isolated in a basaltic matrix in southern La Palma (b, © Google Earth 2020).

La Palma hosts 159 vascular plant species that are endemic to the archipelago and 47 single-island endemics (hereafter SIEs; Beierkuhnlein et al., 2021). The endemic plant species *Cheirolophus junonianus* (Svent.) Holub, comprising its var. *junonianus* and var. *isoplexiphyllus* (Svent.) G. Kunkel (Vitales et al., 2014a, b, Beierkuhnlein et al., 2021), occurs within a range of only 3500 m^2, solely on La Palma (Bañares et al., 2004). Within this small range, individuals of this species occur only on a few outcrops, which are almost exclusively phonolitic rocks with a chemical composition different from most of the surrounding substrates. Therefore, the species is very restricted in its range size to just a few small locations (Muer et al., 2016; Atlantis, 2021) and appears to be restricted to phonolites (Fig. 1a). This example species evokes the question of whether or not phonolites are of special importance for endemic species on the Canary Islands.

We aim to investigate plant species richness, abundance and performance on phonolites compared to surrounding basaltic lavas. Therefore, we investigated the occurrences and traits of plant species in a comparative study matching basaltic and phonolitic rock formations on La Palma of comparable size, shape, and extent to test the following hypotheses:

i. Species diversity: we expect plant species richness on phonolitic rocks to be higher than on basaltic rocks because phonolites offer more favourable plant growth conditions.

ii. ii. Plant performance: we expect plant species populations on phonolites show a larger abundance of individuals that are taller and have greater canopy diameter than neighbouring basalts due to their advantages in resource availability and porosity. We used plant performance as a surrogate for plant fitness.

iii. Island endemism: we expect phonolitic rocks to host more endemic plant species than basaltic rocks because of their high degree of spatial isolation, in combination with the older age of the phonolitic bedrock than the basaltic matrix.

2 | Methods

2.1 | Study site and data sampling

We sampled four phonolitic and four adjacent basaltic rocks in the southern part of La Palma in spring 2018 (Walentowitz et al., 2021; Fig. 2). Locations were identified in the field based on Middlemost (1972). The sampled phonolitic rocks represented most of the overall extent of this habitat on the island, covering a large gradient of microclimate, aspect ("northernness" and "easternness"), and inclination. Local climate data are not available for individual plots, nor for the sites. Interpolated modelled climate data (Karger et al., 2017) show only small variations in temperature and precipitation values for our study sites (Table A2). We chose comparable neighbouring pairs of phonolite and basalt consisting of one cohesive rock formation each. Outcrop pairs were chosen to match the size and microclimatic conditions (aspect, slope). For each selected phonolitic and basaltic rock, we recorded plant species composition and abiotic parameters within 15 plots of 2 m × 2 m that were randomly selected within the range of accessibility on phonolite and basalt. This resulted in a total of 120 plots sampled across the four pairs of phonolitic and basaltic rocks (60 plots on phonolite and 60 plots on basalt).

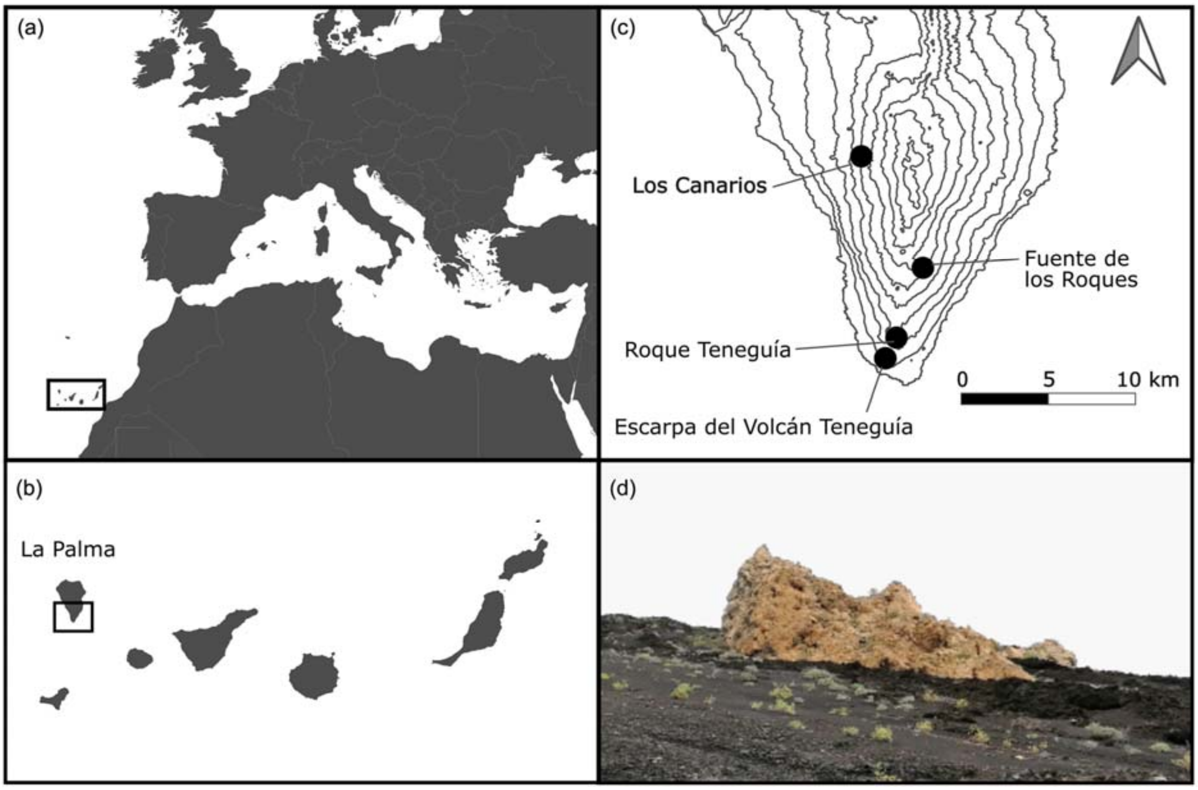

Figure 2: Location of the Canary Islands (a) and La Palma (b). Southern La Palma with our four study sites and contour lines at 200 m intervals (c). Phonolite rock on southern La Palma downwards slopes of the "Roque Teneguía", located in a basaltic matrix (d, © Anna Walentowitz).

Within each plot, we recorded coordinates, aspect, and slope inclination. Then, we estimated rock surface rugosity using thread transects spanning the two plot diagonals: we measured the transect length along the 3D rock surface (Walentowitz et al., 2021). Larger values of rugosity indicate higher levels of microtopography (cracks, hollows, uneven slope), while low values indicate smooth, even surfaces.

All vascular plant species within each plot, including ferns, were identified following the taxonomy of Beierkuhnlein et al. (2021) that use Plants of the World Online (POWO, 2019) as a taxonomic backbone. The biogeographic status of each species (SIE; multi-island endemic, MIE; non-endemic native; and introduced) is based on Muer et al. (2016; see extensive plant list in Appendix A3). The number of individuals per species and plot was counted.

Plant height (length from base of the stem to the tip) and canopy diameter (widest part of the plant parallel to the ground) of all single individuals found were measured as traits. Height, diameter, and species abundances were measured for all vascular plant species. As plant communities were dominated by perennial species, we can expect that vegetational differences evolved through long-term processes and did not reflect the short-term variability of environmental conditions. We are aware that there is a serious debate on the trade-off between different functional traits and their effect on plant growth responses. However, we assume that height and diameter are good proxies for different components such as survival and reproduction that contribute to plant fitness (Laughlin et al., 2020). We furthermore know that numbers of flowers and seeds might be more accurate to measure and monitor over the course of an entire reproductive cycle, but we chose plant height and width as proxies as these can be measured at the same time.

Lichen cover, which is abundant on the basalt, was estimated as the percent cover of each plot. Moss cover was negligible in all the plots.

2.2 | Statistical analysis

Differences in total plant species number and the number of SIEs and MIEs were analysed using Pearson's Chi-squared tests. Percentages of abundance, plant height, diameter, and SIE percentage between plots on phonolites and basalt were analysed using Mann–Whitney U tests. We conducted detrended correspondence analysis (DCA) to investigate the multidimensional aspects of vegetation composition and identify potential fundamental underlying drivers (Fig. A1). Afterwards, we applied a post hoc permutation test (10 000 repetitions) between the environmental variables (substrate, inclination, aspect, and relief) and the DCA ordination axes (Table A3). We tested for differences in aspect, inclination, rock surface rugosity, and lichen cover between phonolite and basalt using Mann–Whitney U tests.

3 | Results

We recorded 68 species of vascular plants (pteridophytes and spermatophytes) overall. Of these species, nine were SIEs restricted to the island of La Palma, 16 were MIEs co-occurring on other islands in the archipelago, 39 were non-endemic natives, and 4 were introduced. The SIE *Cheirolophus junonianus* was only found on phonolite, and most individuals of var. *junonianus* occurred on one isolated outcrop (Roque Teneguía) and individuals of var. *isoplexiphyllus* on another one (Escarpa del Volcán Teneguía, Fig. 2c).

We found higher plant species richness on phonolitic rocks. While 22 species were encountered on both phonolite and basalt, only 11 species were restricted to basalt, and 34 were recorded only on phonolite (Table A4). Endemism groupings showed similar patterns (SIEs – phonolite: 9, basalt: 5; MIEs – phonolite: 15, basalt: 6). Besides the total number of plant species per rock type, we also found higher species richness on phonolite at the plot scale (p=0.0164, Fig. 3a), and higher diversity of SIEs (p=0.00151, Fig. 3b) and MIEs (p=0.00727, Fig. 3d). The percentage of SIEs (p=0.1928, Fig. 3c) and MIEs (p=0.05346, Fig. 3e) relative to total species number did not differ significantly at this scale between phonolitic and basaltic rocks.

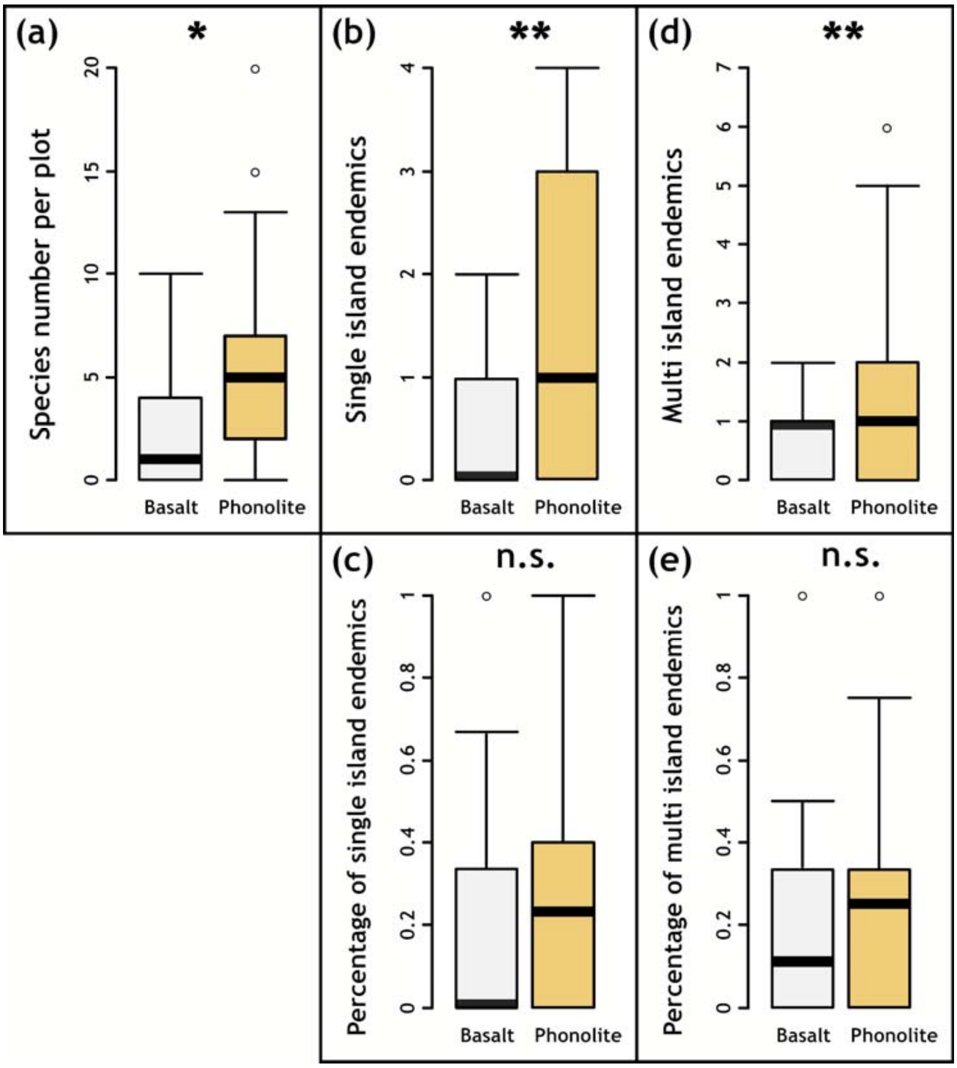

Figure 3: Perennial species per 2 × 2 m plot for basaltic (*n*=60) and phonolite substrates (*n*=60). (a) The number of species per phonolite plot is significantly larger than for basaltic plots. (b) Phonolites have significantly more SIEs and (d) MIEs. However, the numbers of endemic species relative to the total number of species do not differ significantly between substrates (c, e). All analyses were conducted with Pearson's Chi-squared test (a, b, c) and the Mann–Whitney U test (c, e).

On phonolitic rocks, we did not find higher total plant abundance (p=0.169, Fig. 4a). Moreover, there was no significant difference in abundance when only considering the 23 species found in plots on both substrates (p=0.179, Fig. 4b).

For plant species recorded on both rock types, individuals were on average taller and had wider canopies (Fig. 4c–d) on phonolitic than on basaltic rocks (Fig. 4c–d). Plant cover only (excluding lichens) was also significantly higher (p<0.0001, Fig. A2a) on phonolites than on basalt. Lichen cover did not show a significant difference (p=0548, Fig. A2b).

