

# A roadmap to plant functional island biogeography

Julian Schrader<sup>1,2\*</sup> , Ian J. Wright<sup>1</sup> , Holger Kreft<sup>2,3</sup>  and Mark Westoby<sup>1</sup> 

<sup>1</sup>*Department of Biological Sciences, Macquarie University, Sydney, NSW, 2109, Australia*

<sup>2</sup>*Department of Biodiversity, Macroecology and Biogeography, University of Goettingen, Büsgenweg 1, 37077, Goettingen, Germany*

<sup>3</sup>*Centre of Biodiversity and Sustainable Land Use (CBL), University of Goettingen, Büsgenweg 1, 37077, Goettingen, Germany*

## ABSTRACT

Island biogeography is the study of the spatio-temporal distribution of species, communities, assemblages or ecosystems on islands and other isolated habitats. Island diversity is structured by five classes of process: dispersal, establishment, biotic interactions, extinction and evolution. Classical approaches in island biogeography focused on species richness as the deterministic outcome of these processes. This has proved fruitful, but species traits can potentially offer new biological insights into the processes by which island life assembles and why some species perform better at colonising and persisting on islands. Functional traits refer to morphological and phenological characteristics of an organism or species that can be linked to its ecological strategy and that scale up from individual plants to properties of communities and ecosystems. A baseline hypothesis is for traits and ecological strategies of island species to show similar patterns as a matched mainland environment. However, strong dispersal, environmental and biotic-interaction filters as well as stochasticity associated with insularity modify this baseline. Clades that do colonise often embark on distinct ecological and evolutionary pathways, some because of distinctive evolutionary forces on islands, and some because of the opportunities offered by freedom from competitors or herbivores or the absence of mutualists. Functional traits are expected to be shaped by these processes. Here, we review and discuss the potential for integrating functional traits into island biogeography. While we focus on plants, the general considerations and concepts may be extended to other groups of organisms. We evaluate how functional traits on islands relate to core principles of species dispersal, establishment, extinction, reproduction, biotic interactions, evolution and conservation. We formulate existing knowledge as 33 working hypotheses. Some of these are grounded on firm empirical evidence, others provide opportunities for future research.

We organise our hypotheses under five overarching sections. Section A focuses on plant functional traits enabling species dispersal to islands. Section B discusses how traits help to predict species establishment, successional trajectories and natural extinctions on islands. Section C reviews how traits indicate species biotic interactions and reproduction strategies and which traits promote intra-island dispersal. Section D discusses how evolution on islands leads to predictable changes in trait values and which traits are most susceptible to change. Section E debates how functional ecology can be used to study multiple drivers of global change on islands and to formulate effective conservation measures.

Islands have a justified reputation as research models. They illuminate the forces operating within mainland communities by showing what happens when those forces are released or changed. We believe that the lens of functional ecology can shed more light on these forces than research approaches that do not consider functional differences among species.

**Key words:** community assembly, conservation, dispersal, evolution, extinction, functional diversity, functional ecology, island biogeography, species establishment, trait space

## CONTENTS

I. Introduction	2852
II. Section A: dispersal to islands	2853
(1) Dispersal to remote islands	2856

\* Address for correspondence (Tel: +61-298507111; E-mail: jschrad@uni-goettingen.de)

(2) Within-archipelago dispersal	2858
III. Section B: establishment, succession and natural extinction	2858
(1) Establishment and succession	2859
(2) Natural extinctions	2860
IV. Section C: biotic interactions, reproduction and within-island dispersal	2860
(1) Biotic interactions and reproduction	2860
(2) Within-island dispersal	2861
V. Section D: evolutionary shifts in traits and trait syndromes	2862
VI. Section E: global change, threat by invasive species and conservation	2863
VII. Conclusions	2864
VIII. Acknowledgements and author contributions	2864
IX. References	2864
X. Appendix A. Methodological and statistical approaches for functional island biogeography	2868
(1) Island–mainland comparisons	2868
(2) Functional trait spaces	2868
(3) Community (weighted) means	2868
(4) Functional diversity	2868
(5) Null models	2868
(6) Functional groups	2869
(7) Species-interaction networks	2869
(8) Molecular-phylogenetic approaches	2869
(9) Data and resources for functional island biogeography	2869

## I. INTRODUCTION

In this review we hope to persuade readers that much can be gained from considering island biogeography in terms of functional traits that can surely inform us about the processes shaping island assemblages. Functional traits are morphological and phenological characteristics of an organism or species that express aspects of its ecological strategy, scale up from individuals to properties of populations, communities and ecosystems, and can be used to quantify dimensions of ecological variation across organisms, populations, species, communities and ecosystems (Díaz & Cabido, 2001; Westoby *et al.*, 2002; Díaz *et al.*, 2016). Island biogeography describes the spatial distribution of organisms, populations, species, communities or ecosystems on islands and other isolated habitats, and the processes generating these patterns (Whittaker & Fernández-Palacios, 2007). Consequently, we define functional island biogeography as the study of ecological and evolutionary processes that shape the structure, diversity and functioning of island assemblages, as viewed specifically through the lens of functional traits and plant ecological strategies.

Island life has sparked the imagination of generations of scientists. Many species are unable to cross the large distances that separate islands from neighbouring landmasses. Species that do make the crossing and establish often evolve into distinct forms and functions after colonisation. This triggered ideas about evolution for both Darwin and Wallace (Darwin & Wallace, 1858; Darwin, 1859). Other influential theories include the Equilibrium Theory of Island Biogeography (MacArthur & Wilson, 1967), and more modern theories that combine colonisation, speciation and extinction as dynamic processes with the physical characteristics of islands

(Fernández-Palacios *et al.*, 2016; Borregaard *et al.*, 2017). Nevertheless, we are still scratching the surface of understanding processes and outcomes leading to the wealth of island species forms and functions found today.

Early research on islands concentrated on aspects of natural history, describing, for example, species characteristics for long-distance dispersal, adaptive radiations or unique evolutionary pathways of island species, with strong emphasis on deterministically describing island assemblages (Darwin, 1859; Wallace, 1880; Carlquist, 1965, 1974). Carlquist (1965, 1974) developed an important framework to understand species dispersal and evolution on islands. Core principles were that, due to the over- or underrepresentation of certain clades or functional groups, island assemblages are disharmonic entities compared to their mainland counterparts (Carlquist, 1974; König *et al.*, 2021), and that island biotas tend to follow distinct evolutionary pathways known as island syndromes (Carlquist, 1974; Burns, 2019). Carlquist's principles about island life remain relatively underrepresented in modern studies (Midway & Hodge, 2012), perhaps because they do not translate directly into testable predictions.

In MacArthur & Wilson's (1967) Equilibrium Theory of Island Biogeography (hereafter ETIB), species richness on islands is determined as an equilibrium between immigration and extinction rates. Larger and less isolated islands support more species than smaller or more isolated ones. The ETIB's simple and elegant assumption of species being ecologically neutral in predicting diversity patterns on islands triggered a plethora of studies of species richness, paved the way for neutral assembly theory and still forms the basis for many island studies and theories today (Whittaker & Fernández-Palacios, 2007; Whittaker *et al.*, 2017).

A limitation of the ETIB, and other island biogeographical models, is their strong focus on species richness (in the case of

the ETIB) and/or endemism with species implicitly treated as functionally equivalent. Many recent studies in island biogeography have moved beyond a strictly species-richness-centred approach, and called for new and extended frameworks to understand species dispersal and persistence, community assembly, island disharmony and evolutionary pathways on islands and how ecological, biogeographical and evolutionary processes interact with the dynamic abiotic environment (e.g. Whittaker *et al.*, 2014; Jacquet *et al.*, 2017; Ottaviani *et al.*, 2020; Schrader, 2020; König *et al.*, 2021). Functional island biogeography, as an emerging discipline, holds great potential to close the gap between the study of species characteristics and island biogeography (Violle *et al.*, 2014; Patiño *et al.*, 2017; Ottaviani *et al.*, 2020).

On continents, functional biogeography has substantially advanced our understanding of spatial biodiversity patterns (Violle *et al.*, 2014), and has provided firm quantification of, for example, global drivers of leaf size and the leaf economic spectrum (Wright *et al.*, 2004, 2017), wood density (Šimová *et al.*, 2018; Poorter *et al.*, 2019), plant growth forms and height (Šimová *et al.*, 2018; König *et al.*, 2019) and seed size (Moles *et al.*, 2007). Functional approaches in island biogeography are surprisingly underrepresented in the scientific literature today and it still remains largely unknown why traits vary across islands and how (Ottaviani *et al.*, 2020).

Strong dispersal and establishment filters and non-random diversification acting on island biota lead to a biased subset of species compared to the source pool, which can be the closest mainland or a set of other, larger islands (Carlquist, 1974; König *et al.*, 2021). Carlquist called island assemblages ‘disharmonic’ in this sense, but focused almost entirely on taxonomic disharmony using *post hoc* inferences on certain traits as an explanation (König *et al.*, 2021). For instance, ferns are overrepresented on islands, and this is likely due to ferns being efficient long-distance dispersers (Kreft *et al.*, 2010). For our part, we do not find harmony *versus* disharmony helpful for capturing the differences in traits between mainland and island assemblages. But the point stands that island assemblages are often selected subsets of a species pool, which consequently may follow unique but predictable ecological and evolutionary pathways (Whittaker & Fernández-Palacios, 2007; Ottaviani *et al.*, 2020). Because island assemblages are modified compared to equivalent sites on the mainland, they can reveal processes of community assembly that might otherwise be invisible.

Here, we address the potential for integrating functional ecology into island biogeography. We focus on plants, but the general considerations and concepts may extend to other taxa. We review the literature on how functional traits on islands might relate to species dispersal, establishment, extinction, reproduction, biotic interactions, evolution and conservation. In particular, we formulate existing knowledge as a set of 33 working hypotheses.

Our review is organised into five sections: Section A focuses on plant functional traits enabling species dispersal to islands, which we discuss separately for dispersal to (i) remote islands and (ii) within archipelagos. Section B

addresses how functional traits help to predict (i) species establishment and successional trajectories and (ii) natural extinctions on islands. Section C discusses (i) biotic interactions and reproduction strategies of species and (ii) their adaptations to intra-island dispersal. In Section D, we review how evolution on islands may lead to predictable changes in trait values and which traits are most affected by evolution. In Section E, we discuss how global change in form of rising sea levels, habitat destruction and invasive species threatens native island plants and how functional ecology can be used to formulate effective conservation guidelines.