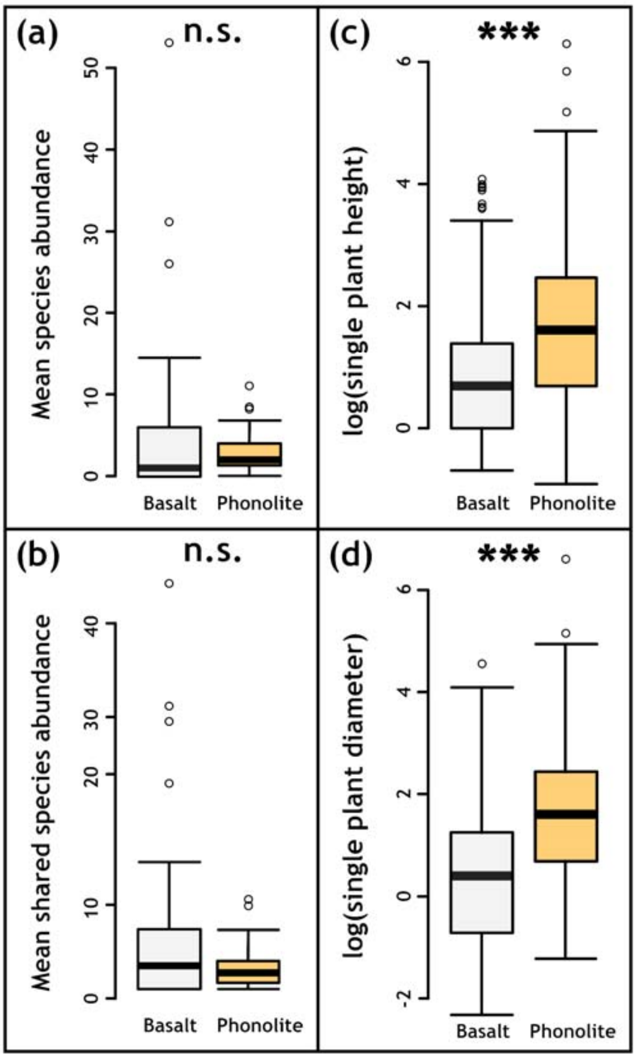

Figure 4: (a) Mean abundance differs significantly between basaltic (n=60) and phonolite substrates (n=60), but (b) considering only shared species on both substrates resulted in no significant difference between basalt (n=39) and phonolite (n=51). (c, d) plant height and diameter (both log10-transformed) are significantly larger on phonolite plots (n=1560) than on basaltic plots (n=1173). Plot size: 2×2 m. All analyses were conducted with the Mann–Whitney U test.

The ordination did not show any difference in the species composition, indicating no aspects of beta-diversity at all (Fig. A1, Table A3). Topographic characteristics of basalt and phonolite plots showed no differences in surface rugosity, aspect (northerness, easterness), or differences in slope inclination (Table A5).

4 | Discussion

The vegetation on phonolitic rocks differs compared to equivalent neighbouring basaltic rocks by exhibiting higher species richness and higher performance of plant individuals and higher total plant cover. Larger numbers of SIEs and MIEs on phonolites also reflect augmented total species numbers on this rock type.

Phonolite rocks on La Palma and other oceanic islands are arranged as habitat islands in a basaltic matrix (Fig. 1b). On La Palma, the total area of phonolite outcrops is tiny compared to the area of the basaltic matrix. Thus, encountering more species on phonolites than on basalt aligns with our hypotheses but defies the area effect on species richness, which predicts species number to be lower on phonolites. Differences in species numbers might be attributed to lower-than-expected species numbers growing on basalt, higher-than-expected species numbers on phonolites, or both. Our findings are congruent with studies that did not find a species–area relationship or relationships with a less steep slope on habitat islands (Matthews et al., 2016; Deák et al., 2018). The existence of unrealised niches due to unsaturated evolutionary dynamics in a young system could explain lower-than expected species numbers on basalt. A possible extinction debt that might lead to the disappearance of species in the future might explain higher-than expected species numbers on phonolitic outcrops. Only the continuous monitoring of populations on both rock types can help to verify these assumptions. Environmental filters (Liu et al., 2020) enhancing growth conditions on phonolite outcrops may also exist, consistent with our findings that plants are larger on phonolites.

The rock types phonolite and basalt differ in their chemical composition resulting in different nutrient availability, which explains our observation of increased plant performance on phonolites. Phonolites consist of the potassium-rich nepheline, which dissolves much faster than other potassium sources (Manning, 2010). Various studies indicate that phonolites and the related nepheline syenite contain a higher proportion of potassium than basalt (Manning, 2010; Roqueto do Reis, 2021). Therefore, ground phonolite rock powder has traditionally been used as an inorganic fertiliser (von Wilpert and Lukes, 1998; Ramos et al., 2006; Schoen et al., 2016). Basaltic rock powder has also been used as fertiliser but is considered a less important source of potassium than phonolite (Manning, 2010). The usage of ground basalt as fertiliser can also be explained by unclear assignments (potassium-rich trachyte is often assigned to basalt; see Maning, 2010). In addition to geochemical differences, the duration of rock weathering is a decisive factor in providing nutrients. The phonolitic outcrops in southern La Palma are substantially older than the surrounding basalt, which stems from very young volcanic eruptions (Carracedo et al., 1999). The youngest nearby eruption of the Teneguía volcano took place only 50 years ago, in 1971.

The age of geological formations influences plant diversity and species compositions (Whittaker et al., 2008; Hulshof and Spasojevic, 2020). As noted in previous studies (Carracedo et al., 1999), the Cumbre Vieja rift on La Palma has evolved throughout several eruptions and therefore contains lava formations from different ages as well as slightly different mineralogical compositions. The current volcanic activity and lava flow at the Cumbre Vieja are a live example of this geological process (Pankhurst et al., 2021). The known phonolite rocks on La Palma are located in the geologically young southern part of the island. As a consequence, the species pool in the surrounding basaltic matrix of these rocks is poor. Under the arid conditions of southern La Palma, only very few early successional species establish on these young basaltic outcrops with not more than initial soil formation (Irl et al., 2019). The few rocky outcrops of phonolite are embedded in this species-poor matrix of young basalt. We observed partly buried phonolites on which the survival of plants or seedlings during volcanic events was improbable (Garantje et al., 1998). Carracedo et al. (1999) showed that the last phonolite formation occurred in 1585, while basaltic eruptions continue until modern times (Pankhurst et al., 2021). 19 plant species, including *Cheirolophus junonianus*, can solely be encountered on phonolitic rocks (Irl et al., 2015; Muer et al., 2016). This confirms that habitat diversity on islands contributes to their total species richness (Hortal et al., 2009).

Besides petro-chemical characteristics and rock age, the surface structure and colour of phonolites might be suspected to drive plant patterns on such rocks. We observed deeper fractures in phonolitic rocks than in other volcanites on La Palma. In addition, phonolitic rocks show a much smoother surface roughness than their surrounding matrix. Basaltic rocks seem to possess a more dynamic relief, mainly attributed to their origin in congealed lava flows, typically found on oceanic islands. Nevertheless, when testing rock surface rugosity, there were no significant differences between phonolitic and basaltic rocks. Hence, we argue that surface characteristics do not play a role in higher plant growth response, richness, and abundance observed on phonolites. Besides fractures, another visual observation was that phonolites are of lighter colour than their surrounding basaltic matrix. We expected that phonolites possess a higher albedo than surrounding rocks and therefore expected them to have a reduced surface temperature compared to volcanic outcrops with darker colouring, such as basalt. However, in an experiment with differently coloured bricks, Hall et al. (2005) showed that the albedo of white surfaces only leads to significantly lower temperature of the material when the surface temperature falls below air temperature. With monthly temperatures between 17 and 25 ∘C within large areas of oceanic islands (Harter et al., 2015), no major temperature differences between basalt and phonolite surfaces can be expected. We therefore consider that this effect has no major impact on plants' habitat suitability.

While a diversity of rocks with different chemical characteristics and at different ages supports species richness on volcanic islands, such rock characteristics do not necessarily contribute to higher percentages of endemic plants or distinct compositional vegetation on individual rocky outcrops. The overall percentage of SIEs on phonolites was not significantly enhanced, refuting our expectations. Thus, the differential geology of phonolites itself does not result in a specialised flora. Obviously, the small outcrops of phonolite on La Palma do not suffice to evolve and maintain a substantial set of endemic species, which contrasts with general assumptions that patterns caused by differing topography or discontinuous parent material can be explained by island biogeographic theory (e.g. Kruckerberg 1991). Consequently, lessons learnt from other outcrops (Kruckerberg, 1991) cannot be adapted to the phonolitic rocks on La Palma, and the functioning of phonolites as islands of speciation within a matrix of basalt does not seem to apply.

Despite the limited spatial extent of phonolites on La Palma, they contribute to insular habitat heterogeneity, which translates into increased species richness and abundance as well as higher plant performance. These phenomena are facilitated by specific characteristics of phonolite rock, like high nutrient availability fortified by longer geological timeframes for erosion and nutrient release compared to basalt. We are not aware of other studies conducted in locations where phonolites can be encountered that explore their potential role as exceptional plant habitat islands, even though phonolites can be found all over the world (Garcia et al., 1986; Ackerman et al., 2015; Hagos et al., 2017). Therefore, further studies are needed to investigate whether the patterns encountered on La Palma may also be found on comparable phonolitic rocks in other areas of the world. Their benefits for biodiversity found in this study need to be recognised and valued. Especially for isolated areas such as islands, phonolites can contribute to small-scale biodiversity hotspots and our findings suggest that they should be conserved.

5 | Conclusion

Phonolites provide unique habitat conditions for plants on oceanic islands compared with surrounding areas. Higher species numbers and abundances as well as higher plant performance underline the importance of these rocks for the vegetation on oceanic islands. Despite the small total area covered by phonolites, they play a significant role in enhancing plant biodiversity on the island of La Palma. Our results suggest that exceptional rock outcrops like phonolites contribute to a better understanding of the formation of plant diversity on volcanic islands. As oceanic islands have always been formed through volcanic activity on the oceanic crusts, the combination of basaltic and phonolitic rocks is highly likely a regular pattern in Earth history.

Code availability

Only standard tests and plotting commands in R were used for data analysis. The code is available on request from the corresponding author.

Data availability

Any data supporting the findings of this study are available within the Supplement of this article and were taken from Walentowitz et al. (2021; https://doi.org/10.1016/j.dib.2021.107229).

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Appendix

Table A1: References of selected chemical components of basaltic and phonolitic substrates. (B) indicates basaltic, (P) phonolitic, and (N) nepheline syenite (phonolite equivalent with larger grain size) substrates or treatments.

Study	System/ study	Ca	Mg	K	Mn	P	Fe
Roqueto do Reis (2021; thesis)	Substrate used in experiments	B) 8.54% P) 1.76% CaO	B) 4.74% P) 0.32% MgO	B) 1.25% P) 8.05% K_2O	B) 0.21% P) 0.25% MnO	B) 0.42% P) 0.07% P_2O_5	B) 14.82% P) 3.87% Fe_2O_3
Garcia et al. (1986)	Field work (Kaula Isl.)	P) 1.74% CaO	P) 1.93% MgO	P) 4.48% K_2O	P) 0.31% MnO	P) 0.64% P_2O_5	P) 3.33% Fe_2O_3; P) 1.74% FeO
Hagos et al. (2017)	Field work (Axum)	P) 1.12% CaO	P) 0.05% MgO	P) 4.94% K_2O	P) 0.30% MnO	P) 0.04% P_2O_5	P) 5.47% Fe_2O_3
Manning (2010)	Review	B) 9.47% N) 2.31% CaO	B) 6.73% N) 0.77% MgO	B) 1.10% N) 5.58% K_2O	B) 0.20% N) 0.15% MnO	B) 0.35% N) 0.13% P_2O_5	B) 3.79% N) 2.25%; Fe_2O_3 B) 7.13% N) 2.05% FeO

Table A2: Interpolated data from climate models for our research sites bases on the CHELSA Climate Data (Karger et al., 2017).

Site	Annual mean temperature [C °]	Annual precipitation [mm]
Los Canarios	16.7	651
Fuente de los Roques	18.2	536
Roque Teneguía	16.5	633
Ecarpa del Volcán Teneguía	18.8	517

Table A3: A post hoc permutation test (10 000 repetitions) between the DCA ordination axes and the environmental variables (substrate, inclination, aspect, and relief) showed no significant differences between phonolite and basalt. Obviously, the variation shown in the DCA does not depend on the substrate (but there is a relationship between northernness and the fourth dimension DCA4).

	DCA1& DCA2	DCA1& DCA3	DCA1& DCA4	DCA2& DCA3	DCA2& DCA4	DCA3& DCA4
Substrate	p = 0.623	p = 0.503	p = 0.768	p = 0.289	p = 0.959	p = 0.439
Inclination	p = 0.490	p = 0.946	p = 0.315	p = 0.523	p = 0.108	p = 0.365
Northerness	p = 0.914	p = 0.526	p = 0.032	p = 0.875	p = 0.933	p = 0.921
Easterness	p = 0.293	p = 0.564	p = 0.310	p = 0.429	p = 0.213	p = 0.426
Rugosity	p = 0.212	p = 0.387	p = 0.324	p = 0.875	p = 0.933	p = 0.921

Table A4: Complete list of all study species encountered on phonolites (P) and basalt (B) including their status as SIE, MIE, native (nat.), and introduced (intr.). The taxonomy follows the standards of Plants of the World Online (POWO 2019) updated and adapted to the FloCan Checklist (Beierkuhnlein et al., 2021).

Species	Family	Rock type	Status	woody	perennial
Aeonium arboreum ssp. *holochrysum* (H.Y.Liu) Bañares	Crassulaceae	B/P	MIE	1	1
Aeonium davidbramwellii H.Y.Liu	Crassulaceae	B/P	SIE	1	1
Aeonium diplocyclum (Webb ex Bolle) T.H.M.Mes	Crassulaceae	B	MIE	1	1
Aichryson bollei Webb ex Bolle	Crassulaceae	P	SIE	0	1
Aira caryophyllea L.	Poaceae	B/P	nat.	0	0
Allium canariense (Regel) N.Friesen & P.Schönfelder	Amaryllidaceae	P	MIE	0	1
Anogramma leptophylla (L.) Link	Pteridaceae	B	nat.	0	0
Anthoxanthum odoratum L.	Poaceae	P	nat.	0	1
Arabidopsis thaliana (L.) Heynh.	Brassicaceae	B/P	nat.	0	0
Arenaria leptocladus (Rchb.) Guss.	Caryophyllaceae	B/P	nat.	0	0
Argyranthemum haouarytheum Humphries & Bramwell	Asteraceae	P	SIE	1	1
Astydamia latifolia (L.f.) Baill.	Apiaceae	P	nat.	1	1
Bituminaria bituminosa (L.) C.H.Stirt.	Fabaceae	P	nat.	1	1
Brassica oleracea L.	Brassicaceae	B	intr.	0	1
Bystropogon origanifolius var. *palmensis*	Lamiaceae	B/P	SIE	1	1
Cardamine hirsuta L.	Brassicaceae	B	nat.	0	0
Cheirolophus junonianus (Svent.) Holub	Asteraceae	P	SIE	1	1
Cosentinia vellea ssp. *bivalens* (Reichstein) Rivas Mart. & Salvo	Pteridaceae	B/P	nat.	0	1
Crassula campestris (Eckl. & Zeyh.) Endl.	Crassulaceae	B	intr.	0	0
Davallia canariensis (L.) Sm.	Davalliaceae	B/P	nat.	0	1
Echium brevirame Sprague & Hutch	Boraginaceae	B/P	SIE	1	1
Erica arborea L.	Ericaceae	P	nat.	1	1
Erigeron bonariensis L.	Asteraceae	P	nat.	0	0
Erodium botrys (Cav.) Bertol.	Geranicaeae	P	nat.	0	0
Festuca muralis Kunth	Poaceae	B	nat.	0	0
Filago germanica (L.) Huds.	Asteraceae	B	nat.	0	0
Galium aparine L.	Rubiaceae	B/P	nat.	0	0
Geranium molle L.	Geraniaceae	P	nat.	0	0
Geranium purpureum Vill.	Geranicaeae	P	nat.	0	0

Hemionitis gluckuk Christenh.	Pteridaceae	P	nat.	0	1
Hemionitis guanchica (Bolle) Christenh.	Pteridaceae	B/P	nat.	0	1
Holcus lanatus L.	Poaceae	P	nat.	0	1
Hyparrhenia hirta (L.) Stapf	Poaceae	B/P	nat.	0	1
Kleinia neriifolia Haw.	Asteraceae	P	MIE	1	1
Lavandula canariensis Mill.	Lamiaceae	P	MIE	1	1
Lobularia canariensis (DC.) L.Borgen	Brassicaceae	P	MIE	1	1
Medicago truncatula Gaertn.	Fabaceae	P	nat.	0	0
Mercurialis canariensis Obbard & S.A.Harris	Euphorbiaceae	P	MIE	0	0
Micromeria herpyllomorpha Webb & Berthel.	Lamiaceae	B/P	SIE	1	1
Monanthes muralis (Webb ex Bolle) Hook.f.	Crassulaceae	B/P	MIE	0	1
Ononis serrata Forssk.	Fabacea	P	nat.	0	0
Opuntia ficus-indica (L.) Mill.	Cactaceae	P	intr.	1	1
Parietaria debilis G.Forst.	Urticaceae	P	nat.	0	0
Paronychia canariensis (L.f.) Link	Caryophyllaceae	P	MIE	1	1
Periploca laevigata Aiton	Apocynaceae	P	nat.	1	1
Phagnalon purpurascens Sch.Bip.	Asteraceae	P	nat.	1	1
Pinus canariensis C.Sm. ex DC.	Pinaceae	P	MIE	1	1
Polycarpaea aristata (Aiton) C.Sm. ex DC.	Caryophyllaceae	B/P	MIE	0	1
Polycarpaea tenuis Webb ex Christ	Caryophyllacea	P	MIE	0/1	1
Polypodium macaronesicum A.E.Bobrov	Polypodiaceae	B/P	nat.	0	1
Pteridum aquilinium (L.) Kuhn	Pteridaceae	P	nat.	0	1
Pterocephalus porphyranthus Svent.	Caprifoliaceae	P	SIE	1	1
Rubia fruticosa Aiton	Rubiaceae	P	nat.	1	1
Rumex bucephalophorus ssp. canariensis (Steinh.) Rchb.f.	Polygonaceae	B	nat.	1	1
Rumex lunaria L.	Polygonaceae	B/P	MIE	1	1
Schizogyne sericea (L.f.) DC.	Asteraceae	B/P	nat.	1	1
Sideritis barbellata Mend.-Heuer	Lamiaceae	B/P	SIE	1	1
Solanum villosum Mill.	Solanaceae	P	nat.	0	1
Sonchus hierrensis (Pit.) Boulos	Asteraceae	P	MIE	1	1
Sonchus oleraceus L.	Asteraceae	B/P	nat.	0	0
Stachys arvensis (L.) L.	Lamiaceae	B/P	nat.	0	0
Todaroa aurea (Aiton) Parl.	Apiaceae	P	MIE	0	1
Tolpis laciniata Webb	Asteraceae	B/P	MIE	0	1
Trifolium arvense L.	Fabaceae	B	nat.	0	0
Tuberaria guttata (L.) Fourr.	Cistaceae	B	nat.	0	1
Umbilicus gaditanus Boiss.	Crassulaceae	B/P	nat.	0	1
Valeriana dentata (L.) All.	Valerianaceae	P	intr.	0	0
Wahlenbergia lobelioides (L.f.) Link ssp. *lobelioides*	Campanulaceae	B	nat.	0	0

Table A5: Environmental plot characteristics. Inclination on phonolites was (despite efforts to sample similar environments) significantly higher than on basalt. Components of exposition (northernness and easternness) and rugosity showed no significant differences (unpaired Whitney test).

	Rugosity (m)	Northerness	Easterness	Inclination (°)
Mean Basalt	3.557	0.01407	0.04970	43.0
Mean Phonolite	3.643	-0.09062	0.04303	53.8
p-value	0.7781	0.6525	0.8827	0.0277

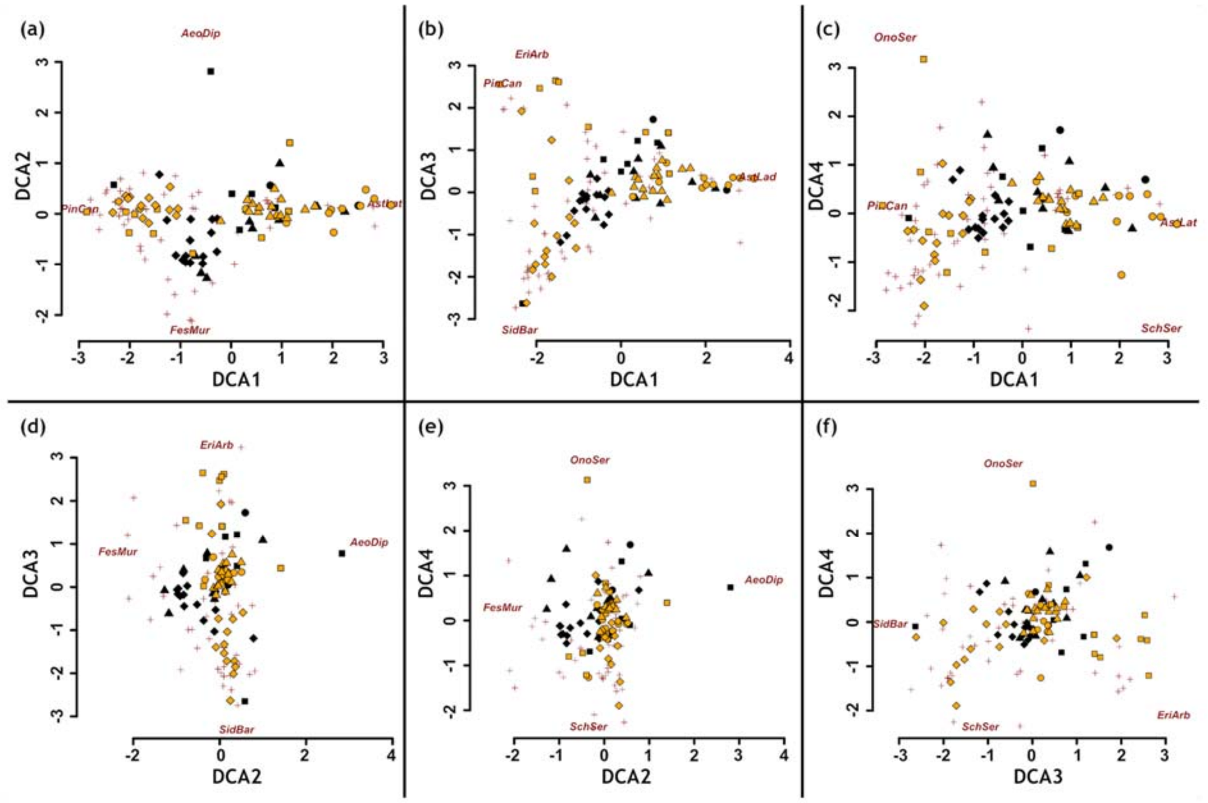


Figure A1: Detrended correspondence analysis (DCA) shows no clear difference between phonolite and basaltic rock vegetation. Yellow dots show phonolite plots, black dots basalt plots, and dark red a subset of species centroids. Species names chosen based on the most extreme values along the gradients.

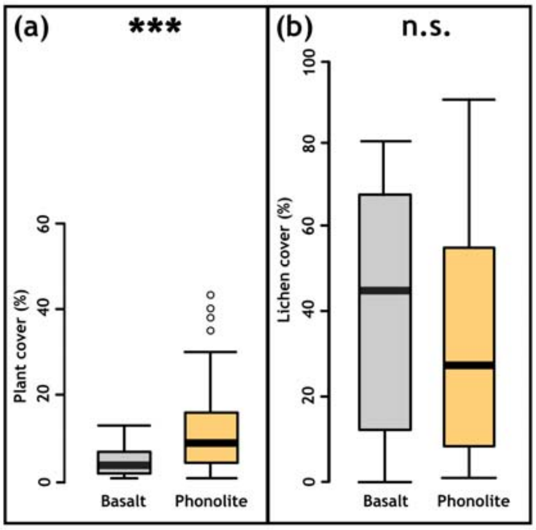


Figure A2: Vegetation cover on basaltic and phonolite plots. (a) Plant cover showed significant ($p < 0.001$, Mann–Whitney U test) and (b) lichen cover showed no significant difference between the substrates ($p > 0.05$, Mann–Whitney U test).

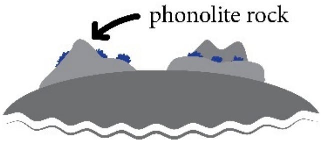
Manuscript 8

Field work to assess the impact of geodiversity on biodiversity of phonolite rocks on La Palma, Canary Islands. © Anna Walentowitz

Summary

Vegetation and plot data from phonolite rocks and basaltic outcrops obtained during fieldwork on La Palma (Canary Islands) in 2018 was published in alignment with open-access policies (Hampton *et al.* 2015; Michener 2015). The dataset can be used in biogeographic and ecological studies, and in support of biodiversity conservation. Manuscript 7 is built on the basis of the data published in this data paper.

Journal
Data in Brief



Vegetation plot and trait data from phonolitic and basaltic rocks on La Palma (Canary Islands, Spain)

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Data in Brief (2021) 37, 107229

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Abstract

Geodiversity promotes biodiversity by increasing habitat heterogeneity. In times of a global biodiversity decline, data about diversity on such geological elements gains importance, also regarding conservation and restoration. In the Canary Islands, phonolitic rocks are geological elements of volcanic origin that represent additional habitat for species. In the southern part of the island La Palma, phonolite rocks can be encountered in matrices of young lava. We provide biotic and abiotic records from 60 plots of 2 m × 2 m, sampled on phonolitic and neighbouring basaltic outcrops at four different sites that cover a wide environmental gradient. The recorded parameters were species abundances (percentage cover), plant individuals' frequency (number of plant individuals per plot and species), plant growth height (in cm), and canopy diameter (in cm). Additionally, lichen cover (percentage cover) was estimated. To describe site specific characteristics, we recorded plot surface dynamics (3D rock surface), aspect, and inclination. This data set covers vegetation and trait data comparing phonolites and basalts on La Palma. It can be used for island biogeography, vegetation ecology and conservation sciences to help support fundamental research related to insular biodiversity and endemism, and to identify priority areas for protection and preservation in the Canary Islands.

Keywords: Biodiversity, *Cheirolophus junonianus*, Endemic species, Habitat islands, Oceanic islands, Phonolite Species richness

Specifications Table

Subject	Biodiversity
Specific subject area	The vegetation plot data provided is of interest for island biogeography, vegetation ecology and relevant for questions related to insular endemism and biodiversity.
Type of data	Table
How data were acquired	Field observations and measurements.
Data format	Raw
Parameters for data collection	We collected data from 60 square 2 m × 2 m vegetation plots sampled on phonolite and on basaltic rock. In each plot, species composition, abundance (estimated percentage cover), frequency (number of individuals per species), plant height (cm), and canopy diameter (cm) were sampled. Additional information about lichens cover was measured. Finally, essential geomorphological information were collected for each plot: surface rugosity (3D rock surface), aspect and inclination.
Description of data collection	Data collection took place in spring 2018 (10–15. March). The four phonolites were selected based on Middlemost (1972) [1] and adjacent basaltic outcrops of comparable size were chosen. Biotic parameters: • Plant species were identified in the field or, in unclear cases, at our field station. Taxonomy follows the standards of "Plants of the World Online" (POWO 2019) [2]. Additional species' information, namely family, if perennial/annual and status (single- or multi-island endemic, native, introduced) were collected from Muer et al. (2016) [3] and the ATLANTIS database [4]. • Absolute frequency was calculated for each species sampled in each 2 m × 2 m plot. • Plant cover per species and total lichen cover were estimated as a fraction of the plot area and expressed as percentages.