In each section, we formulate a set of working hypotheses (Table 1), review the evidence supporting them and suggest directions for future research. Hypotheses invoke processes (eight hypotheses) and outcomes (25 hypotheses). Processes include prevailing dispersal vectors, successional pathways or principles of evolution. Outcomes describe trait patterns shaped by these processes, such as prevalence of seeds with anemochorous appendages on remote islands. Taken together, our hypotheses can be used as a provisional framework for predicting plant species traits on islands. Our aim is that, over time, these working hypotheses can be solidified or falsified and replaced. Together, this should advance our understanding of how insularity shapes island biota.

## II. SECTION A: DISPERSAL TO ISLANDS

Many islands worldwide are of oceanic origin or have been submerged at some point in their ontogeny. All extant terrestrial species (or their ancestors) once dispersed there. But even for islands that were never submerged, such as most continental-shelf or land-bridge islands, colonisation by dispersal can be an important influence on their species assemblages (MacArthur & Wilson, 1967; Cody, 2006).

In order to reach an island, propagules may have to cross large expanses of ocean. The distance over water acts as a dispersal filter, selecting out propagules not possessing traits linked to the prevailing dispersal vectors (Fig. 1A). Vectors enabling dispersal over water are wind, sea currents, vegetation rafts and volant or swimming animals (Nathan *et al.*, 2008; Gillespie *et al.*, 2012). The respective traits suitable to harness these vectors are small size and/or anemochorous appendages, floating and/or saltwater-resistant propagules or edible fruits or those suitable for epizoochorous dispersal (Carlquist, 1974; Nathan *et al.*, 2002). The degree of island isolation – either in form of sheer distance to the next source pool, unfavourable wind and water currents, surrounding landmass proportions or the presence of stepping stones (Weigelt & Kreft, 2013) – has profound effects on the relative representation of these dispersal vectors and thus the prevalence of certain dispersal traits in island assemblages (Keppel, Lowe & Possingham, 2009; Gillespie *et al.*, 2012). We discuss dispersal filters under two categories: (i) dispersal to remote islands (>100 km) and (ii) intra-archipelago dispersal or dispersal from nearby source pools (a few km to <100 km; Fig. 1A; Gillespie *et al.*, 2012).

Table 1. Summary and overview of the 33 hypotheses on plant functional island biogeography. Hypotheses are numbered according to appearance in the text and divided into processes (P) and outcomes (O). Island variables indicate geoenvironmental factors suitable to address and test hypotheses. Plant functional traits linked to hypotheses are listed in the 'Traits' column. Methods and statistical approaches are explained in the Appendix (Section X). CWM, community (weighted) mean; FD, functional diversity; FG, functional group; FTS, functional trait spaces; IMC, island–mainland comparison; NM, null model

Section	Hypotheses	Island variables	Traits	Methods and statistics	References
Section A Remote islands	P H1	Dispersal to remote islands is coupled to (i) seabird dispersal, (ii) wind dispersal or (iii) ocean currents.	Island area and isolation		Renner (2004); Gillespie <i>et al.</i> (2012); Alsos <i>et al.</i> (2015); Vargas <i>et al.</i> (2015)
	O H2	On oceanic islands, successful colonisers have traits suitable for long-distance dispersal.	Island isolation	Seed mass, propagule appendages, floating and saltwater resistance	FG Carlquist (1974); Gillespie <i>et al.</i> (2012)
	O H3	The proportion of species with propagules small enough to be easily carried by wind, or adapted to wind and water dispersal increases with island isolation.	Island isolation	Seed mass and size, propagule appendages	FG CWM Carlquist (1974)
	O H4	Plants specialised for dispersal by seabirds have external attachments and their prevalence in a community increases with island isolation.	Island isolation	Propagule appendages	FG CWM Aoyama <i>et al.</i> (2012); Nogales <i>et al.</i> (2012)
Section A Within-archipelago dispersal	P H5	Endozoochorous dispersal is the most successful dispersal vector within archipelagos rich in volant frugivores; wind dispersal is predominant in archipelagos poor in volant frugivores.	Island location and climate		Meehan <i>et al.</i> (2002); Kissling <i>et al.</i> (2009); Carvajal-Endara <i>et al.</i> (2017); Onstein <i>et al.</i> (2017)
	O H6	Seed mass of propagules with anemochorous appendages decreases with island isolation and increases for fleshy, scented and colourful propagules.	Island isolation	Seed mass	FG CWM Schrader <i>et al.</i> (2021b)
	O H7	For plants with fleshy and colourful fruits, fruit size is coupled to the size of volant frugivores and to other traits such as gape width.	Island frugivore diversity	Fruit mass, size, colour and type	FG CWM Wheelwright (1985); Onstein <i>et al.</i> (2017)
Section B Establishment and succession	P H8	Species establishment success after dispersal depends on the strength of prevailing abiotic and biotic interaction filters and is mediated by traits.	Island age, area and isolation, habitat diversity, communities present		Carlquist (1974); Whittaker <i>et al.</i> (1997); Schrader <i>et al.</i> (2021a)
	O H9	Species establishing on very small or young islands or in pioneering habitats have traits tolerating high initial adversity, including salt spray, sand blasting, high irradiation, strong wind near the ground and sometimes nutrient-poor conditions.	Island area and age	Plant height, stem density, leaf mass per area, leaf N and P content, leaf cuticle thickness	CWM FTS Neufeld <i>et al.</i> (2017); Schrader <i>et al.</i> (2021b)
	O H10	With increasing island age, area and heterogeneity, species assemblages change – expressed by a shift in trait compositions.	Island age, area and habitat diversity	All traits relevant to describe species communities	CWM FTS FD IMC Whittaker <i>et al.</i> (1989); Burns & Neufeld (2009); Karadimou <i>et al.</i> (2018); Schrader <i>et al.</i> (2021a, 2021b)
	O H11	With degree of island isolation, the proportion of species with pioneer traits increases, even in late-successional communities.	Island isolation	Plant height, stem density, leaf mass per area	FG Cordell <i>et al.</i> (1998)
Section B Natural extinctions	P H12	Extinction risk on islands can be predicted from functional traits and is coupled to (i) population-level processes and stochasticity, (ii) disturbance and catastrophic events caused by geological events such as mega landslips, volcanic activity, sea level transgressions, island subsidence, erosion and tsunamis, (iii) habitat loss or (iv) co-extinctions of mutualists.	Island area, sea level change, disturbance, mutualist diversity		Burns & Neufeld (2009); Gray (2019)

(Continues)

Table 1. (Cont.)

Section	Hypotheses		Island variables	Traits	Methods and statistics	References
Section C Biotic interactions and reproduction	O H13	Extinction risk is greater at the margins of island trait spaces where traits indicate <i>(i)</i> specialised mutualistic relationships, <i>(ii)</i> slow life cycles and <i>(iii)</i> low seed output.		Seed output, dispersal syndrome, plant height, stem density, mycorrhizal type	FG CWM	Sakai <i>et al.</i> (2002); Burns & Neufeld (2009); Whittaker <i>et al.</i> (2014)
	P H14	Diversity of mutualists including pollinators and animal seed dispersers decreases with increasing island isolation.	Island isolation			Bawa (1980); Givnish (2010); Hiraiwa & Ushimaru (2017); Delavaux <i>et al.</i> (2019); Razanajatovo <i>et al.</i> (2019); Taylor <i>et al.</i> (2019)
	O H15	Functional diversity of traits linked to mutualistic relationships and reproduction decreases with island isolation.	Island isolation	Mycorrhiza, pollination mode, flower morphology	FD	Hiraiwa & Ushimaru (2017); Delavaux <i>et al.</i> (2019)
	O H16	With increasing island isolation, the proportion of species increases that <i>(i)</i> have generalist pollination strategies, <i>(ii)</i> are self-compatible or <i>(iii)</i> reproduce vegetatively.	Island isolation	Flower morphology, pollination syndromes, vegetative reproduction	FG	Baker (1955); Delavaux <i>et al.</i> (2019); Razanajatovo <i>et al.</i> (2019); Taylor <i>et al.</i> (2019)
	O H17	The presence, absence and frequency of different pollination strategies and traits related to pollination (e.g. flower size, colours, length of nectar spurs and rewards) in island communities depends on the presence, absence and frequency of insects and other pollinators.	Communities present	Pollination syndromes	CWM FG	Bawa (1980); Givnish (2010); Alsos <i>et al.</i> (2015); Grossenbacher <i>et al.</i> (2017)
Section C Within-island dispersal	P H18	Selection for dispersal within islands can favour different vectors compared to those that initially brought species to the island.	Diversity of animals on islands			Cody & Overton (1996); Olesen & Valido (2003); Albert <i>et al.</i> (2020)
	O H19	Low-lying islands or sites, such as atolls, have a high proportion of water-resistant propagules and those with sticky or bristly appendages.	Island elevation and type	Anemochorous appendages, salt water resistance	FG CWM IMC	Carlquist (1974)
	O H20	High-elevation sites on islands have high proportion of <i>(i)</i> species with small seeds and <i>(ii)</i> propagules with anemochorous appendages.	Island elevation	Seed mass, anemochorous appendages	FG CWM	Kreft <i>et al.</i> (2010); Keppel <i>et al.</i> (2016)
Section D Evolution	O H21	Islands with well-developed vertebrate communities also have a high proportion of zoochorous-dispersed plants.	Diversity of animals on islands	Fruit type and colour	NM IMC	Whittaker <i>et al.</i> (1997); García-Verdugo <i>et al.</i> (2014)
	P H22	Evolution of traits follows predictable trajectories across islands depending on the degree of isolation, vacancy of niches and priority effects, level of competition and presence of herbivores and/or mutualists.	Island isolation, area, habitat diversity, species communities present			Jorgensen & Olesen (2001); Silvertown (2004); Givnish (2010); Gillespie <i>et al.</i> (2012); García-Verdugo <i>et al.</i> (2017); Biddick <i>et al.</i> (2019); Burns (2019)
	O H23	Absence of mutualists results in trait shifts towards generalist strategies.	Island isolation, communities present	Pollination and dispersal syndromes	FTS FG	Jorgensen & Olesen (2001); Grossenbacher <i>et al.</i> (2017)
	O H24	Propagules with anemochorous appendages, water resistance or small seeds evolve towards <i>(i)</i> fleshiness, <i>(ii)</i> loss of appendages or <i>(iii)</i> larger seed masses.	Island area, age and isolation	Fruit type and mass, propagule appendages, salt water resistance	FTS IMC	Cody & Overton (1996); Givnish <i>et al.</i> (2009); Kavanagh & Burns (2014); García-Verdugo <i>et al.</i> (2017)
	O H25	Insularity causes trait convergence, i.e. large species or organs become smaller and small species or organs become larger.	Island type and isolation	Leaf size, flower and fruit size, plant height	IMC CWM	Biddick <i>et al.</i> (2019); Burns (2019)
	O H26	On oceanic islands, herbaceous species tend to evolve secondary woodiness.	Island climate, communities present	Woodiness, stem specific density	IMC FG	Carlquist (1974); Lens <i>et al.</i> (2013); Burns (2019)

Table 1. (Cont.)