	• Plant height for each individual was measured from the stem base to the top of the plant (in cm). Canopy diameter was measured as the maximum lateral spread of a plant (in cm). Abiotic parameters: • Plot surface rugosity (3D rock surface) was measured by placing a thread diagonally across a plot as close to the rock surface as possible. Both diagonals were measured, from the top-left to the bottom-right corner and from the top-right to the bottom-left corner. The longer the thread length needed to cover the diagonals, the higher the 3D rock surface dynamics. • Aspect was recoded with a compass and expressed in degree. • Inclination was estimated and expressed in degree.
Data source location	Region: Southern La Palma (Canary Islands) Country: Spain Coordinates of sampling sites: 28°35′01.1″N 17°52′10.2″W 28°30′56.4″N 17°50′00.1″W 28°28′51.6″N 17°51′23.5″W 28°28′40.4″N 17°51′31.8″W
Data accessibility	With the article

Value of the Data

- Habitat island studies can benefit from phonolite rocks as these island-like systems are volcanic outcrops within a matrix of surrounding basaltic rocks.
- Island biogeographers can benefit from the dataset to answer questions related to insular biodiversity and endemism, and conservationists to identify priority areas for protection and preservation.
- Global extinction risk studies are mostly focused on endemic species with small range sizes, such as the isolated habitats and populations in this study.
- Research related to the role of geodiversity for biodiversity, especially on oceanic islands, might benefit from our dataset.

1 | Data Description

We provide raw data in the form of a data table. Details about the investigated parameters are available in Table 1. An illustration of the sampling design can be found in Fig. 1.

Table 1: Table describing the investigated parameters available as raw data. The column Plot indicates a running plot ID. Longitude and Latitude are UTM coordinates (zone 28N). Rugosity1 and Rugosity2 are the two measured values of rock rugosity (3D surface). Lichen_cover is the estimated total cover of lichen for the whole plot. Species are species names of the individual sampled individuals. Species_cover indicates the estimated value of the cover of all individuals of the same species on the plot. Height is the measured plant height of all individuals in cm. Canopy_diameter is the measured canopy diameter of all individuals in cm. Rock_type indicates whether the plot is on a phonolitic or basaltic rock. "B" stands for basaltic and "P" for phonolitic rock. Perennial indicates if a species is perennial ("1") or not ("0"). Species status indicates if a species is endemic to the Canary Islands ("MIE", multi-island endemic) to La Palma only ("SIE", single-island endemic), native ("nat."), or introduced ("intr.").

Column name	**Data type**	**Unit**	**Range**	**Measurement method**	**Reference of the method**	**Levels of factors**
Plot	Nominal-scaled	–	–	Defined	-	-
Longitude	Ratio-scaled	m	218761–222706	GPS	EPSG 32628	-
Latitude	Ratio-scaled	m	3158040–3165299	GPS	EPSG 32628	-
Aspect	Interval-scaled (circular data)	°	0–355	Compass with inclinometer	-	-
Inclination	Interval-scaled (circular data)	°	0–90	Compass with inclinometer	-	-
Rugosity1	Ratio-scaled	cm	245–735	Raffia thread & measuring tape	Fig. 1	-
Rugosity2	Ratio-scaled	cm	258–565	Raffia thread & measuring tape	Fig. 1	-
Lichens_ cover	Ratio-scaled	%	1–90	Estimation	-	-
Species	Nominal-scaled	-	–	Own knowledge and literature work	[2,3]	-
Species_ cover	Ratio-scaled	%	1–30	Estimation	-	-
Height	Ratio-scaled	cm	0–550	Measuring tape	-	-
Canopy_ diameter	Ratio-scaled	cm	0.1–750	Measuring tape	-	-
Rock_type	Binary-scaled	–	–	Knowledge	-	"B", "P"
Perennial	Binary-scaled	–	–	Knowledge	-	"1", "0"
Species status	Nominal-scaled	–	–	Literature work	[3]	"SIE", "MIE", "intr.", "nat."

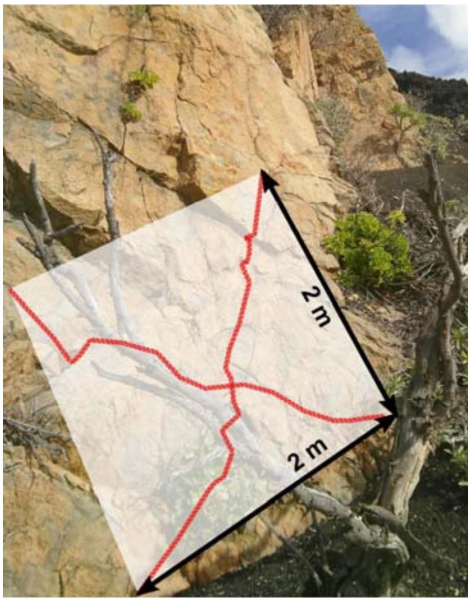

Fig. 1: Illustration of our plot design. The two black arrows indicate the plot area (2 × 2 m) in relation to the rock's inclination. The two red lines illustrate how we estimated the rock's rugosity (3D surface) using a raffia thread following the rocks surface from the bottom-left to the top-right and from the top-left to the bottom-right corner.

2 | Experimental Design, Materials and Methods

2.1 | Study design

The study focuses on phonolitic rocks and adjacent basaltic outcrops on southern La Palma. We selected four sampling sites based on geologic information about locations of phonolites given by Middlemost [1] that cover a wide environmental gradient on the island (Fig. 2). At all sites, phonolitic and adjacent basaltic outcrops were sampled. We placed plots on neighbouring rocks of comparable size. At all sites and on both phonolitic and basalitc rocks we measured a set of vegetational and environmental parameters to account for plot characteristics.

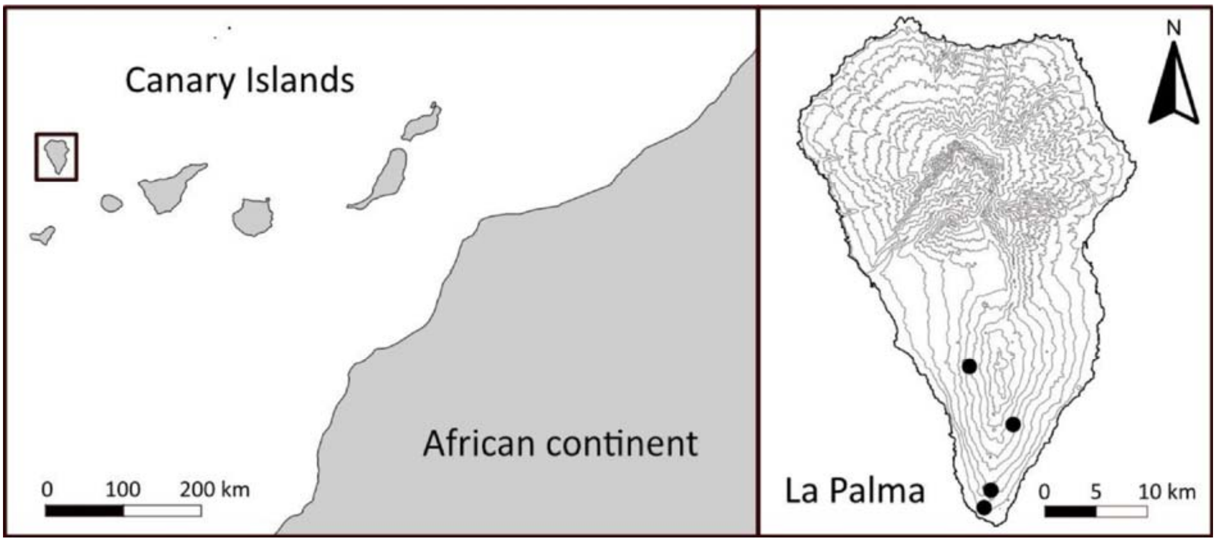

Fig. 2: Data collection took place in the Canary Islands (left) on the island of La Palma (right) at four sites in the southern part of the island (black dots).

2.2 | Data collection

The data collection took place in spring 2018 (10–15. March) and have previously been used for one publication [5]. We collected data from 60 square 2 m × 2 m vegetation plots sampled on phonolite and 60 square 2 m × 2 m vegetation plots sampled on basalt, respectively. (Total of 120 plots with 15 plots per outcrop at four locations on phonolite and four respective locations on basalt) The plots were randomly selected for each outcrop. The placement of plots was restricted to the range within accessibility. All plots were marked with GPS coordinates. The species (vascular plants) were identified and all individuals per species (frequency) were counted within each plot. Plant height and canopy diameter for all individuals were measured with a measuring tape (in cm). The total cover of each species and the total cover for existing lichens were estimated.

We collected basic topographic information for each plot. Aspect was determined with the help of a geologic compass (expressed in degree). Northness and eastness were calculated as the cosine and sinus from the aspect measurements. Inclination was estimated and raffia threats were chosen to measure the rugosity (3D rock surface as a proxy for plot surface dynamics). These were laid out as close as possible to the surface, arranged from the top-left to the bottom-right and from the bottom-left to the top-right corner of each plot (Fig. 1).

Ethics Statement

We had a permit by the Cabildo de La Palma to take samples on the Roque de Teneguía, an archaeological site. We determined the plant species and took the measurements on this rock of high cultural importance of the Canary history with special consideration and care.

Acknowledgments

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Supplementary Materials*

Supplementary material associated with this article can be found in the online version at doi: 10.1016/j.dib.2021.107229.

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* Author's comment: The supplementary materials of manuscript 8 is not included in the printed and electronic version of this thesis due to the number of pages. The supplementary materials can be accessed through the indicated doi.

Manuscript 9

Collage of plant species illustrating the diversity and beauty of species forming the flora of the Canary Islands. © Anna Walentowitz

Summary

The Canary Islands have been used extensively as natural laboratories to study ecological and evolutionary principles (e.g., Whittaker & Fernández-Palacios 2007). In support of such work, we compiled an extensive checklist of the Canary Island flora. To ease the use of the updated checklist for macroecological and biogeographical studies and to enable compatibility with large online databases, we unified the list according to the taxonomic reference database Plants of the World Online (POWO 2022). Furthermore, we match our checklist with other floras and frequently used ecological databases (e.g., TRY, GBIF). The generated pant species checklist is freely accessible in support of open-data policies.

FloCan - A Revised Checklist for the Flora of the Canary Islands

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Abstract

The flora of the Canary Islands has been subject to botanical studies for more than 200 years. Several biodiversity databases are available for the archipelago. However, there are various drivers of change in real biodiversity and the knowledge about it constantly needs to be kept track of. Island floras are both: exposed to species loss and to species introductions, either through natural processes or by anthropogenic drivers. Additionally, the evolution of endemic plant species plays a substantial role. Endemic species are sensitive to population decline due to small population sizes and possible low competitiveness against incoming species. Additionally, there is continuous progress in systematics and taxonomy. Species names or their taxonomic attribution can be modified. Here, we check published plant lists for the Canary Islands and literature, and compile currently accepted taxa into an updated checklist. For this FloCan checklist, several sources were compiled, checked for completeness and quality, and their taxonomy was updated. We illustrate how far plant names are considered in regional or global databases. This work represents the current state of knowledge on Canary Island plant diversity, including introduced and recently described taxa. We provide a comprehensive and updated basis for biogeographical and macroecological studies. Particularly, the number of non-native species is being extended substantially. The adaptation to standard international nomenclature supports integration into large-scale studies.

Keywords: alien species; archipelago; biodiversity; databases; endemism; evolutionary arena; GBIF; invasive species; island biogeography; island biota; Macaronesia; macroecology; non-native alien species; plants; TRY; EU Biodiversity Strategy

1 | Introduction

The Flora of the Canary Islands archipelago has attracted botanists for centuries. Alexander von Humboldt, for example, spent a week on Tenerife in the year 1799. During this short stay, he described the elevational distribution of plant species at the slope of Mount Teide. The iconic figure displaying the altitudinal distribution key species was published after his return to Europe in 1826 [1]. In the same year as Humboldt's ascent to Mont Teide, in 1799, the first natural history book on the Canary Islands comprising species lists, and written by Viera y Clavijo, was released [2].

Knowing about Humboldt's experiences, Charles Darwin was keen to see the vegetation of Tenerife in January 1832 when the Beagle arrived offshore. However, nobody was allowed to leave the Beagle at the harbour of Santa Cruz de Tenerife due to quarantine restrictions because of the Cholera epidemic in London at that time. Darwin depicts the situation in his report published in 1839 [3] "*Oh misery, misery—we were just preparing to drop our anchor within 1/2 a mile of Santa Cruz when a boat came alongside bringing with it our death-warrant. The consul declared we must perform a rigorous quarantine of twelve days. Those who have never experienced it can scarcely conceive what a gloom it cast on every one: Matters were soon decided by the Captain ordering all sail to be set & make a course for the Cape Verd Islands. We have left perhaps one of the most interesting places in the world, just at the moment when we were near enough for every object to create, without satisfying, our utmost curiosity". Captain Fitzroy, manoeuvring the Beagle, wrote about this situation "this was a great disappointment to Mr Darwin, who had cherished a hope of visiting the peak. To see it, to anchor and be on the point of landing, yet be obliged to turn away without the slightest prospect of beholding Tenerife again, was indeed to him a real calamity*". Having a strong background in botany, Darwin might have had an eye-opening experience if this incidence had not prevented him from exploring the flora of the Canary Islands.

The middle of the 19th century saw a strong stimulation of botanical assessments with the outstanding “Histoire naturelle des Iles Canaries” written by Philip Barker Webb and Sabin Berthelot (and Afred Moquin-Tandon) [4]. This book became the most important landmark for a complete flora of the archipelago. A few decades later, Hermann Christ [5,6] published another list of plant species in the archipelago. During the 20th century, an extensive series of floristic studies and species lists were edited with the pioneering work of Charles-Josef Pitard [7]. Increasingly new contributions by botanists such as Bornmüller, Buch, Sventenius, Broussonet, Masferrer, Burchard, Hansen, Kunkel, Sunding, Bramwell, Santos Guerra, and Schönfelder, to name but a few, increased the knowledge about the Canarian flora [8-13]. Additionally, nowadays the archipelago continues to attract the attention of international naturalists and scientists. This long legacy of botanical research evokes the impression that the plant species of the islands are well known, and it may be one of the best investigated regions of the planet. However, even though the Canary Islands were colonised and settled by Europeans centuries ago and have become an attractive destination for tourists, no complete survey of the entire islands could ever be conducted. The steep terrain of remote mountain slopes, inaccessible gorges (barrancos), and rugged cliffs at their coastline are restricting human investigations and hamper accessibility [14,15]. Substantial parts of the archipelago cannot be reached and are not even accessible to climbers due to the loose parent material of young volcanic rock.

In recent years, several new plant species have been described in the archipelago [16-21]. However, the publication of a new species does not translate directly into being incorporated and accepted in standard international databases. This process takes time. Additionally, expert knowledge exists about species that exist in nature but has not yet been addressed in official and accepted scientific publications. Several species are known and mentioned by experts but not officially described yet. This even applies to woody species of considerable size and with clear morphological distinction (Figure 1).

Figure 1: On the island of La Palma (Canary Islands) just one species of the genus *Carlina* L. with narrow leaves is listed in most floras. This species (*C. falcata* Svent.) (a) is relatively abundant and widespread on the island. However, in remote parts of northern cliffs a subspecies of *Carlina canariensis* (L.f.) Cav. was recorded recently (b), which has not been scientifically described up to now. A regular publication of this taxon following the rules of ICN (International Code of Nomenclature for algae, fungi, and plants) is in preparation. This illustrates that even for well-known genera of woody species, new species’ descriptions are still to be expected.

Furthermore, plant species recorded in the past have been reported to have disappeared (e.g., *Hypecoum procumbens* L. or *Grammitis quaerenda* Bolle), to have extinguished populations, or to have become extinct [22]. Some endemic plant species are currently at the brink of extinction (e.g., *Lotus eremiticus* A. Santos). This is a common syndrome on islands, where species populations can be small and viable population sizes can easily be undershot. Comparable examples exist in the Galapagos islands for previously important key species from the endemic genus *Scalesia* [23] or on Mauritius, exhibiting the prominent example of *Sideroxylon grandiflorum* [24]. Others are likely to have disappeared in the past and might only be reflected as genera in rare studies of pollen records [25]. Many islands have an extensive legacy of biodiversity loss. However, there is little quantitative evidence for this due to the limited preservation of plant remains.

Because of the continuous progress in plant systematics and taxonomy, there is a need to update and unify nomenclature, particularly for those genera or families under debate and for those experiencing considerable upheaval. Understandably, it is mostly those groups that have undergone rapid radiation and diversification in the archipelago, respectively, where the identification of species and their relatedness is work in progress [26-28].

During recent decades, several floras and species lists of the Canary Islands have been published and updated as online databases reflecting the state of knowledge and its rapid development. Here, we can just mention prominent examples of this vast literature [22-35]. It is difficult to decide on one work as a standard. Some are mainly rooted in regional and local knowledge; others are better related to international taxonomic standards; some are more recently published; others follow a more rigorous understanding of systematics; some are continuously updated online databases; others are printed books. When looking closer at some taxa, there is disagreement in many details, including the acceptance of species and differences in the perceptions of their systematic and taxonomic status. However, there is a general need to unify and update taxonomic and spatial information on species [36] to reflect real biodiversity at its best and to enable, e.g., inter-island comparison.

Regional flora and checklists of the Canary Islands are increasingly used in macro-ecological and biogeographical studies [37-39], which, however, may reflect just a subsection of the real species diversity of the archipelago [40,41]. The resulting findings may be questionable if a substantial part of the existing species is being ignored [42]. Furthermore, outdated taxonomy might inhibit or weaken studies at larger scales.

Openly available public webpages on endemic plants of the Canary Islands, for instance in Wikipedia, differ strongly in content between languages. The Spanish site lists 122 endemic plant species [43]; the English version linked to the same page informs about only 68 endemic plant species [44]! This illustrates that there is not a clear common ground on this topic. A reason for these differences might be the definition of endemism. It is by its nature scale-dependent [45,46] and may be subjectively defined if the area it is related to is not clearly limited [47]. Additionally, there is human bias to be considered meaning that people might be used to certain species names or taxa that have a high value in nature conservation, and that persist even if there is scientific evidence that such names can no longer be accepted and must be updated.

The advancement of knowledge and confusion due to new findings for the Canary Island flora is understandable at best with the example of the dragon tree (*Dracaena draco* (L.) L.). The dragon tree is maybe the most iconic plant species in the archipelago. Alexander von Humboldt was already fascinated by the impressive life form of several specimen in the valley of Orotava, Tenerife, back in his days. Then, 200 years later in 1997, a small population of a subspecies of *Dracaena draco* was found in the Moroccan

High Atlas Mountains (subsp. ajgal Benabid & Cuzin). In consequence, *Dracaena draco* was no longer a Macaronesian endemic species (to the Canary Islands and Cabo Verde) but an endemic subspecies (*D. draco* subsp. *draco*) for these islands. One year later, in 1998, another *Dracaena* species *Dracaena tamaranae* A. Marrero, R.S. Almeida & M. Gonzalez-Martin was found on the island of Gran Canaria, again adding an endemic *Dracaena* species to the archipelago [48]. Such surprises and discoveries would rather be expected for less famous plants or for cases where the deterministic traits are not so obvious but are astonishing for the most well-known plant taxa of the islands.

Another prominent example is the Canary Island laurel tree, a key species of the laurel forest, which is best preserved in this archipelago. *Laurus novocanariensis* Rivas Mart., Lousã, Fern. Prieto, E. Días, J.C. Costa & C. Aguiar was named *Laurus azorica* (Seub.) Franco before and even further back in time was named *Laurus canariensis* Webb & Berthel. non Willd. To add to the confusion, *Laurus canariensis* Willd. is a published but invalid synonym for another Lauracean species of the island: *Apollonias barbujana* (Cav.) Bornm. In summary, *Laurus novocanariensis*, as it is currently named, was an archipelago endemic species first, became a Macaronesian endemic, and back again an archipelago endemic taxon. The name has changed due to an increasing understanding of phylogenetic relatedness. However, it may happen that in the future this taxon could be understood as a synonym to *Laurus nobilis* L. from the Mediterranean which would mean that one more classified endemic species would be lost from the list of plant species just in the human understanding of biological taxonomy—without any consequences for nature [49].

Changes in the number of species that are described for islands are mostly due to newly introduced and even invasive species. These species are being introduced by past and present trade and travelling activities that connect the islands to other parts of the world [50]. This applies strongly to the Canary Islands that have been used as a testing ground for the acclimatisation of exotic species from the New World that were intended to be introduced to the Mediterranean as early as in the 16th century [51]. The subtropical and oceanic climate supports the establishment of many species across tropical and subtropical biogeographic realms. The differentiation of climatic conditions within the archipelago and even within topographically diverse islands with pronounced elevational zones and differences in precipitation and moisture regimes between leeward and windward sides adds to the spectrum of available habitats for the establishment of non-native biota [52]. Many plants have been introduced for ornamental purposes. Those species may remain confined to gardens or parks, but they may also start reproducing and spreading after a certain time lag and establish a legacy of offspring. However, the same mechanism applies for newly introduced species as for unknown endemics; they must first be detected before they can be registered in any database or list. Too often knowledge about cultivated ornamental plants that were established outside their natural range has been ignored until such species turned “wild” and created problems and damage.

Another process that is modifying the diversity of islands is extinction. Many of these extinction events may have occurred unnoticed since invasive species, unknown herbivores such as rabbits or goats, or other predators and pathogens have been introduced. However, the pressure of introduced herbivores on island species that have not evolved defence mechanisms is still pertinent [53]. Many endemic plant species have dramatically declined in distribution and abundance with the consequence of becoming hyper-endemic [46], surviving as remnant populations at the brink of extinction. In the case of *Lotus eremiticus* A. Santos only one “population” of few specimens remains in nature, most probably built up by a single clone [54]. One single (local) disturbance event could erase such a species globally. Considering the vulnerability of such hyper-endemics, it becomes evident that the human impact has clearly reduced intraspecific diversity. Generally, it is not a given fact that island taxa exhibit low genetic diversity as concluded from their small populations [55,56].

The genus *Aeonium* is iconic to the archipelago and is also considered as an example of adaptive radiation. Of the 42 species of the genus, 36 are endemic to the Canary Islands. Surprisingly, the phylogenetically oldest species do not originate from the continent (Morocco, Eastern Africa, Yemen), but the continental species instead represent the young branches of the phylogenetic tree [57]. The earth history of "Paleo-Macaronesia" is one explanation for this pattern [58].

Many more volcanic islands more existed in this tectonically complex area at the edge of the oceanic and the continental crust during the last 80 Mio. years. These former islands have disappeared from the ocean surface due to erosion. However, they can be detected with the help of bathymetry as guyots at the sea level of the Last Glacial Maximum 200 (LGM), which was their basis for erosion [59]. Furthermore, the spatial fluctuation of island area during the Pleistocene had an influence on plant species richness [60].

Increasingly, modern molecular methods allow for new insights into the distinction of species and to their attribution to higher phylogenetic units, influencing nomenclature, systematics, and biogeography [61-64]. Realistically, this process is a continuous one that will not end soon because of the immense diversity of plant populations and the historical focus on mere morphological traits for classification. Hidden relations between taxa need to be uncovered, and cryptic species that resemble other published species need to be identified. Consequently, data sources for regional and trans-regional assessments need to be updated continuously and adapted to international standards in nomenclature to avoid artefacts just through deviating terminologies.

The Canary Islands are an outstanding example of an essential field for ecological research, the preservation of endemic taxa, and for biogeographical studies. Here, we offer an overview of the current knowledge and perception of the flora of the Canary Islands, knowing that near future developments in phylogeny and discoveries of new species might modify this picture. Nevertheless, we identify that the customary reference to one specific list of plant species has an influence on the scientific statements made. Based on the comparison of established approaches, databases, and lists of the Canary Islands, we identified common general taxonomic agreement but also inconsistencies. Based on this overview, we present an updated and revised flora for the archipelago that is open for additions and corrections.

2 | Materials and Methods

We first reviewed and compiled published species lists for the Canary Islands [8-13,22,29-35]. The resulting plant species list was then complemented with individual publications on specific taxonomic groups for specific regions or islands. In addition, documented cultivated ornamental plants and crops were included. This study is focused on the 7 major islands of the Canary Islands archipelago: El Hierro, La Palma, La Gomera, Tenerife, Gran Canaria, Fuerteventura, and Lanzarote. With very few exceptions, all taxa are attributed to their occurrence on these islands.

Small islets in the close vicinity of Lanzarote and Fuerteventura were excluded as they have been covered in a recent study that provided a checklist for these islets [65]. However, there were no additional species listed in comparison with our checklist.

Criteria for accepting a taxon in this new FloCan plant checklist for the Canary Islands were the reliability of records and whether the respective species or subspecies name is accepted or considered a synonym following international standards of nomenclature and systematics. In the case of questionable records, additional proof was explicitly searched, and if a record for a given species on an individual island or for the entire archipelago was not found, this species was deleted from the list. The same applied if a plant population was considered an independent subspecies (or species), but this taxonomic categorization did not align with international standards. However, such synonyms or erroneously reported species are also maintained in an appendix to allow checking for the existence of these taxa in the future. For highly debated taxa, we also consider current scientific literature on plant phylogenetics (e.g., [66] for the genus *Micromeria*).

The resulting list was then compared to international standard taxonomic checklists prioritising those species that are listed in Plants of the World online (POWO) [67]. As a result, published species names in one list or dataset can translate into subspecies and vice versa.

Additionally, we consulted World Flora Online (WFO) [68] for all taxa, which is the replacement of The Plant List (TPL) [69] that has not been updated since 2013. Therefore, TPL was not considered explicitly in this checklist to avoid redundance and outdated viewpoints. We further compared all taxa with Catalogue of Life [70], which generally accepts more taxa as valid names than World Flora Online. We do not suggest that one of these databases is superior to another one. However, for standardisation we decided to follow the suggested plant names of one checklist, generally Plants of the World Online, indicating nevertheless whether other databases share the same name for a respective plant species, or suggest a synonym as the accepted name.

Additionally, we checked names in GBIF [71], which is not a taxonomic database, but is frequently used and to be considered a standard to obtain species' distribution data. Furthermore, we screened the TRY [72,73] database for plant functional traits. These international databases differ in terms of scientific scrutiny and their general philosophy. For example, TRY does not provide author citation, which is a substantial part of botanical names.

In this study, databases are not evaluated. Rather it shall be illustrated which taxa are considered under the name given in this checklist (or under a synonym) in these prevalent databases. We follow, with only very few exceptions, in the naming for plant species, genus, family, and subspecies the standards of POWO. Other infraspecific units (e.g., varieties) are only considered in a few cases. There is no clear agreement across checklists to which degree infraspecific taxa should be considered below the level of subspecies.

Deviating nomenclature or missing representation in other plant lists is protocolled. This option in our checklist illustrates which taxa are generally accepted and where no consistent opinion across published plant species lists can be seen. There are cases where the same species' name was published by several authors. Confusion could result from missing author citations if one of these apparently equitable names is defined as a synonym of another accepted species.

For list comparison we used a semi-automatised approach and compared our species list with global databases via the "taxize" package [74] applied in R [75]. Every species for which several or no results were given were rechecked manually. However, this filter was complemented by individual reviews and revisions for all taxa, to overcome, for example, deviating spelling of names. Botanical publications that are based on taxa should follow the International Code of Nomenclature for algae, fungi, and plants (ICN) as a global compilation of published plant names in scholarly publications serves the International Plant Names Index (IPNI) [76]. However, IPNI is not aiming to provide the latest state of knowledge for the progress in taxonomy and its reflection in botanical nomenclature.