Section	Hypotheses		Island variables	Traits	Methods and statistics	References
Section E Global change, threat by invasive species and conservation	O H27	Island species lose defence mechanisms against herbivores.	Herbivore diversity	Spinescence, secondary, chemical compounds	IMC CWM	Bowen & Van Vuren (1997); Burns (2016); Meredith <i>et al.</i> (2019)
	H28	Adaptive island radiations should lead to a detectable and predictable expansion of functional trait space.	Island area, age and isolation	All traits relevant to describe species communities	FTS	Givnish <i>et al.</i> (2009); Blonder <i>et al.</i> (2016)
	P H29	Invasive species, progressive loss and fragmentation of natural habitats and rising sea levels are the main drivers of island species extinctions and this is mediated by traits.	Anthropogenic pressure, island elevation, number of herbivores			Arellano-Cataldo & Smith-Ramírez (2016); Moser <i>et al.</i> (2018); Aikio <i>et al.</i> (2020); Westerband <i>et al.</i> (2021)
	O H30	Species with slow reproductive cycles and poor dispersal abilities are most threatened by extinction.	Anthropogenic pressure, island elevation	Plant height, number of seeds, dispersal syndrome, stem density	FG FTS	Harter <i>et al.</i> (2015); Gray (2019)
	O H31	Species that have lost defence mechanisms against herbivores are more likely to suffer negative impacts from introduced feral herbivores.	Herbivore diversity	Spinescence, secondary chemical compounds, leaf mass per area, plant height	FG CWM FTS	Bowen & Van Vuren (1997)
	O H32	Alien plants with traits connected to high competitive and dispersal ability and/or unspecific pollination syndromes are more likely to become invasive on islands.	Non-native species diversity, infrastructure	Seed output, plant height, leaf mass per area, flowering period, pollination syndrome	FTS FG	Baruch & Goldstein (1999); Marx <i>et al.</i> (2016); Westerband <i>et al.</i> (2021)
	O H33	Islands with a low trait diversity in the native flora should be more susceptible to invasion.	Native and non-native species diversity	All traits relevant to describe species communities	FTS FD	Denslow (2003)

## (1) Dispersal to remote islands

### Processes:

H1. Dispersal to remote islands is coupled to (i) seabird dispersal, (ii) wind dispersal or (iii) ocean currents.

### Outcomes:

H2. On oceanic islands, successful colonisers have traits suitable for long-distance dispersal.

H3. The proportion of species with propagules small enough to be easily carried by wind, or adapted to wind and water dispersal increases with island isolation.

H4. Plants specialised for dispersal by seabirds have external attachments and their prevalence in a community increases with island isolation.

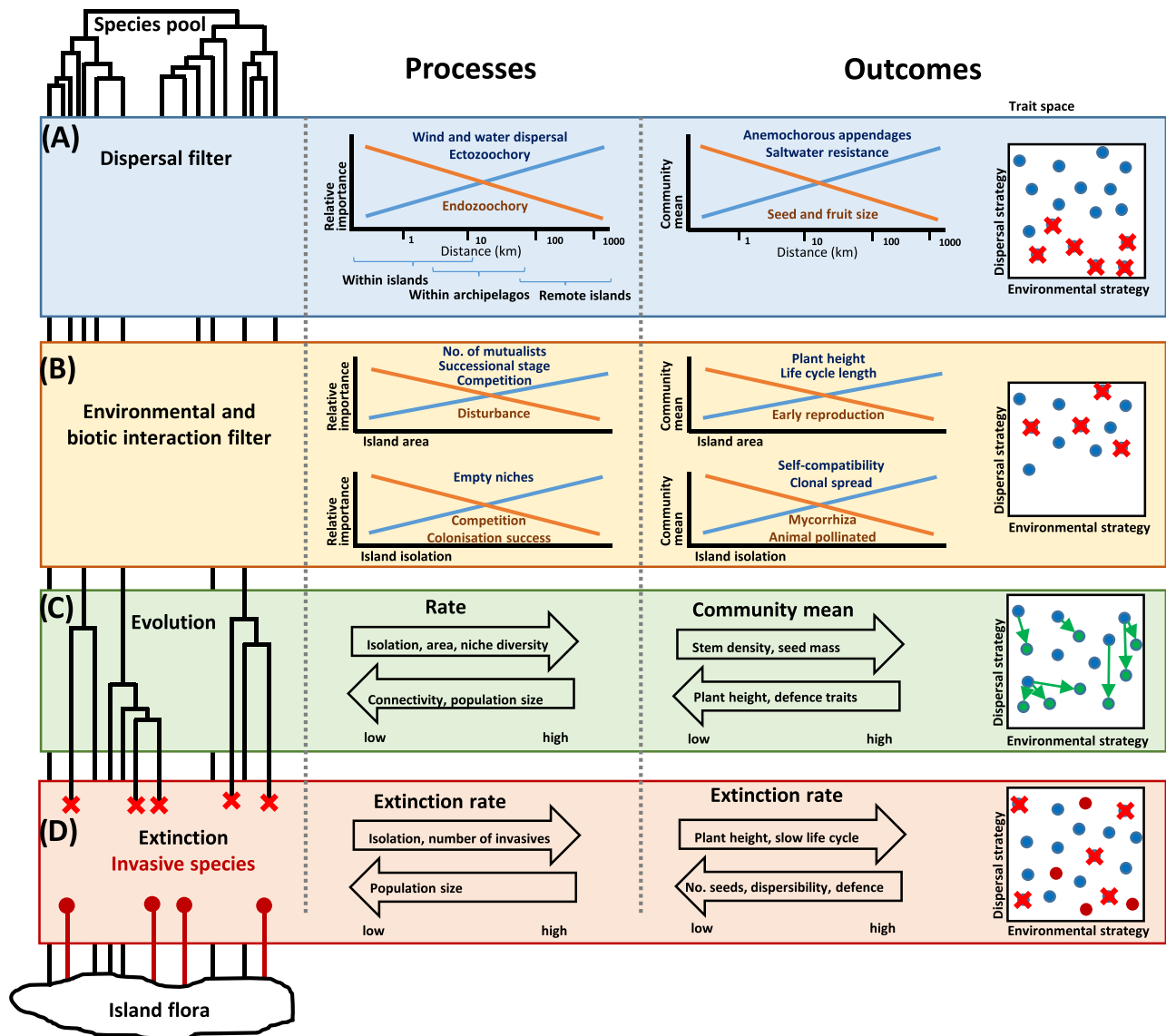
Dispersal to remote islands is a rare event, occurring for only tiny fractions of all seeds produced and including a highly stochastic component (Nathan, 2006; Vargas *et al.*, 2012; Heleno & Vargas, 2015). Only very occasionally has arrival of long-distance dispersed propagules been documented (e.g. Costin, 1965; Smith, 2012). Conventionally, dispersal traits are inferred from the species found on islands rather than from direct observations of dispersal events (Vargas *et al.*, 2012).

Propagule traits associated with dispersal by wind are appendages slowing the rate of fall (e.g. pappus or wings) or

very small size as in ferns and orchids. Species with these traits often have wide distributions and can become relatively abundant on remote islands (Kessler *et al.*, 2011). For example, wind-dispersed pteridophytes are overrepresented in island floras with an average of 15.3% compared to only 3.6% in mainland floras (Kreft *et al.*, 2010). Moreover, the proportion of pteridophytes is positively related to the remoteness of islands (Kreft *et al.*, 2010).

The standard dispersal to remote islands by water occurs through propagules that possess traits that make them buoyant, resistant to salt and long-lasting to withstand weeks of floating (Vargas *et al.*, 2015). These propagules can be of different sizes, ranging from a few mm (e.g. *Pemphis acidula* or *Hibiscus tiliaceus*) to ca. 30 cm (*Cocos nucifera*). Dispersal by water may also occur *via* vegetation mats or rafts carried down rivers or otherwise detached from the mainland by strong storms or waves. These can carry propagules as well as whole plants (Renner, 2004). Dispersal by rafts can also transport propagules unspecialised for long-distance dispersal (Renner, 2004; Nathan *et al.*, 2008). Water-dispersed species are generally associated with beach or shoreline vegetation where they can represent the predominant dispersal strategy in a community (Vargas *et al.*, 2014).

Seabirds (and to a lesser degree migrating songbirds; Viana *et al.*, 2016) are also common dispersal vectors to remote islands. This dispersal vector is less affected by island size as seabirds find islands irrespective of size (Carlquist, 1974). Seabirds frequently traverse long distances over water in search for islands on which to roost or nest (Arjona *et al.*, 2018). Seabird dispersal can in principle be



**Fig 1.** Conceptual framework of functional island biogeography for species assemblages (left side), processes (middle) and outcomes (right). (A) Species from the regional pool first have to overcome the dispersal filter. With increasing island isolation, the relative importance of dispersal by wind, water and ectozoochory increases, while that of endozoochory decreases. Prevailing dispersal vectors have strong imprint on community trait values. The proportion of propagules with anemochorous appendages and salt water resistance increases with increasing isolation, whereas seed and fruit size decreases. In island trait space, species with specific dispersal strategies may be missing. (B) Environmental and biotic interaction filters subsequently will act on species assembly. With increasing island area, diversity of mutualists, successional stage and competition increases. With increasing isolation, competition and colonisation success of species decreases while available niches increase. Community means of traits indicating high competitive ability (e.g. low leaf mass per area; greater plant height) will increase with island area. Community trait means suitable to withstand adverse environmental conditions will peak on smaller islands (e.g. short life cycles or early reproduction). Community means of plants with mutualistic relationships will decrease with isolation and plants with generalistic strategies increase. Environmental and biotic interaction filters will further affect trait space. (C) Rate of evolution on islands increases with isolation, niche diversity and island area and decreases with population size. Community trait means likely to change during evolution are stem density, seed mass (both increasing), plant height and defence traits (both decreasing). Evolving species may move into empty trait space (green arrows and dots). (D) Extinction on islands increases with island isolation and number of invasives but decreases with island area and population size. Traits accelerating extinction risk are being tall and having poor defence traits. Species with high seed output, dispersal ability and potent defence traits are less likely to suffer extinction. Species at the margins of trait space may have a higher risk of extinction. Invasive species will either occupy empty trait space (red dots) or compete with natives for trait space and increase extinction risk through competition. Distances in A are according to Gillespie *et al.* (2012). Left side is modified after Weigelt *et al.* (2015) and Taylor *et al.* (2019).