Island biota and endemic species, but also recently published data on taxa with revised nomenclature, are likely to be underrepresented in global databases. This needs to be considered to avoid data bias in trans-regional biodiversity studies. In our checklist, the current state of representation of Canary Island plants in these databases is protocolled, even though such data repositories will further develop towards higher completeness and representation. This comparison serves as orientation on the reliability of research that uses such open data sources without scrutinising and comparing every single species.

In addition to published floras and plant lists, we reviewed the current botanical literature, focusing on studies about recently documented established non-native species and taxonomic studies for selected species groups [77-108]. These studies are sources for additional species records and changes in plant names, which are not yet included in global or regional databases.

To indicate taxa that are highly debated compared to others, we checked the number of published synonyms in POWO. Infraspecific taxa such as subspecies and varieties are also listed if they are officially published. We separate our analyses for different taxonomic levels. In some genera (e.g., *Aeonium*, *Micromeria*) a series of hybrids are described. Hybrids are listed in a separate table in order not to ignore this aspect of biodiversity, but also to show that such organisms, that might appear with a certain regularity, have not evolved (yet) to accepted species.

Finally, we suggest an updated plant list including information on the spatial distribution of taxa across the Canary Islands and their status. We classify native species as probably native and surely native. Non-native species were categorised as probably non-native in cases where this is not certain, surely non-native and invasive non-native (i.e., intruding into and substantially modifying natural ecosystems). The term "non-native" is being used as a synonym of the term "alien". Our study aims to improve the picture of the currently existing taxa on the island, but also to acknowledge that numerous taxa are unanimous or under debate.

3 | Results

This new FloCan checklist informs about the current state of knowledge of the flora of the Canary Islands considering regional floras and international taxonomic databases as well as specific publications (Supplement Materials Part S1–S6). It aims at providing a transparent overview of the acceptance of species and infraspecific names, suggesting a revised checklist. The total number of accepted taxa in this checklist sums up to 2812 (1781 native, 1031 non-native), comprising 2416 species (1452 native, 964 non-native) and 396 infraspecific taxa (329 native, 67 non-native) (Supplement Materials Part S1, Main Table for species and Infraspecific taxa).

There are substantial differences between islands in the number and proportion of native and non-native taxa, species, and infraspecific taxa (A species list can be found in Supplement Materials Part S2). The proportion of native taxa is high for the arid islands with less topographic diversity in the eastern part of the archipelago (Fuerteventura and Lanzarote) (Figure 2). Islands with a large human population such as Tenerife or Gran Canaria posess a large number of non-native species. Generally, there are not many non-native infraspecific taxa, which reflects that such biota are an indicator of ongoing speciation.

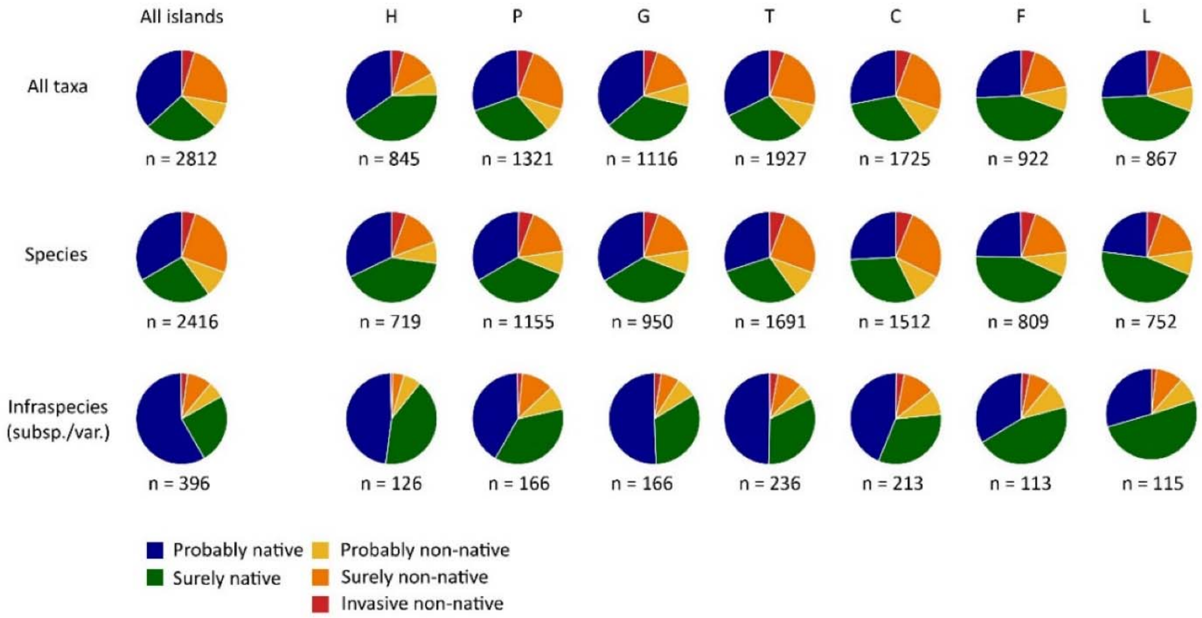

Figure 2: Categories of native and non-native taxa in the Canary Islands and for the individual islands El Hierro (H), La Palma (P), La Gomera (G), Tenerife (T), Gran Canaria (C), Fuerteventura (F) and Lanzarote (L) based on the here presented checklist. Proportions are given at the level of all taxa, and separately for species and infra specific taxa (sub-species and varieties). Absolute numbers of taxa are given below the pie charts. Generally, the proportion of accepted native infraspecific units (subspecies, varieties) is higher compared with the accepted species. Highest numbers of taxa are listed for the large islands with pronounced topography and diverse climatic conditions.

Within the native taxa (Figure 3), we find a consistent proportion of endemic taxa between approx. 20 and 40 per cent. The proportion of single-island endemic species (SIE) is only higher in comparison with multi-island (archipelago) endemics (MIE) for the sum of all taxa and species across all islands. On individual islands, the proportion of MIE is always larger than that of SIE. The arid islands with less pronounced relief again show comparable patterns, dominated by native species that are non-endemic. Surprisingly, the proportion (and absolute number) of SIE is very small also for El Hierro, whereas the other mountainous islands exhibit a consistently high proportion of SIE. Infraspecific taxa exhibit higher proportions of SIE and MIE compared to species or taxa level consistently for all individual islands but show the opposite pattern for the entire archipelago.

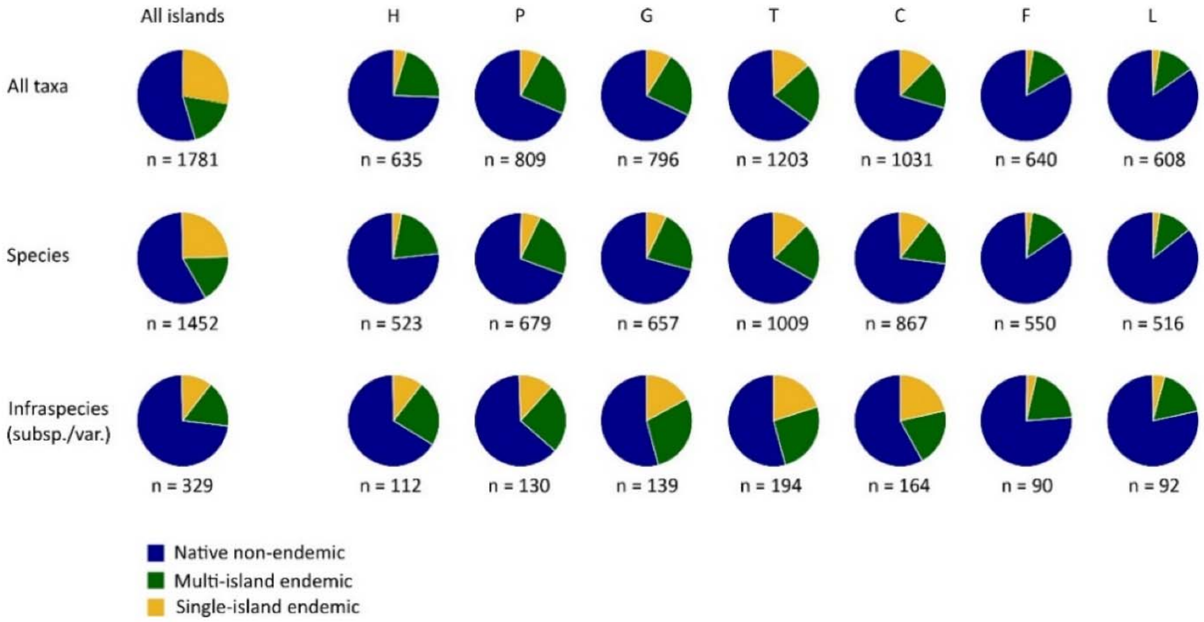

Figure 3: Categories for native taxa subdivided into native non-endemic species (blue), multi-island endemics (green) and single island endemics (yellow). Proportions are given at the level of all taxa, and separately for species and infraspecific taxa (sub-species and varieties). Absolute numbers of taxa are given below the pie charts (n). The relations are illustrated for the entire Canary Islands archipelago (All islands) and for the individual islands El Hierro (H), La Palma (P), La Gomera (G), Tenerife (T), Gran Canaria (C), Fuerteventura (F) and Lanzarote (L). Surprisingly, approximately one quarter of all species in the entire archipelago are SIE. The highest proportions of endemic taxa relate to the islands with pronounced topography and diverse climatic conditions (H, P, G, T, C).

As this FloCan checklist provides an updated list of plant taxa, including their representation in other existing floras and databases, we want to illustrate to what degree other lists are deviating from the here suggested taxonomy (Figure 4). Uncertainty is generally high for infraspecific taxa. The reflection of accepted taxa is good in GBIF. However, many accepted taxa, mainly endemic and infraspecific taxa are not well represented in the TRY database, which can cause bias in ecological studies.