*via* bird droppings after seed consumption on the mainland or other islands (endozoochory), or attached externally to plumage or feet (epizoochory). However, as few seabirds consume seeds, endozoochory likely plays a minor role in long-distance dispersal by such species. Sticky or bristly appendages can attach to the feet or plumage of birds (Aoyama, Kawakami & Chiba, 2012). The frequency of such events is still debated, but some propagules lacking other traits for long-distance dispersal have colonised islands, and this has been interpreted as *via* mud attached to bird feet (Nogales *et al.*, 2012; Vargas *et al.*, 2015). Seabirds often gather on low-lying, small and/or isolated islands free of predators (Ellis, 2005), possibly explaining why seabird-dispersed propagules are especially common on these islands (Fosberg, 1953; Stoddart, 1992).

Because dispersal to remote islands is hardly ever observed directly, the extent to which the observed trait mixture should be attributed to dispersal *versus* to environmental filters has remained contentious (Carvajal-Endara *et al.*, 2017; König *et al.*, 2021). There may be potential to quantify dispersal by tracing genetic lineages within species or populations from the mainland to islands and among islands, or by trait reconstruction of the ancestral coloniser by using species-level phylogenies (see Appendix, Section X.8).

## (2) Within-archipelago dispersal

### Processes:

H5. Endozoochorous dispersal is the most successful dispersal vector within archipelagos rich in volant frugivores; wind dispersal is predominant in archipelagos poor in volant frugivores.

### Outcomes:

H6. Seed mass of propagules with anemochorous appendages decreases with island isolation and increases for fleshy, scented and colourful propagules.  
H7. For plants with fleshy and colourful fruits, fruit size is coupled to the size of volant frugivores and to other traits such as gape width.

Most islands worldwide are embedded in archipelagos or are in close vicinity to the mainland (Weigelt, Jetz & Kreft, 2013). Dispersal events are more frequent than to remote islands. Assemblages can be thought of as metacommunities covering multiple islands (Burns & Neufeld, 2009; Schrader *et al.*, 2020), and can show rapid temporal species turnover within individual islands (Chiarucci *et al.*, 2017). Species turnover is likely driven by recurrent dispersal vectors, such as constant winds and ocean currents (Gillespie *et al.*, 2012), or high inter-island connectivity *via* birds or bats (Burns, 2005; García-Verdugo *et al.*, 2014; Onstein *et al.*, 2017).

Within-archipelago dispersal by wind, water and seabirds often requires dehiscent fruits. Seeds dispersed by fruit-eating birds or bats offer fleshy rewards, and may be coloured or scented according to the vector (García-Verdugo *et al.*, 2014). Bird and bat dispersal is much more important within archipelagos compared to remote islands. While seabirds still disperse plants within archipelagos or from the mainland to nearby islands *via* epizoochory, endozoochorous dispersal by frugivorous birds and bats can become the main dispersal mode (Whittaker, Bush & Richards, 1989; Fall, Drezner & Franklin, 2007). Endozoochorous plant dispersal is especially pronounced in tropical and temperate regions rich in volant frugivorous birds and bats (Kissling, Böhning-Gaese & Jetz, 2009). In tropical Tonga, about 79% of all native trees and lianas are dispersed by endozoochory (Meehan, McConkey & Drake, 2002); and on small islands off the west coast of Canada plant communities are dominated by fleshy-fruited species dispersed by birds (Burns, 2005). Islands in the arid subtropics or at higher latitudes are less rich in frugivores, with wind dispersal the main dispersal vector there (Howe & Smallwood, 1982; Alsos *et al.*, 2015), indicating that patterns of insularity could be modified by broad-scale differences among biomes, such as climate. Fruit size and weight likely play an important role in dispersal distance by endozoochory. Larger birds that consume larger fruits also fly longer distances over water than smaller birds that eat smaller fruits (Wheelwright, 1985; Onstein *et al.*, 2017). This relationship between bird and fruit size can lead to increasing community mean fruit sizes on more isolated islands within archipelagos (Schrader *et al.*, 2021b). However, the relationship between fruit size and island isolation is still poorly supported and deserves future research.

Traits that particularly reflect dispersal filters within archipelagos or in systems close to mainland include seed and fruit size, fruit colour and type and plant height (Burns, 2005; Thomson *et al.*, 2011; Schrader *et al.*, 2021a, 2021b). Community means and functional diversity metrics of these traits from different data resources (plots, species lists, point counts, etc.; see Section X.9) on islands and mainland can be used to assess the roles and strengths of dispersal filters, with null models correcting for differences in species richness and island area among islands (Section X.5; Schrader *et al.*, 2021a).

## III. SECTION B: ESTABLISHMENT, SUCCESSION AND NATURAL EXTINCTION

After dispersal, species establishment depends on both the abiotic (e.g. space, environmental matching) and biotic conditions (competitors and mutualists present), and these can differ greatly among islands (Carvajal-Endara *et al.*, 2017; Aikio *et al.*, 2020). Young oceanic islands or atolls often have poorly developed soil, filtering out species not adapted to pioneer and/or early successional habitats (Carlquist, 1974; Whittaker *et al.*, 1989; Schrader *et al.*, 2019). Older oceanic and/or continental islands impose biotic filters in the form



of mature ecosystems where high competitive ability is needed for newcomers to establish (Silvertown, 2004; Emerson & Gillespie, 2008). Some species require specific habitats to establish that might be entirely absent on a focal island (Carvajal-Endara *et al.*, 2017; Schrader *et al.*, 2019). Species not adapted to prevailing abiotic and biotic conditions fail to establish or go extinct if island conditions change [anthropogenic extinctions and effects on functional traits are discussed in Section VI. (Section E)]. Here, we discuss traits in the light of (i) species establishment and succession and (ii) natural extinction.

### (1) Establishment and succession

Processes:

H8. Species establishment success after dispersal depends on the strength of prevailing abiotic and biotic interaction filters and is mediated by traits.

Outcomes:

H9. Species establishing on very small or young islands or in pioneering habitats have traits tolerating high initial adversity, including salt spray, sand blasting, high irradiation, strong wind near the ground and sometimes nutrient-poor conditions.

H10. With increasing island age, area and heterogeneity, species assemblages change – expressed by a shift in trait compositions.

H11. With degree of island isolation, the proportion of species with pioneer traits increases, even in late-successional communities.

Carlquist (1974) observed that species adapted to dispersal to remote islands are often also associated with early-successional habitats, possibly for two reasons. First, traits associated with long-distance dispersal, such as having small seeds, are also found in species adapted to an early-successional growth and establishment strategy. Thus, only species possessing traits able to pass the dispersal filters can colonise an island. Second, the island environment itself demands early-successional establishment strategies, imposing a further establishment filter (also termed environmental or abiotic and biotic filter) on top of the dispersal filter. However, both arguments could lead to similar trait patterns and the relative roles of dispersal and establishment filters provides future research opportunities (e.g. Carvajal-Endara *et al.*, 2017). With increasing island area and age, species communities mature as expressed by a shift from early- to late-successional communities (Whittaker *et al.*, 1989; Karadimou *et al.*, 2018).

However, not many studies in relation to island area and age have focussed on traits and on succession (in the sense of primary succession) as an interpretation. Community trait responses to successional trajectories on mainland communities

– which are relatively well understood (e.g. Westoby, 1998; Westoby *et al.*, 2002; Reich, 2014) – can therefore act as model for island communities. For instance, in tropical mainland regions woody species follow two distinct strategies to deal with adverse establishment conditions. At sites with strong dry seasons, species have conservative life-history strategies with high stem density, emphasis on deep early roots and drought-tolerant leaves. Under more equable rainfall, emphasis is on rapid initial growth expressed by low stem density and leaf mass per area, early reproduction and short life cycles. As succession proceeds and plants grow taller, community mean trait values move to intermediate values for wood density and leaf mass per area (Craven *et al.*, 2015; Poorter *et al.*, 2019). Traits of species on small islands show a similar pattern. Here, species are often small, and have either large or tiny leaves and low or high wood density (Burns & Neufeld, 2009; Schrader *et al.*, 2021a, 2021b). With increasing island area and age, species communities change, as expressed by a shift in trait compositions from early- to late-successional assemblages (Whittaker *et al.*, 1989; Whittaker, Jones & Partomihardjo, 1997; Karadimou *et al.*, 2018). Species communities on larger islands are likely determined by stochastic processes and higher niche diversity (Schrader *et al.*, 2021a), and should over time become more similar to those on a comparable mainland site (Karadimou *et al.*, 2018).

The shift from early- to late-successional communities does not necessarily mirror trajectories seen on the mainland. For instance, late-successional species with high competitive abilities can be absent from islands due to strong dispersal filters, with the result that pioneer species persist into late succession. A striking example is the Hawaiian endemic tree *Metrosideros polymorpha* Gaudich., a species with an enormous ecological range and common in both early- and late-successional habitats (Cordell *et al.*, 1998; James *et al.*, 2004). *M. polymorpha* has tiny, wind-dispersed seeds and is among the first species to colonise recent lava flows (Wright *et al.*, 2000). At the same time, *M. polymorpha* is also the dominant species in native mature tree communities. It has relatively high competitive abilities expressed by growing tall and having high water transport efficiency (Stratton, Goldstein & Meinzer, 2000). The great habitat range occupied by *M. polymorpha* is possibly explained by the fact that life on the Hawaiian islands is less competitive than on the mainland as relatively few species dispersed to Hawaii (Carlquist, 1974). In the absence of highly competitive late-successional species, *M. polymorpha* evolved to exploit niches on Hawaii that would be occupied by other species on the mainland, possibly through character release of certain traits. A similar example is *Pinus canariensis* C.Sm. growing in mountain regions on the Canaries (López *et al.*, 2007; Navascués & Emerson, 2007).

The prevalence of highly dominant species on oceanic islands is largely unknown but represents an exciting avenue for future research (H11). For instance, it will be interesting to clarify traits involved with this wide amplitude, apart from those found important in *M. polymorpha* and *P. canariensis* (H11), shedding light on the usual mainland situation where different species occupy different successional stages. Further, it is unclear how closely community trait means on

young, small and/or disturbed islands resemble those of early succession on the mainland (H9). For instance, small islands could be special in the sense that repeated disturbance by waves and salt water retains communities in a state of early successional equilibrium, similar only to coastal habitats on the mainland. Potential late-successional stages of island communities could thus depend on island area, frequency of disturbances and the pool size of interspecific competitors. This can be studied by comparing community trait means or functional diversity of communities from differently sized islands with those of different successional levels from the mainland using plot data from islands and mainlands.

## (2) Natural extinctions

### Processes:

H12. Extinction risk on islands can be predicted from functional traits and is coupled to (i) population-level processes and stochasticity, (ii) disturbance and catastrophic events caused by geological events such as mega landslips, volcanic activity, sea level transgressions, island subsidence, erosion and tsunamis, (iii) habitat loss or (iv) co-extinctions of mutualists.

### Outcomes:

H13. Extinction risk is greater at the margins of island trait spaces where traits indicate (i) specialised mutualistic relationships, (ii) slow life cycles and (iii) low seed output.

Plant extinctions on islands are connected to several processes that often intermix. These processes include genetic bottlenecks, decreasing island area and habitat loss due to erosion, increasing competition and herbivory by newly arriving species or extinctions of mutualists – all leading to decreasing population sizes and ultimately to (local) species extinctions (Whittaker & Fernández-Palacios, 2007; Gray, 2019). Also disturbance by storms, waves or volcanic activities can have severe effects on population sizes (Burns & Neufeld, 2009; Borregaard *et al.*, 2017). For instance, species with traits not well adapted to ocean disturbances, like salt water and mechanical damage by waves, are more likely to go extinct on small islands. Persisting species are often better adapted to these disturbances by having tough leathery leaves and being taller (Burns & Neufeld, 2009). While disturbances can happen spontaneously at any time to (almost) all islands, changes in habitat availability and island area and elevation are often the result of island ontogeny and changes in sea levels that have profound effects on species assemblages (Fernández-Palacios *et al.*, 2016; Borregaard *et al.*, 2017). In particular, smaller island areas tend to have higher extinction rates and hence lower numbers of species at equilibrium (MacArthur & Wilson, 1967). Species more likely to go extinct by chance are those with traits connected to slow life cycles (e.g. high wood density or leaf mass per area), low reproduction rates (e.g. low number of seeds) or abiotic dispersal

(e.g. dry fruited; Sakai, Wagner & Mehrhoff, 2002). Species maintaining large metapopulations either through prolific output of propagules and/or high dispersibility by having low seed mass or winged propagules are less vulnerable to habitat loss (Sakai *et al.*, 2002). Natural plant extinctions can further be coupled to extinctions of mutualists, such as animal pollinators or dispersal agents. Examples are large-fruited plants that depend on large birds for dispersal, or plants with specialised pollination syndromes, such as often observed in dioecious species, that can suffer co-extinction if their mutualists disappear (Baker & Cox, 1984; Meehan *et al.*, 2002; Heinen *et al.*, 2018).

Causes of plant extinctions on islands are still poorly understood (but see, e.g. Cody, 2006). Most discussion has been about small population sizes in general without a clear focus on processes and traits involved in actual extinctions (H12). Future research should address whether and which traits increase extinction risk in island plants. For instance, species with high trait plasticity may be better adapted to changing environmental conditions and thus offset extinction risk. Species most susceptible to extinctions may have unique traits located at the margins of community trait spaces (H13; Fig. 1C). However, neither of these hypotheses connected to intraspecific trait plasticity and trait space are well supported by empirical evidence. Functional trait spaces and measures of functional rarity and species trait plasticity – such as intraspecific functional diversity (see Section X.4) – may be utilised together with population dynamics of island species.

## IV. SECTION C: BIOTIC INTERACTIONS, REPRODUCTION AND WITHIN-ISLAND DISPERSAL

Many island plants depend on mutualistic relationships to germinate, establish, reproduce or disperse, such as interaction with mycorrhizae or pollination and dispersal by animals. On islands, mutualisms require both the plants and the mutualists to colonise successfully. Hence, the diversity and magnitude of biotic interactions on islands depends strongly on the degree of isolation (Taylor *et al.*, 2019). Intra-island dispersal can also be facilitated by biotic interactions including non-volant animals – vectors not available for dispersal to islands.

### (1) Biotic interactions and reproduction

#### Processes:

H14. Diversity of mutualists including pollinators and animal seed dispersers decreases with increasing island isolation.

#### Outcomes:

H15. Functional diversity of traits linked to mutualistic relationships and reproduction decreases with island isolation.

H16. With increasing island isolation, the proportion of species increases that (i) have generalist pollination strategies, (ii) are self-compatible or (iii) reproduce vegetatively.

H17. The presence, absence and frequency of different pollination strategies and traits related to pollination (e.g. flower size, colours, length of nectar spurs and rewards) in island communities depends on the presence, absence and frequency of insects and other pollinators.

As colonisation rate decreases with island isolation (MacArthur & Wilson, 1967), it can be expected that the diversity and complexity of biotic interactions also decreases. The proportion of mycorrhizal plants in island assemblages has been shown to decrease with increasing island isolation, most likely as a consequence of a decline in successful colonisation by their symbionts (Delavaux *et al.*, 2019). Some taxa such as orchids that are well adapted for dispersal to remote islands are nevertheless underrepresented on oceanic islands due to lack of symbionts (Taylor *et al.*, 2019).

Absence of animal pollinators from islands can lead to underrepresentation of certain plant groups or to profound changes in species reproduction strategy (Bawa, 1980; Givnish, 2010; Alsos *et al.*, 2015; Grossenbacher *et al.*, 2017). Clonal reproduction and self-compatibility are significantly more common on oceanic islands than on the mainland (Baker, 1955; Razanajatovo *et al.*, 2019). Compared to the mainland, island communities feature a higher proportion of pollination generalists, expressed by a lack of pollinator exclusion mechanisms, with short corolla tubes and nectar spurs and easily accessible flowers with dull colours (Olesen, Eskildsen & Venkatasamy, 2002; Hiraiwa & Ushimaru, 2017). Within the families Asteraceae, Brassicaceae and Solanaceae, 66% of island species are self-compatible compared to only 41% of mainland species (Grossenbacher *et al.*, 2017). Traits such as flower morphology, pollination mode, clonal activity, self-compatibility or those facilitating mycorrhizal association are useful to understand why certain clades are under- or overrepresented on islands (Olesen & Valido, 2003; Traveset & Riera, 2005; Taylor *et al.*, 2019).

Biotic interactions on islands have been subject to intensive research (e.g. Alsos *et al.*, 2015; Delavaux *et al.*, 2019; Razanajatovo *et al.*, 2019; Taylor *et al.*, 2019). However, empirical evidence on frequency and generalisation across islands is scarce. Future research should test whether traits linked to biotic interactions are less common compared to the mainland and how they scale with island isolation and area (H15 & H16). Indices of functional diversity in combination with null models, or mainland communities representing the null expectation (see Section X.5), could be coupled to standardised plot data from island and mainland communities (Section X.9). Reliance on mutualists,

indicated by network approaches (Heleno *et al.*, 2011; Schleuning, Fründ & García, 2015), can also be treated as a trait for this purpose, with H17 predicting that proportions of species reliant on mutualists will be lower in remote islands.

## (2) Within-island dispersal

Processes:

H18. Selection for dispersal within islands can favour different vectors compared to those that initially brought species to the island.

Outcomes:

H19. Low-lying islands or sites, such as atolls, have a high proportion of water-resistant propagules and those with sticky or bristly appendages.

H20. High-elevation sites on islands have high proportion of (i) species with small seeds and (ii) propagules with anemochorous appendages.

H21. Islands with well-developed vertebrate communities also have a high proportion of zoochorous-dispersed plants.

Within-island dispersal becomes important after species colonisation and initial establishment [see Section III (Section B)]. Species dispersal patterns within islands are complex as species could disperse (i) using the same vectors as harnessed for inter-island dispersal such as wind, (ii) using novel dispersal vectors such as animals not able to cross water or (iii) by evolving novel traits such as increased seed mass after colonisation and loss of anemochorous appendages [- Section V (Section D)]. Often, dispersal vectors and mechanisms important for inter-island dispersal are less efficient to reach different regions within an island. On Krakatau island, a newly formed volcano in Indonesia, the first plant colonisers possessed traits linked to wind and water dispersal. Plants with traits for zoochorous dispersal appeared later when biotic requirements of animal dispersers were met (Whittaker & Jones, 1994; Whittaker *et al.*, 1997). Ferns and orchids, for example, often occur in mountainous interiors (Kreft *et al.*, 2010; Keppel *et al.*, 2016). Endozoochorous dispersal, mainly by birds and bats, can also be important for within-island dispersal, especially on tropical islands (Gillespie *et al.*, 2012; García-Verdugo *et al.*, 2014).

In addition, novel dispersal vectors can become available after reaching an island that play little or no role in dispersal to islands. These include dispersal by non-volant animals such as fruit-eating lizards or tortoises, mammals, non-flying birds or insects (Olesen & Valido, 2003; Albert, Flores & Strasberg, 2020). The shift in relative importance of dispersal vectors can create new ecological ties between plants and dispersers often leading to novel evolutionary adaptations [- Section V (Section D)]. This link can become so specialised as

to risk cascading extinctions: loss of plant species after their zoochorous dispersal vector becomes extinct (Heinen *et al.*, 2018; Albert *et al.*, 2020).

Within-island dispersal might restrict distribution within islands and make chance extinction more likely. However, this is an indirect effect compared to the filter imposed by the capacity to disperse to islands in the first place. Selection subsequent to initial colonisation is known sometimes to shift dispersal mode. The consequences of these different effects will depend on island remoteness and size, on the differences between shoreline and interior habitats, and on animal vectors that have reached the island. Quantified frequencies of dispersal traits comparing both between islands and between habitats within islands (H19 & H20) can measure the consequences of these different effects.