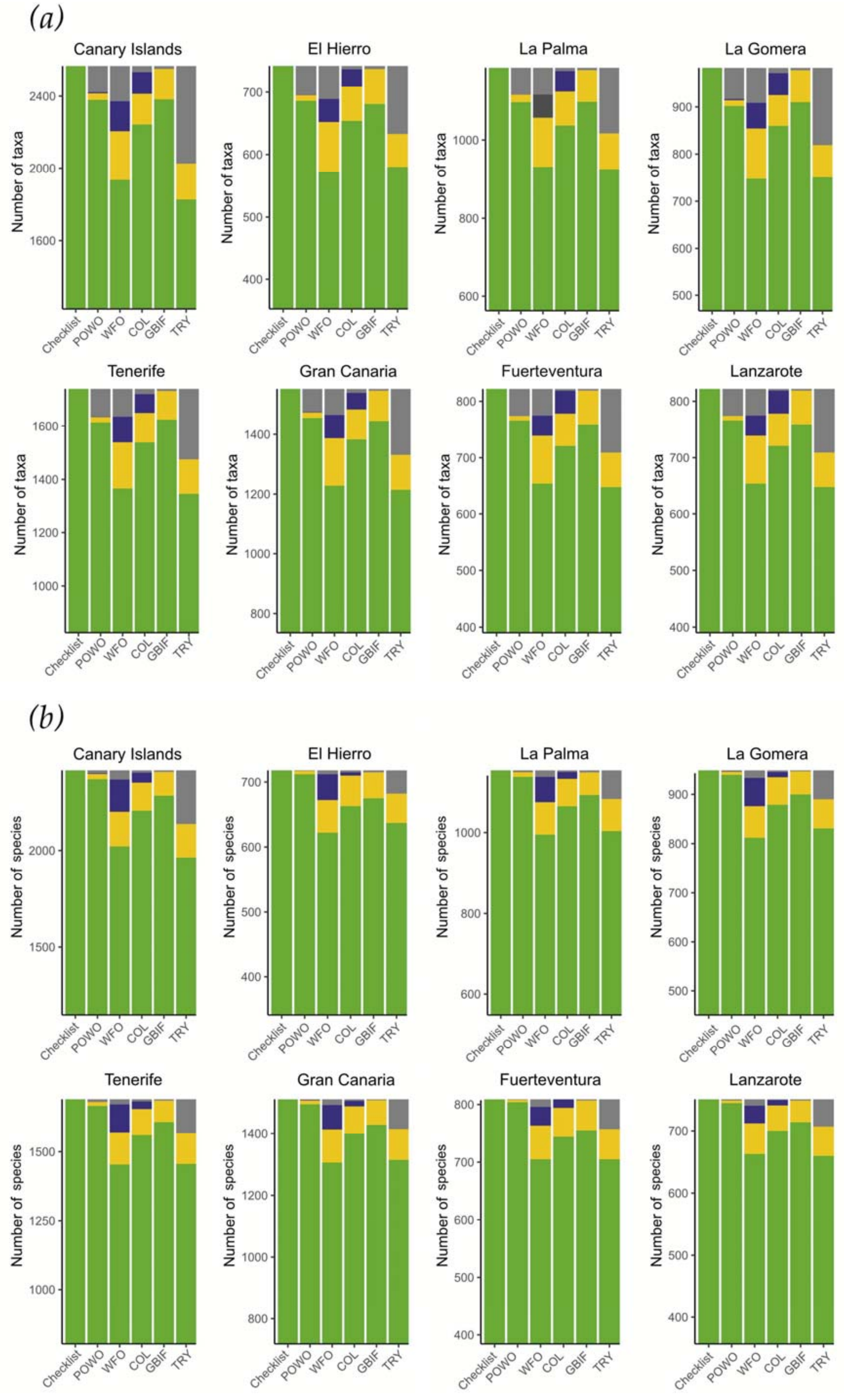

Figure 4 continued

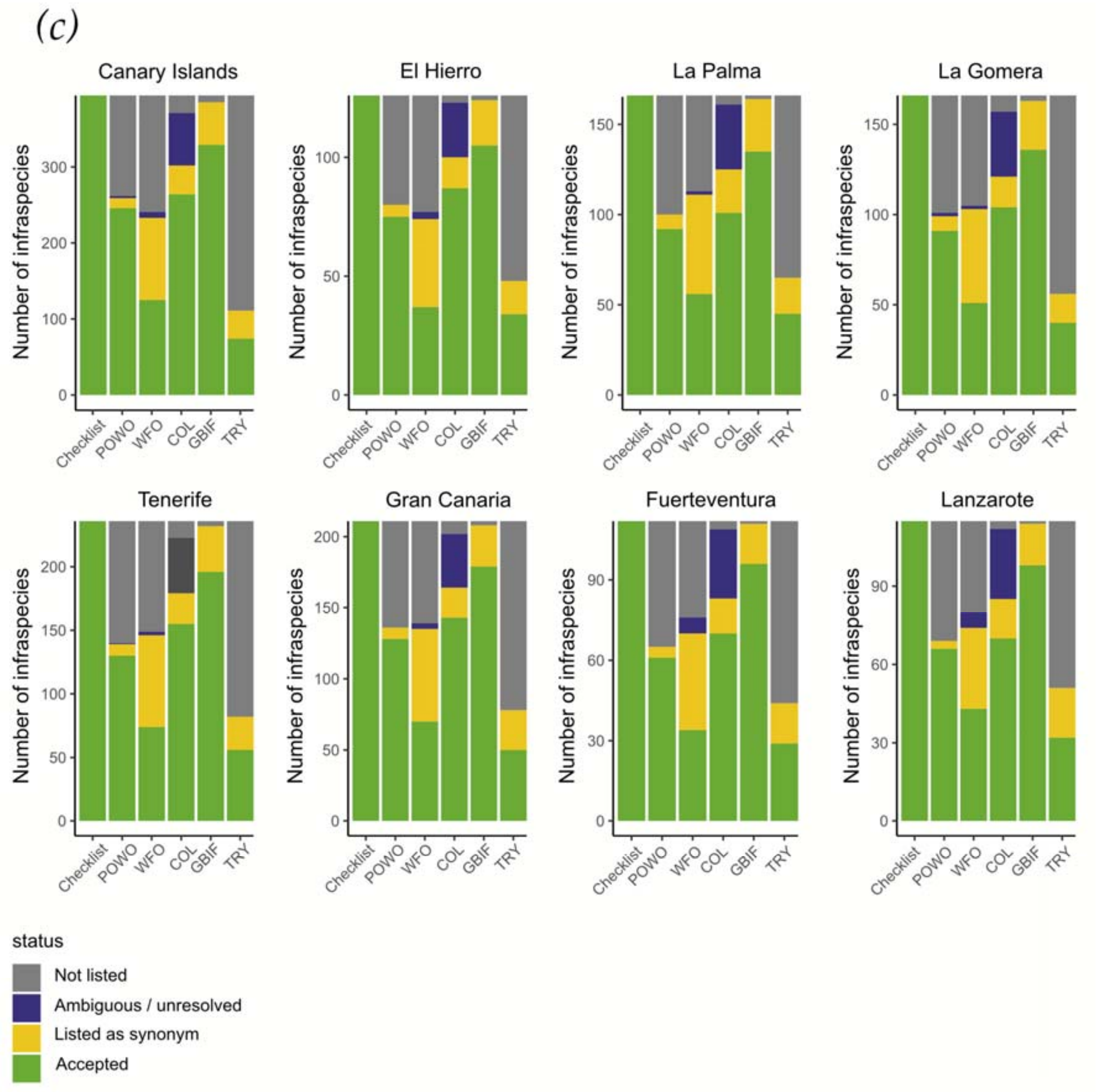

Figure 4: Representation of the accepted taxa suggested in this checklist for the Canary Islands in global databases. (a) for all taxa, (b) for species, and (c) for infraspecific taxa (subspecies and varieties). Note that scales for (a,b) do not begin with 0 taxa/species but start at 50% of each individual y-axis to work out differences. Axis (c) for infraspecific taxa start in 0. Numbers of accepted taxa diverge between POWO and WFO, reflecting that POWO was taken as a reference. COL numbers are close to those of POWO, which supports the decision to select this database for reference. The patterns for individual islands resemble the pattern of the entire archipelago.

Generally, the compiled list of taxa is well reflected in two currently applied reference lists for the flora of the Canary Islands [22,34] (Figure 5). However, a substantial number of taxa appear in these lists as not-accepted synonyms, and also in international reference databases (Figure 4).

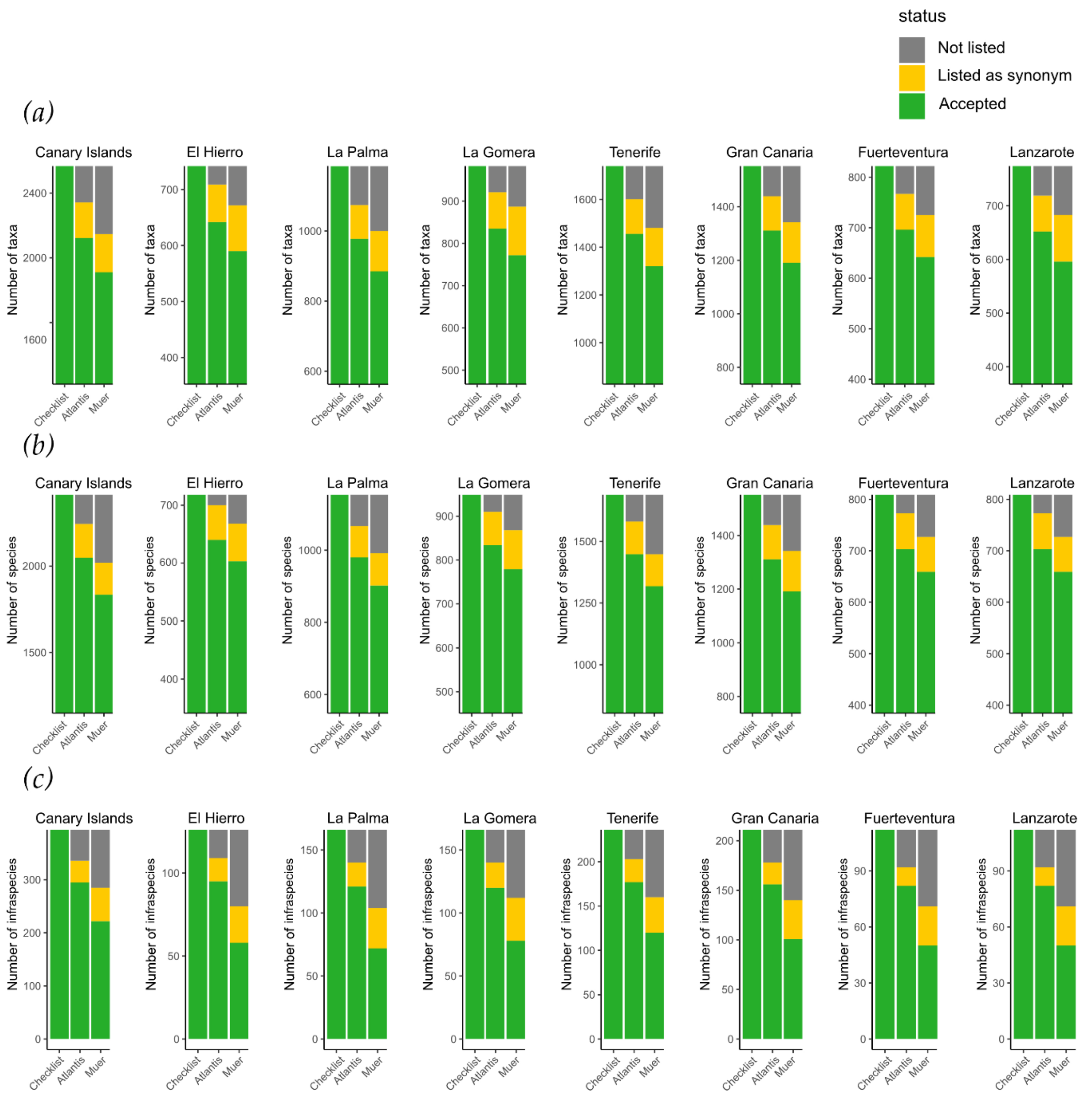

Figure 5: Comparing numbers of the here presented FloCan Checklist (without hybrid taxa, synonyms, and non-naturalized ornamental garden and park plants) with the Atlantis database [22] and with the taxa of Muer et al. [34] separately for (a) taxa, (b) species and (c) infraspecies (subspecies, varieties). Categories given are “not listed” in the respective database, “listed as synonym” and “accepted”. This comparison illustrates how many of the accepted taxa in FloCan are also reflected in other established references.

In addition to the main checklist, we add a list of currently not considered taxa that were published for the Canary Islands before, illustrating the reason for exclusion such as being a synonym of another accepted taxon or an obviously erroneous record or misunderstanding (Supplement Materials Part S5). As it does not make sense to list all synonyms ever published, which can sum up to more than 100 for a single species, we report those synonyms in detail in Supplement Materials Part S6 that are used in the above-mentioned datasets and floras referred to in this checklist to guide readers towards accepted names in this checklist.

Published hybrids are listed in addition, in a separate list (Supplement Materials Part S3), as this field is highly likely to be incomplete, and less clearly regulated. Particularly in specific genera (e.g., *Micromeria*) several hybrids are described. As hybrid speciation can be an important process, hybrids contribute to the biodiversity of the Canary Islands.

Furthermore, we add a list of not (yet) naturalized plants planted in gardens and parks (Supplement Materials Part S4), focusing on recorded perennial, long-lived plants because those species might naturalise and establish in the future. This list contains non-native exotic species that have not been found and reported yet to produce natural offspring. The species of this list are not included in the here presented analyses as we could not compile an exhaustive list of these species given the information available.

In Table 1, we provide a comparison for the taxa accepted in the FloCan Checklist (Supplement Materials Part S1, Main Table) with other modern plant lists such as Atlantis Biota or Muer et al. Major differences relate to the consideration of recently recorded non-native species, but also to taxonomic revisions.

Table 1: Numbers of accepted plant taxa (families, genera, species, subspecies, varieties) in the FloCan checklist for the Canary Island archipelago in comparison with other current plant lists (Atlantis, Muer) and with reference to the accepted taxa in international taxonomic data bases Plants of the World Online (POWO), Catalogue of Life (COL), World Flora Online (WFO), GBIF and TRY.

Taxonomic Level	FloCan	Atlantis Biota	Muer et al.	POWO	COL	WFO	GBIF	TRY
Year	2021	2021	2016	2021	2021	2021	2021	2021
Families	171	162	155	171	166	164	170	166
Genera	863	747	699	854	815	775	832	788
Species	2416	2050	1834	2370	2207	2022	2284	1965
Infraspecifics	396	295	222	247	264	125	329	74

Differences in the number of families are related to deviating reflection of changes in plant taxonomy and systematics. The splitting up of the family Scrophulariaceae is one of several examples of fundamental changes in plant families. Additionally, the increasing consideration and recording of exotic species contributes to an increase in plant families, respectively.

Progress in the exploration of species and in systematics reveals that a flora (plant list) is a moving target due to processes such as the increasing identification of endemism (Table 2) through records of new species or molecular identification of their taxonomic separation. Another process contributing to the ongoing changes in regional biodiversity is the establishment of non-native species (Table 3). Both processes are considered in the updated FloCan checklist.

Table 2: Numbers of endemic species and endemic infraspecific taxa (subspecies, varieties) in current plant lists of the Canary Island archipelago.

Taxonomic Level	FloCan	Atlantis Biota	Muer et al.
Year	2021	2021	2016
Species	608	541	499
Infraspecifics	197	147	152

Table 3: Numbers of non-native species and non-native infraspecific taxa (subspecies, varieties) in current plant lists of the Canary Island archipelago.

Taxonomic Level	FloCan	Atlantis Biota	Muer et al.
Year	2021	2021	2016
Species	964	781	662
Infraspecifics	67	44	16

4 | Discussion

This new checklist reflects the current state of knowledge on the Flora of the Canary Islands, one of the most important evolutionary arenas in the holarctic realm [109]. This knowledge is under constant change and development. Therefore, it seems impossible to provide one final product, even in the case of the Canary Islands archipelago, which has been subject to botanical studies since the beginning of the 19th century. New species are still being found that were not known to science before, while small endemic populations of species are at the brink of extinction. Additionally, new non-native species are introduced as crops, ornamental plants or accidentally, and then may become established in the natural or semi-natural environment close to settlements or along roadsides. Some of these species become invasive, intruding into natural communities, and modifying ecosystems and their functioning, partly resulting in a deterioration of ecosystem services. Such ongoing and even accelerated changes resulting from the mostly undersaturated floras of islands combined with increasing connectivity due to transport and traffic make island biota a moving target.

For only very few taxa, no occurrence records could be attributed to specific islands, although these taxa occur or have occurred in the archipelago. Such species are listed in some sources as occurring in the archipelago, but without a precise location on specific islands or without confirmation during the last decades. One endemic plant species (*Solanum nava* Webb. & Berthel.) is likely completely extinct now, although this was already thought to be the case in the 1970s. One species has most likely become regionally extinct (*Grammitis quaerenda* Bolle), and three others have not been recorded for years (*Glinus lotoides* L., *Hypecoum procumbens* L., *Picris hieracioides* L.). Nevertheless, such taxa were not excluded as there is a chance of rediscovery. Other species with no clear local records in this list are part of complex groups that require specialist knowledge (e.g., *Taraxacum campylodes* G.E. Haglund). Currently missing clear local records also apply to some ornamental plants such as *Acanthus spinosus* L., *Amphilophium crucigerum* (L.) L.G. Lohmann, or *Syagrus weddelliana* (H.Wendl.) Becc. and to some tree species that have been planted in forestry (e.g., *Pinus sylvestris* L.).