## V. SECTION D: EVOLUTIONARY SHIFTS IN TRAITS AND TRAIT SYNDROMES

Oceanic island floras are renowned for their spectacular evolutionary radiations which considerably contribute to diversity and endemism and entail novel trait combinations. The speed and extent of evolution on islands is thereby tightly linked to the degree of isolation (Whittaker & Fernández-Palacios, 2007; Givnish, 2010). Three processes can drive evolution on islands. First, after colonisation a species can change in isolation, evolving through time into a new species (Stuessy *et al.*, 2006). This may (i) lead to random or unchanged trait combinations by genetic drift when the island's environmental settings are similar to the mainland source region or (ii) result in directional change if the island environment differs from the ancestral area and therefore imposes a selection pressure on the colonising species (García-Verdugo & Fay, 2014; Emerson & Patiño, 2018). Second, distinct environmental and biotic characteristics of islands can favour tendencies including loss of dispersibility by wind, loss of defence against herbivores and size changes in plant organs (Burns, 2019). These 'island syndromes' describe directional changes in traits driven by differences between islands and mainlands *per se* and are found across islands of different regions and origins (Carlquist, 1974; Burns, 2019). The third process is evolutionary adaptation in the direction of occupying empty niches or escaping competition. Here, evolutionary trajectories and trait changes are likely to be different across species and islands. They are expected to depend on the ecological strategy of the colonist and on the species communities already present (Silvertown, 2004). This sort of shift can be seen as an instance of character displacement, two populations or species differentiating their traits when in sympatry to reduce competition for resources (Emerson, 2002; Losos & Ricklefs, 2009). However, the prevalence of character displacement in island plants is not yet well understood (Beans, 2014), providing distinct opportunities for future research.

The second and third evolutionary processes can result in similar trait outcomes. A prominent example is secondary woodiness, which can be interpreted as (i) an island syndrome as a result of moderate oceanic climates and an absence of herbivores on islands that lead to longer vegetative periods and allow herbs to grow taller; or (ii) a result of evolution into vacant niches (Darwin, 1859; Carlquist, 1974; Lens *et al.*, 2013). Consequently, we refrain from attributing trait patterns to each of these but rather summarise processes and outcomes relevant for both [for further discussion see Whittaker & Fernández-Palacios (2007), Lens *et al.* (2013), Whittaker *et al.* (2017) and Burns (2019)].

Processes:

H22. Evolution of traits follows predictable trajectories across islands depending on the degree of isolation, vacancy of niches and priority effects, level of competition and presence of herbivores and/or mutualists.

Outcomes:

H23. Absence of mutualists results in trait shifts towards generalist strategies.

H24. Propagules with anemochorous appendages, water resistance or small seeds evolve towards (i) fleshiness, (ii) loss of appendages or (iii) larger seed masses.

H25. Insularity causes trait convergence, i.e. large species or organs become smaller and small species or organs become larger.

H26. On oceanic islands, herbaceous species tend to evolve secondary woodiness.

H27. Island species lose defence mechanisms against herbivores.

H28. Adaptive island radiations should lead to a detectable and predictable expansion of functional trait space.

Species evolution can happen under two main scenarios, both with specific outcomes on traits (which also intermix to a certain degree; Emerson & Patiño, 2018). First, after colonisation a species can evolve anagenetically when an island endemic evolves from a single ancestor (Stuessy *et al.*, 2006). Anagenetic evolution is especially prevalent on uniform islands that only feature a limited set of habitats. If, and under which environmental factors, species traits evolve after anagenetic evolution is not well understood. García-Verdugo *et al.* (2020) showed that populations of the same species from Macaronesian islands repeatedly evolved larger leaves and have lower photosynthetic rates compared to their mainland source populations, hinting towards directional change in response to low seasonality.

The second scenario describes the radiation of a single coloniser into a set of new species. This change – often termed cladogenesis – can be directional in response to prevailing abiotic and biotic factors (adaptive radiation) or random, and is especially common on isolated, oceanic and

heterogeneous islands, such as Hawaii or the Canaries. These islands offer a wealth of different, often vacant, niches, have low immigration rates and relaxed competition (Silvertown, 2004; Stuessy *et al.*, 2006). Examples of species clades that adaptively radiated into different forms and functions from a single ancestor are the Hawaiian silverswords or lobeliads (Givnish *et al.*, 2009; Blonder *et al.*, 2016), or the 36 recent species of the genus *Aeonium* in the Canaries (Silvertown, 2004). These taxa occupy all major habitats of their respective archipelagos today, probably with clear imprints in their trait values. Examples are trait evolution towards monocarpy, developmental heterophylly, sexual dimorphism, growth form and floral morphology (Givnish, 2010).

High dispersibility of a species is beneficial for colonising distant islands. After colonisation, however, high dispersibility results in large losses of propagules to the sea. In response, island plants adapted to wind dispersal tend to limit their dispersal ability by producing larger and fewer seeds, thereby decreasing the chances that their propagules disperse back into the sea, especially on small islands (Cody & Overton, 1996; Givnish *et al.*, 2009; Kavanagh & Burns, 2014; but see García-Verdugo *et al.*, 2017).

Relaxed competition on islands due to depauperate assemblages is another driver of trait changes in island plants (character release). Island communities often show a narrower range of heights compared to the mainland (Burns, 2016; Negoita *et al.*, 2016). Movement of herbaceous colonists towards secondary woodiness may arise from absence of woody competition, at least partly [Darwin, 1859; see Lens *et al.* (2013) for further discussion]. Although there may be a trend towards secondary woodiness within herbaceous clades that colonise, whole assemblages are likely to be less woody than those on the mainland. This has not been well quantified to date.

In the absence of diverse herbivore faunas, island plants are often characterised by a loss of defence traits indicated by lower levels of spinescence compared to their mainland relatives (Burns, 2016). However, it is still debated how general the loss of defence mechanisms is in island plants, including chemical defence (e.g. Meredith *et al.*, 2019; Moreira *et al.*, 2019). Other traits likely to respond similarly across many islands are prevalence of clonal spread, self-compatibility and generalist reproduction as responses to limited pollination success (Jorgensen & Olesen, 2001; Grosenbacher *et al.*, 2017; Taylor *et al.*, 2019).

Evolution of island plants can also result in remarkable intra- and interspecific size changes of the whole plant or organs, also known as the 'island rule'. Examples include smaller plants or organs becoming larger and larger plants or organs becoming smaller (Carlquist, 1974; Burns, 2019). Leaf size and plant stature seem to be specifically affected by the island rule (Biddick, Hendriks & Burns, 2019). Size changes are suggested to be linked to ecological drift or differences in competition, predation or environmental conditions between islands and mainlands, but the underlying processes are poorly understood (Biddick *et al.*, 2019; Biddick & Burns, 2021).

Future research should investigate whether certain traits are especially susceptible to evolutionary change in both anagenetic (less well known) and cladogenetic (better established) evolution, and if so, understanding their causation. Traits linked to competition and biotic interactions may indicate selection pressure on islands. For this, community means of native non-endemic species and endemics should be compared (Section X.3). Intraspecific traits of island and mainland communities of the same species (for natives) or their nearest ancestors (for endemics) may reveal the direction and speed of trait evolution (H23–H27), and may inform on the prevalence of character displacement (as a response to avoid direct competition) or release (species diversifying in many directions due to the absence of competition) in island plants. Cross-island comparisons of island endemics and large island radiations could provide evidence for whether changes in species traits are directional and thus predictable across islands (H23, H28).

## VI. SECTION E: GLOBAL CHANGE, THREAT BY INVASIVE SPECIES AND CONSERVATION

Islands are at the forefront of biodiversity loss (Nogué *et al.*, 2021). Most documented extinctions worldwide have occurred on islands, and about 5–10% of endemic island plants globally are threatened by extinction (Caujapé-Castells *et al.*, 2010). Species extinctions can happen under natural conditions [Section III (Section B)] but are dramatically increased by global change (Gray, 2019).

Processes:

H29. Invasive species, progressive loss and fragmentation of natural habitats and rising sea levels are the main drivers of island species extinctions and this is mediated by traits.

Outcomes:

H30. Species with slow reproductive cycles and poor dispersal abilities are most threatened by extinction.

H31. Species that have lost defence mechanisms against herbivores are more likely to suffer negative impacts from introduced feral herbivores.

H32. Alien plants with traits connected to high competitive and dispersal ability and/or unspecific pollination syndromes are more likely to become invasive on islands.

H33. Islands with a low trait diversity in the native flora should be more susceptible to invasion.

Global change includes fragmentation and destruction of natural habitats, rising temperature and sea levels and introductions of invasive species, leading to decreasing population sizes of native species and subsequent extinctions (Caujapé-

Castells *et al.*, 2010; Gray, 2019). Other factors can be limited reproduction, pollination or facilitation as consequence of extinction of mutualists (Cox & Elmqvist, 2000; Harter *et al.*, 2015; Heinen *et al.*, 2018). Woody perennials and those relying on biotic interactions including for reproduction and dispersal and producing fruits with few seeds experienced the highest extinction risk in the past, whereas generalists and those adapted to changing conditions have been more likely to persist (Gray, 2019). Island assemblages with low functional redundancies are especially vulnerable to extinctions from disrupted ecological interactions induced by climate change (Harter *et al.*, 2015).

Invasive species represent another major threat to native island plants. On some remote islands, plant assemblages are up to 90% invasive species (Pyšek *et al.*, 2017). Invasive plants are superior competitors over natives mediated through traits linked to fast growth, high fecundity and resistance against external disturbances expressed by lower leaf mass per area, longer flowering periods and higher efficiency in capturing limiting resources (Baruch & Goldstein, 1999; Durand & Goldstein, 2001; Marx *et al.*, 2016; Westerband, Knight & Barton, 2021). Invasive plants can also interfere with plant–animal mutualisms, likely leading to disrupted ecological networks (Heleno *et al.*, 2013; Carpenter *et al.*, 2020). Introduced herbivores like ungulates, rabbits or insects threaten native plants that have lost traits for defence due to the absence of herbivores, especially if predators of the herbivores are also absent (Bowen & Van Vuren, 1997).

Knowing the functional ecology of invaders and the trait space or interaction networks of the natural flora may help to predict the risk of invasion and to develop effective conservation measures against invasive species (Fig. 1D; Sections X.2 and X.7). Future research should develop trait-based frameworks predicting extinction risk of island, species and communities. A challenge will be to single out species most susceptible to extinction. Plot-based abundance measures of island species in combination with traits linked to slow life cycles, biotic interactions and defence could be used to develop risk assessments (H30 & H31). Whether and which functional traits play a role in the invasibility of island communities should also be a focus of future research (H32 & H33). Two separate questions are: (i) which traits explain invasion success of alien plants and (ii) which traits indicate the susceptibility of island plants to invasive species. Functional diversity, trait spaces and interaction networks (Sections X.2 and X.7) could indicate whether the ecological strategy of non-invasives and invasives differ, predicting which alien species are most likely to outcompete natives and become invasive (Fig. 1D). This may shed light on the idea that invasion success is connected to exploiting new resources on islands through novel trait combinations (e.g. invasive species increase the functional diversity of island assemblages), by outcompeting natives through similar albeit more competitive trait combinations and/or through escape from their herbivores (Whittaker *et al.*, 2014; Marx *et al.*, 2016).

## VII. CONCLUSIONS

- (1) Functional island biogeography is an emerging discipline lying at the interface of ecology, biogeography and evolutionary biology that has great potential further to enhance the reputation of islands as evolutionary and ecological laboratories and research models. We define functional island biogeography as the study of ecological and evolutionary processes that shape the structure, diversity and functioning of island assemblages, as viewed specifically through the lens of functional traits and plant ecological strategies.
- (2) Functional traits provide information about the underlying processes shaping island assemblages and a deeper understanding of how plants assemble on islands and why island assemblages often differ remarkably from the mainland. These differences shed light also on the forces operating in mainland assemblages.
- (3) Selection on traits can differ remarkably among islands, for both biotic (species and communities present) and abiotic (isolation, area, age, elevation, geology, precipitation and temperature) reasons. To understand fully the distribution and strategies of species assemblages, both abiotic and biotic factors need to be included in functional island biogeography.
- (4) Recent decades have seen a surge in studies integrating plant functional traits to island biogeography. We condensed this literature into a set of 33 working hypotheses. These provide a roadmap for future research and can be used as a provisional framework that can be solidified or falsified and replaced.

## VIII. ACKNOWLEDGEMENTS AND AUTHOR CONTRIBUTIONS

Funding was provided to J. S. by the DAAD (Project ID: 57445626), by the German Research Foundation with a research scholarship (No: SCHR1672/1-1) and by a Macquarie University Research Fellowship. H. K. acknowledges funding from the German Research Foundation (Research Unit FOR 2716 DynaCom). Open Access funding enabled and organized by Projekt DEAL.

**Author contributions:** J. S., I. J. W., H. K. and M. W. conceived the research ideas. J. S. led the writing with major contributions from I. J. W., H. K. and M. W.

## IX. REFERENCES

- AIKIO, S., RAMULA, S., MUOLA, A. & VON NUMERS, M. (2020). Island properties dominate species traits in determining plant colonizations in an archipelago system. *Ecography* **43**, 1041–1051.
- ALBERT, S., FLORES, O. & STRASBERG, D. (2020). Collapse of dispersal trait diversity across a long-term chronosequence reveals a strong negative impact of frugivore extinctions on forest resilience. *Journal of Ecology* **108**, 1386–1397.
- ALSOS, I. G., EHRLICH, D., EIDENSEN, P. B., SOLSTAD, H., WESTERGAARD, K. B., SCHÖNSWETTER, P., TRIBSCH, A., BIRKELAND, S., ELVEN, R. &

- BROCHMANN, C. (2015). Long-distance plant dispersal to North Atlantic islands: colonization routes and founder effect. *Arb Plants* **7**, plv036.
- AOYAMA, Y., KAWAKAMI, K. & CHIBA, S. (2012). Seabirds as adhesive seed dispersers of alien and native plants in the oceanic Ogasawara Islands, Japan. *Biodiversity and Conservation* **21**, 2787–2801.
- ARELLANO-CATALDO, G. & SMITH-RAMÍREZ, C. (2016). Establishment of invasive plant species in canopy gaps on Robinson Crusoe Island. *Plant Ecology* **217**, 289–302.
- ARJONA, Y., NOGALES, M., HELENO, R. & VARGAS, P. (2018). Long-distance dispersal syndromes matter: diaspore-trait effect on shaping plant distribution across the Canary Islands. *Ecography* **41**, 805–814.
- BAKER, H. G. (1955). Self compatibility and establishment after 'long distance' dispersal. *Evolution* **9**, 347–349.
- BAKER, H. G. & COX, P. A. (1984). Further thoughts on diocism and islands. *Annals of the Missouri Botanical Garden* **71**, 244–253.
- BARUCH, Z. & GOLDSTEIN, G. (1999). Leaf construction cost, nutrient concentration, and net CO<sub>2</sub> assimilation of native and invasive species in Hawaii. *Oecologia* **121**, 183–192.
- BABA, K. S. (1980). Evolution of dioecy in flowering plants. *Annual Review of Ecology and Systematics* **11**, 15–39.
- BEANS, C. M. (2014). The case for character displacement in plants. *Ecology and Evolution* **4**, 862–875.
- BIDDICK, M. & BURNS, K. C. (2021). A simple null model predicts the island rule. *Ecology Letters* **24**, 1646–1654.
- BIDDICK, M., HENDRIKS, A. & BURNS, K. C. (2019). Plants obey (and disobey) the island rule. *Proceedings of the National Academy of Sciences* **116**, 17632–17634.
- BLONDER, B. (2018). Hypervolume concepts in niche- and trait-based ecology. *Ecography* **41**, 1441–1455.
- BLONDER, B., BALDWIN, B. G., ENQUIST, B. J. & ROBICHAUX, R. H. (2016). Variation and macroevolution in leaf functional traits in the Hawaiian silversword alliance (Asteraceae). *Journal of Ecology* **104**, 219–228.
- BORREGAARD, M. K., AMORIM, I. R., BORGES, P. A. V., CABRAL, J. S., FERNÁNDEZ-PALACIOS, J. M., FIELD, R., HEANEY, L. R., KREFT, H., MATTHEWS, T. J., OLESEN, J. M., PRICE, J., RIGAL, F., STEINBAUER, M., TRIANTIS, K. A., VALENTE, L., et al. (2017). Oceanic island biogeography through the lens of the General Dynamic Model: assessment and prospect. *Biological Reviews* **92**, 830–853.
- BOWEN, L. & VAN VUREN, D. (1997). Insular endemic plants lack defenses against herbivores. *Conservation Biology* **11**, 1249–1254.
- BRUELHEIDE, H., DENGELER, J., JIMÉNEZ-ÁLFARO, B., PURSCHKE, O., HENNEKENS, S. M., CHYTRÝ, M., PILLAR, V. D., JANSEN, F., KATTGE, J., SANDEL, B., AUBIN, I., BIURRUN, I., FIELD, R., HAIDER, S., JANDT, U., et al. (2019). sPlot – a new tool for global vegetation analyses. *Journal of Vegetation Science* **30**, 161–186.
- BURNS, K. C. (2005). A multi-scale test for dispersal filters in an island plant community. *Ecography* **28**, 552–560.
- BURNS, K. C. (2016). Size changes in island plants: independent trait evolution in *Alyxia ruscifolia* (Apocynaceae) on Lord Howe Island. *Biological Journal of the Linnean Society* **119**, 847–855.
- BURNS, K. C. (2019). *Evolution in Isolation: The Search for an Island Syndrome in Plants*. Cambridge University Press, Cambridge.
- BURNS, K. C. & NEUFELD, C. J. (2009). Plant extinction dynamics in an insular metacommunity. *Oikos* **118**, 191–198.
- BUTLER, E. E., DATTA, A., FLORES-MORENO, H., CHEN, M., WYTHERS, K. R., FAZAYELI, F., BANERJEE, A., ATKIN, O. K., KATTGE, J., AMIAUD, B., BLONDER, B., BOENISCH, G., BOND-LAMBERTY, B., BROWN, K. A., BYUN, C., et al. (2017). Mapping local and global variability in plant trait distributions. *Proceedings of the National Academy of Sciences* **114**, E10937–E10946.
- CARLQUIST, S. J. (1965). *Island Life: A Natural History of the Islands of the World*. The Natural History Press, New York.
- CARLQUIST, S. J. (1974). *Island Biology*. Columbia University Press, New York.
- CARPENTER, J. K., WILMSHURST, J. M., MCCONKEY, K. R., HUME, J. P., WOTTON, D. M., SHIELS, A. B., BURGE, O. R. & DRAKE, D. R. (2020). The forgotten fauna: native vertebrate seed predators on islands. *Functional Ecology* **34**, 1802–1813.
- CARVAJAL-ENDARA, S., HENDRY, A. P., EMERY, N. C. & DAVIES, T. J. (2017). Habitat filtering not dispersal limitation shapes oceanic island floras: species assembly of the Galápagos archipelago. *Ecology Letters* **20**, 495–504.
- CAUJAPÉ-CASTELLS, J., TYE, A., CRAWFORD, D. J., SANTOS-GUERRA, A., SAKAI, A., BEAVER, K., LOBIN, W., VINCENT FLORENS, F. B. B., MOURA, M., JARDIM, R., GÓMES, I. & KUEFFER, C. (2010). Conservation of oceanic island floras: present and future global challenges. *Perspectives in Plant Ecology, Evolution and Systematics* **12**, 107–129.
- CHIARUCCI, A., FATTORINI, S., FOGGI, B., LANDI, S., LAZZARO, L., PODANI, J. & SIMBERLOFF, D. (2017). Plant recording across two centuries reveals dramatic changes in species diversity of a Mediterranean archipelago. *Scientific Reports* **7**, 5415.
- CODY, M. L. (2006). *Plants on Islands: Diversity and Dynamics on a Continental Archipelago*, First Edition. University of California Press, Berkeley.
- CODY, M. L. & OVERTON, J. M. (1996). Short-term evolution of reduced dispersal in island plant populations. *Journal of Ecology* **84**, 53–61.
- CORDELL, S., GOLDSTEIN, G., MUELLER-DOMBOIS, D., WEBB, D. & VITOUSEK, P. M. (1998). Physiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. *Oecologia* **113**, 188–196.
- COSTIN, A. B. (1965). Long-distance seed dispersal to Macquarie Island. *Nature* **4981**, 317.
- COX, P. A. & ELMQVIST, T. (2000). Pollinator extinction in the Pacific Islands. *Conservation Biology* **14**, 1237–1239.
- CRAVEN, D., HALL, J. S., BERLYN, G. P., ASHTON, M. S. & VAN BREUGEL, M. (2015). Changing gears during succession: shifting functional strategies in young tropical secondary forests. *Oecologia* **179**, 293–305.
- CUTTS, V., HANZ, D. M., BARAJAS-BARBOSA, M. P., ALGAR, A. C., STEINBAUER, M. J., IRL, S. D. H., KREFT, H., WEIGELT, P., FERNÁNDEZ-PALACIOS, J. M. & FIELD, R. (2021). Scientific floras can be reliable sources for some trait data in a system with poor coverage in global trait databases. *Journal of Vegetation Science* **32**, e12996.
- DARWIN, C. (1859). *On the Origin of Species*. Murray, London.
- DARWIN, C. & WALLACE, A. (1858). On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. *Journal of the Proceedings of the Linnean Society of London. Zoology* **3**, 45–62.
- DELAVAL, C. S., WEIGELT, P., DAWSON, W., DUCHICELA, J., ESSL, F., VAN KLEUNEN, M., KÖNIG, C., PERGL, J., PYŠEK, P., STEIN, A., WINTER, M., SCHULTZ, P., KREFT, H. & BEVER, J. D. (2019). Mycorrhizal fungi influence global plant biogeography. *Nature Ecology & Evolution* **3**, 424–429.
- DENSLow, J. S. (2003). Weeds in paradise: thoughts on the invasibility of tropical islands. *Annals of the Missouri Botanical Garden* **90**, 119–127.
- DÍAZ, S. & CABIDO, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* **16**, 646–655.
- DÍAZ, S., KATTGE, J., CORNELISSEN, J. H. C., WRIGHT, I. J., LAVOREL, S., DRAY, S., REU, B., KLEYER, M., WIRTH, C., PRENTICE, I. C., GARNIER, E., BÖNISCH, G., WESTOBY, M., POORTER, H., REICH, P. B., et al. (2016). The global spectrum of plant form and function. *Nature* **529**, 167–171.
- DURAND, L. Z. & GOLDSTEIN, G. (2001). Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. *Oecologia* **126**, 345–354.
- ELLIS, J. C. (2005). Marine birds on land: a review of plant biomass, species richness, and community composition in seabird colonies. *Plant Ecology* **181**, 227–241.
- EMERSON, B. C. (2002). Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. *Molecular Ecology* **11**, 951–966.
- EMERSON, B. C. & GILLESPIE, R. G. (2008). Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology & Evolution* **23**, 619–630.
- EMERSON, B. C. & PATIÑO, J. (2018). Anagenesis, cladogenesis, and speciation on islands. *Trends in Ecology & Evolution* **33**, 488–491.
- FALL, P. L., DREZNER, T. D. & FRANKLIN, J. (2007). Dispersal ecology of the lowland rain forest in the Vava'u island group, Kingdom of Tonga. *New Zealand Journal of Botany* **45**, 393–417.
- FERNÁNDEZ-PALACIOS, J. M., RIJSDIJK, K. F., NORDER, S. J., OTTO, R., DE NASCIMENTO, L., FERNÁNDEZ-LUGO, S., TJØRVE, E. & WHITTAKER, R. J. (2016). Towards a glacial-sensitive model of island biogeography. *Global Ecology and Biogeography* **25**, 817–830.
- FISCHER, G., NACHTERGAELE, F., PRIELER, S., VAN VELTHUIZEN, H., VEREIST, L. & WIBERG, D. (2008). *Global Agro-Ecological Zones Assessment for Agriculture (GAEZ 2008)*. IIASA, Laxenburg and FAO, Rome.
- FOSEBERG, F. R. (1953). Vegetation of central Pacific Atolls, a brief summary. *Atoll Research Bulletin* **23**, 1–26.
- GARCÍA-VERDUGO, C., BALDWIN, B. G., FAY, M. F. & CAUJAPÉ-CASTELLS, J. (2014). Life history traits and patterns of diversification in oceanic archipelagos: a meta-analysis. *Botanical Journal of the Linnean Society* **174**, 334–348.
- GARCÍA-VERDUGO, C. & FAY, M. F. (2014). Ecology and evolution on oceanic islands: broadening the botanical perspective. *Botanical Journal of the Linnean Society* **174**, 271–275.
- GARCÍA-VERDUGO, C., MAIRAL, M., MONROY, P., SAJEVA, M. & CAUJAPÉ-CASTELLS, J. (2017). The loss of dispersal on islands hypothesis revisited: implementing phylogeography to investigate evolution of dispersal traits in *Periploca* (Apocynaceae). *Journal of Biogeography* **44**, 2595–2606.
- GARCÍA-VERDUGO, C., MONROY, P., PUGNAIRE, F. I., JURA-MORAWIEC, J., MOREIRA, X. & FLEXAS, J. (2020). Leaf functional traits and insular colonization: subtropical islands as a melting pot of trait diversity in a widespread plant lineage. *Journal of Biogeography* **47**, 2362–2376.
- GILLESPIE, R. G., BALDWIN, B. G., WATERS, J. M., FRASER, C. I., NIKULA, R. & RODERICK, G. K. (2012). Long-distance dispersal: a framework for hypothesis testing. *Trends in Ecology & Evolution* **27**, 47–55.
- GIVNISH, T. J. (2010). Ecology of plant speciation. *Taxon* **59**, 1329–1366.
- GIVNISH, T. J., MILLAM, K. C., MAST, A. R., PATERSON, T. B., THEIM, T. J., HIPPI, A. L., HENSS, J. M., SMITH, J. F., WOOD, K. R. & SYTSMA, K. J. (2009). Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society B: Biological Sciences* **276**, 407–416.