In Supplement Materials Part S4 we provide an additional list of plant species recorded in gardens and parks. This list aims to create awareness about possible additional invasion processes even if the specimens do not yet show natural regeneration and dispersal. We encourage, however, the monitoring of these species, as some of these have been recorded to become invasive in other places of the world (e.g., *Artemisia absinthium* L.). Some herbaceous species on this list, such as *Sanguisorba minor* L. could naturalise rapidly without necessarily becoming invasive. As several of these garden and park species are trees and shrubs, they might invade and modify natural ecosystems. Nevertheless, such a list can only be incomplete as there is a constant import of ornamental plants. For the reasons of non-proven natural regeneration and incompleteness, this list was separated from the general checklist. Consequently, the main FloCan checklist does not comprise these ornamental garden plants. Here, we exclude them from the analyses, even if they can become non-native members of the natural vegetation quite rapidly.

Progress in taxonomy and systematics results in modified attribution of organisms to species, subspecies and even genera and families. This may be uncomfortable for practitioners that are used to specific terms and may even affect legal regulations with fixed terminology and nomenclature, but it is an intrinsic and essential condition of botanical sciences. Because of this continuously ongoing struggle to improve the understanding of nature, there is no complete agreement on all facets of taxonomy within the scientific community. Even if there are clear rules and regulations for accepting a scientific name, it may take time until such insights are generally accepted and translated into floristic inventories. However, deviating viewpoints will always exist.

Global databases are "work in progress" constantly being subject to change. Moreover, they can be incomplete, particularly for island biota. This applies mainly to the TRY database [72], which includes only very few infraspecific taxa, does not inform about species names' authors (which can result in errors due to synonyms), and misses many endemic species. However, the frequent use of such sources in large-scale studies implies the necessity to clarify to which degree island biota are covered and which restrictions need to be considered.

A global invader can serve as an example for a possible confusion of plant names. *Pennisetum setaceum* (Forssk.) Chiov. appears in GBIF [71] as *Pennisetum setaceum* (Forssk.) Chiov. as well as *Cenchrus setaceus* (Forssk.) Morrone, with deviating occurrence records for the Canary Islands. A total of 8970 records are provided for *C. setaceus* for all Canary Islands but only 4473 records are given for *P. setaceum*, including no reference for the island La Gomera (status 28 June 2021). This illustrates that a critical screening of available data is recommended because this is just one species, and a fully automated data mining can hardly recognise such errors that can even occur for widespread species when the nomenclature has changed or synonyms have been published. This species is listed in our checklist as *Cenchrus setaceus* (Forssk.) Morrone. This is also the name of the species in the Atlantis Biota data base of the Cabildo Insular of the Canary Islands [22]. However, it appears under a synonym in Muer et al. [34]. Our reference database for international standards, Plants of the World Online [67], also accepts this name, as well as Catalogue of Life [70], whereas it is seen as ambiguous in World Flora Online [68]. Comparable thorough screening across databases was done for all taxa in our checklist.

If endemic plants on oceanic islands are seen as a reflection of ongoing evolutionary processes, infraspecific variation cannot be ignored. Subspecies or varieties may not be very precisely defined and can be seen as beyond the biological species concept. However, speciation has many facets, including hybrid speciation and apomixis. Hence, biogeographical assessments which are aiming to characterise the moving target of evolution cannot ignore such infraspecific units. Again, it was Charles Darwin who was very aware of this fact. In August 1857 he wrote to J.D. Hooker: "*I am got extremely interested in tabulating according to mere size of genera, the species having any varieties marked by greek letters or otherwise: the result as far as I have yet gone seems to me one of the most important arguments I have yet met with, that varieties are only small species—or species only strongly marked varieties. The subject is in many ways so very important for me; I wish much you would think of any well-worked Floras with from 1000–2000 species, with the varieties marked. It is good to have hair-splitters & lumpers*" [110]. Hopefully, Charles Darwin would have been happy with the plant list provided herewith.

Today, big data algorithms are applied in biogeographic research relying on the correctness of species names, records and occurrence. (e.g., [38-42,60,111,112]). Such analyses are dependent on the expert knowledge fed into databases and their maintenance and quality control. However, there are many sources of error in databases because real-time control cannot be implemented and autotomized, or AI (artificial intelligence) algorithms are not (yet) able to replace expert knowledge, including specific challenges for certain taxa that exhibit, for instance, apomictic processes for reproduction. Additionally, the progress in phylogenetic research is not equal across taxonomic groups, with some being more thoroughly scrutinised because there is a larger scientific community working with these. In contrast, others are more neglected with the consequence of a possibly outdated nomenclature.

The Canary Islands are of outstanding importance to biodiversity covered by the European Union and should be considered strongly in the implementation of the EU Biodiversity Strategy for 2030 [113]. Ongoing land use changes, pressures related to tourism, climate change and additionally, the negative impact of introduced alien herbivores [114] are calling for a reinforced commitment in nature conservation [115]. The designation of protected areas is a common tool in conservation, requiring a sound knowledge of the uniqueness of biota, including infraspecific taxa. Databases and checklists are an important basis for such strategies [116]. The Canary Island protected area network is a work in progress. Besides the management of protected areas, the entire archipelago should be seen as a cradle of nature [109]. To achieve the objective to preserve its biodiversity of the future, laws and regulations need to be efficiently implemented, but in addition, enhanced support in human resources and financial endowment is required.

This FloCan checklist is the result of an in-depth survey on regional literature and web-based platforms, including own experience, data recording in the field and screening of international standard databases. It reflects the current understanding of taxa and the recent information about species records. Each flora, however, is a work in progress or can even be seen as a “moving target”. Additional non-native species can be expected to establish, and even endemic species not yet known to science can be discovered in remote places. Additionally, cryptic taxa can be hidden under the disguise of morphological similarity and will be detectable with molecular methods. Here, we update the state of knowledge in the present moment. Nevertheless, our transparent approach to illustrate converging, but also deviating perceptions and points of view in common plant lists enables more critical and realistic biogeographical assessments.

5 | Conclusions

The Canary Island archipelago is a hotspot of plant endemism and a safe site for remnant populations of plant taxa that have become extinct on neighbouring continents during Pleistocene and even Holocene climatic fluctuations. The oceanic climate, combined with pronounced topography, offers suitable habitats for a wide range of species and plant functional groups. However, the total species richness is, like on all islands, relatively low due to dispersal filters. Non-native species have become abundant since humans contributed to their transport, establishment, and provision of disturbed and anthropogenic habitats. Processes that are contributing to phytodiversity, such as invasion, extinction, or evolution, are progressing with varying momentum and different speeds. Furthermore, they do not proceed equally on all islands or in all ecosystems. The global importance of the Canary Islands requires a continuous survey and monitoring of biodiversity. The FloCan checklist aims to reflect the state of knowledge in July 2021 and is very likely to be amended and adapted in the future. Progress in phylogenetics may modify the status of well-known taxa. Still, new species are being discovered, and more and more non-native species are likely to become establish and detected. Additionally, ornamental plants may start regenerating after a lag period or develop possible invasive population dynamics under climate change. Therefore, this study explicitly includes many non-native plants that were missing in previous lists. Being adapted to the current international taxonomy standards, this list can be used for trans-regional or even global biogeographical studies.

Data Availability Statement

The data provided by this study are documented in the Supplementary Materials.

Acknowledgments

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Supplementary Materials*

The following material is available online at https://www.mdpi.com/article/10.3390/d13100480/s1, Part S1: FloCan Main List (Accepted plant species and infraspecific taxa); Part S2: FloCan Plant Species List; Part S3: Published hybrids (not included in biogeographical analyses); Part S4: Recorded non-naturalized garden plants and plants in public places such as parks (not included in biogeographical analyses); Part S5: List of previously reported plants that were excluded and explanation for exclusion; Part S6: Synonyms used in currently published plant lists (but not accepted in FloCan).

* Author's comment: The supplementary materials of manuscript 9 is not included in the printed and electronic version of this thesis due to the number of pages. The Supplementary materials can be accessed through the indicated permanent link.

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The listed references refer to the introductory chapters 1-5 and the manuscript summaries preceding each of the nine manuscripts presented in this thesis.

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Appendix

Appendix 1

During the writing process of my doctoral thesis, I contributed to the following peer-reviewed scientific publications, which were not included in my doctoral thesis as these differ from the overarching topic of the thesis.

Manuscript A1:
Title: The biome inventory –Standardizing global biogeographical land units
Authors: Jan-Christopher Fischer, **Anna Walentowitz**, Carl Beierkuhnlein
Journal: *Global Ecology and Biogeography* (2022) 00, 1–12

Manuscript A2:
Title: Outdoor cycling activity affected by COVID-19 related epidemic-control-decisions
Authors: Anne-Maria Schweizer, Anna Leiderer, Veronika Mitterwallner, **Anna Walentowitz**, Gregor Hans Mathes, Manuel Jonas Steinbauer
Journal: *PLOS ONE* (2021) 16(5), e0249268

Manuscript A3:
Title: Impact of climatic conditions on radial growth of non-native *Cedrus libani* compared to native conifers in Central Europe
Authors: Nikola Zsolnay, **Anna Walentowitz**, Gregor Aas
Journal: *PLOS ONE* (2023) 18(5), e0275317

Manuscript A4:
Title: Endemic species predation by the introduced smooth-billed ani in Galápagos
Authors: Sophia C. Cooke, David Anchundia, Emma Caton, Lucy E. Haskell, Heinke Jäger, Yatindra Kalki, Óscar Mollá, Jacqueline Rodríguez, Tristan D. Schramer, **Anna Walentowitz**, Birgit Fessl
Journal: *Biological Invasions* (2020) 22, 2113–2120

Appendix 2

Table A2: Presentation of own research at scientific conferences.

Conference	Date	Contribution, Title & Authors
Island Biology Conference (La Réunion, France)	8 – 13 July 2019	Poster: Natural recruitment of *Scalesia pedunculata* on Galápagos after control of invasive plants, by Anna Walentowitz
BayCEER Workshop 2019 (Bayreuth, Germany)	10 Oct. 2019	Poster: Impacts of the invasive grass species *Pennisetum setaceum* on plant diversity patterns on La Palma (Canary Islands), by Anna

		Walentowitz, Severin D.H. Irl, Aurelio Jesús Acevedo Rodríguez, Ángel Palomares-Martínez, Vanessa Vetter, Barbara Zennaro, Félix M. Medina, Carl Beierkuhnlein
Deutscher Kongress für Geographie 2019 (Kiel, Germany)	25 – 30 Sept. 2019	Talk: Natural recruitment of the endemic tree species *Scalesia pedunculata* after invasive woody plant species control, by Anna Walentowitz, Michael Manthey, Heinke Jäger Poster: Impacts of the invasive grass species *Pennisetum setaceum* on plant diversity patterns on La Palma (Canary Islands), by Anna Walentowitz, Severin D.H. Irl, Aurelio Jesús Acevedo Rodríguez, Ángel Palomares-Martínez, Vanessa Vetter, Barbara Zennaro, Félix M. Medina, Carl Beierkuhnlein
EGU General Assembly 2021 (online)	19 – 30 April 2021	Talk: Trait spaces of non-native plants at community level in the Canary Islands, by Anna Walentowitz, Carl Beierkuhnlein
IBS Early Career Biogeographers Conference (online)	22 – 14 Oct. 2021	Talk: How island ecosystems - the labs of biogeographers – are affected by outdoor recreational activities, by Anna Walentowitz, Manuel Steinbauer
10th Biennial conference of the International Biogeography Society (Vancouver, Canada)	2 – 6 June 2022	Talk: How plant dispersal syndromes shape the relationship of species richness with area and isolation, by Anna Walentowitz, Claudia Troiano, Julie B. Christiansen, Manuel Steinbauer, Anders S. Barfod
BfN Workshop Aktuelle Biodiversitätsforschung 2022 (Island Vilm, Germany)	15 – 19 Aug. 2022	Talk: Biodiversität auf Inseln im Anthropozän, by Anna Walentowitz
Neobiota 12th International Conference on Biological Invasions (Tartu, Estonia; online participation)	12 – 16 Sept. 2022	Talk: Paleoecological perspective on the abundance of alien plant species on islands, by Anna Walentowitz, Manuel Steinbauer, Bernd Lenzner, Nichola Strandberg, Simon Connor, Álvaro Castilla Beltrán, Franz Essl, Sandra Nogué
Bauhin (Basel, Switzerland)	15 – 16 Sept. 2022	Poster: Flora of the Canary Islands – Revised Checklist to a Classic Arena of Botany, by Anna Walentowitz, Carl Beierkuhnlein, Walter Welss
BayCEER Workshop 2022 (Bayreuth, Germany)	13. Oct. 2022	Talk: Palaeoecological trajectories of non-native vegetation on islands, by Anna Walentowitz, Manuel Steinbauer, Bernd Lenzner, Nichola Strandberg, Simon Connor, Simon Haberle, Álvaro Castilla Beltrán, Franz Essl, Sandra Nogué

Appendix 3

During my time as a PhD candidate, I reviewed manuscripts submitted to be considered for publication to the *Journal of Biogeography*, *Diversity and Distributions*, and *Environmental Conservation*.

Eidesstattliche Versicherungen und Erklärungen

(§ 9 Satz 2 Nr. 3 PromO BayNAT)

Hiermit versichere ich eidesstattlich, dass ich die Arbeit selbstständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe (vgl. Art. 64 Abs. 1 Satz 6 BayHSchG).

(§ 9 Satz 2 Nr. 3 PromO BayNAT)

Hiermit erkläre ich, dass ich die Dissertation nicht bereits zur Erlangung eines akademischen Grades eingereicht habe und dass ich nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden habe.

(§ 9 Satz 2 Nr. 4 PromO BayNAT)

Hiermit erkläre ich, dass ich Hilfe von gewerblichen Promotionsberatern bzw. -vermittlern oder ähnlichen Dienstleistern weder bisher in Anspruch genommen habe noch künftig in Anspruch nehmen werde.

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Hiermit erkläre ich mein Einverständnis, dass die elektronische Fassung meiner Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung unterzogen werden kann.

(§ 9 Satz 2 Nr. 8 PromO BayNAT)

Hiermit erkläre ich mein Einverständnis, dass bei Verdacht wissenschaftlichen Fehlverhaltens Ermittlungen durch universitätsinterne Organe der wissenschaftlichen Selbstkontrolle stattfinden können.

Bayreuth, 30. November 2022