- GÖTZENBERGER, L., BOTTA-DUKÁT, Z., LEŠ, J., PÄRTEL, M., ZOBEL, M. & DE BELLO, F. (2016). Which randomizations detect convergence and divergence in trait-based community assembly? A test of commonly used null models. *Journal of Vegetation Science* **27**, 1275–1287.
- GRAY, A. (2019). The ecology of plant extinction: rates, traits and island comparisons. *Oryx* **53**, 424–428.
- GROSSENBACHER, D. L., BRANDVAIN, Y., AULD, J. R., BURD, M., CHEPTOU, P. O., CONNER, J. K., GRANT, A. G., HOVICK, S. M., PANNELL, J. R., PAUW, A., PETANIDOU, T., RANDLE, A. M., DE CASAS, R. R., VAMOSI, J., WINN, A., et al. (2017). Self-compatibility is over-represented on islands. *New Phytologist* **215**, 469–478.
- HARTER, D. E. V., IRL, S. D. H., SEO, B., STEINBAUER, M. J., GILLESPIE, R. G., TRIANTIS, K. A., FERNÁNDEZ-PALACIOS, J.-M. & BEIERKUHNEIN, C. (2015). Impacts of global climate change on the floras of oceanic islands - projections, implications and current knowledge. *Perspectives in Plant Ecology, Evolution and Systematics* **17**, 160–183.
- HEINEN, J. H., VAN LOON, E. E., HANSEN, D. M. & KISSLING, W. D. (2018). Extinction-driven changes in frugivore communities on oceanic islands. *Ecography* **41**, 1245–1255.
- HELENO, R., BLAKE, S., JARAMILLO, P., TRAVESET, A., VARGAS, P. & NOGALES, M. (2011). Frugivory and seed dispersal in the Galápagos: what is the state of the art? *Integrative Zoology* **6**, 110–129.
- HELENO, R. H., OLESEN, J. M., NOGALES, M., VARGAS, P. & TRAVESET, A. (2013). Seed dispersal networks in the Galápagos and the consequences of alien plant invasions. *Proceedings of the Royal Society B: Biological Sciences* **280**, 1–9.
- HELENO, R. H. & VARGAS, P. (2015). How do islands become green? *Global Ecology and Biogeography* **24**, 518–526.
- HIRAIWA, M. K. & USHIMARU, A. (2017). Low functional diversity promotes niche changes in natural island pollinator communities. *Proceedings of the Royal Society B: Biological Sciences* **284**, 20162218.
- HOWE, F. & SMALLWOOD, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics* **13**, 201–228.
- JACQUET, C., MOUILLOT, D., KULBICKI, M. & GRAVEL, D. (2017). Extensions of Island Biogeography Theory predict the scaling of functional trait composition with habitat area and isolation. *Ecology Letters* **20**, 135–146.
- JAMES, S. A., PUTTOCK, C. F., CORDELL, S. & ADAMS, R. P. (2004). Morphological and genetic variation within *Metrosideros polymorpha* (Myrtaceae) on Hawai'i. *New Zealand Journal of Botany* **42**, 263–270.
- JORGENSEN, T. H. & OLESEN, J. M. (2001). Adaptive radiation of island plants: evidence from Aeonium (Crassulaceae) of the Canary islands. *Perspectives in Plant Ecology, Evolution and Systematics* **4**, 29–42.
- KARADIMOU, E., KALLIMANIS, A. S., TSIRIPIDIS, I., RAUS, T., BERGMEIER, E. & DIMOPOULOS, P. (2018). Functional diversity changes over 100 yr of primary succession on a volcanic island: insights into assembly processes. *Ecosphere* **9**, e02374.
- KARGER, D. N., CONRAD, O., BÖHNER, J., KAWOHL, T., KREFT, H., SORIA-AUZA, R. W., ZIMMERMANN, N. E., LINDER, H. P. & KESSLER, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data* **4**, 170122.
- KARGER, D. N., KESSLER, M., CONRAD, O., WEIGELT, P., KREFT, H., KÖNIG, C. & ZIMMERMANN, N. E. (2019). Why tree lines are lower on islands-climatic and biogeographic effects hold the answer. *Global Ecology and Biogeography* **28**, 839–850.
- KATTGE, J., BÖNISCH, G., DÍAZ, S., LAVOREL, S., PRENTICE, I. C., LEADLEY, P., TAUTENHAHN, S., WERNER, G. D. A., AAKALA, T., ABEDI, M., ACOSTA, A. T. R., ADAMIDIS, G. C., ADAMSON, K., AIBA, M., ALBERT, C. H., et al. (2020). TRY plant trait database – enhanced coverage and open access. *Global Change Biology* **26**, 119–188.
- KAVANAGH, P. H. & BURNS, K. C. (2014). The repeated evolution of large seeds on islands. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20140675.
- KEPPEL, G., GILLESPIE, T. W., ORMEROD, P. & FRICKER, G. A. (2016). Habitat diversity predicts orchid diversity in the tropical south-west Pacific. *Journal of Biogeography* **43**, 2332–2342.
- KEPPEL, G., LOWE, A. J. & POSSINGHAM, H. P. (2009). Changing perspectives on the biogeography of the tropical South Pacific: influences of dispersal, vicariance and extinction. *Journal of Biogeography* **36**, 1035–1054.
- KESSLER, M., KLUGE, J., HEMP, A. & OHLEMÜLLER, R. (2011). A global comparative analysis of elevational species richness patterns of ferns. *Global Ecology and Biogeography* **20**, 868–880.
- KISSLING, W. D., BÖHNING-GAESE, K. & JETZ, W. (2009). The global distribution of frugivory in birds. *Global Ecology and Biogeography* **18**, 150–162.
- KÖNIG, C., WEIGELT, P., SCHRADER, J., TAYLOR, A., KATTGE, J. & KREFT, H. (2019). Biodiversity data integration—the significance of data resolution and domain. *PLoS Biology* **17**, e3000183.
- KÖNIG, C., WEIGELT, P., TAYLOR, A., STEIN, A., DAWSON, W., ESSL, F., PERGL, J., PYŠEK, P., VAN KLEUNEN, M., WINTER, M., CHATELAIN, C., WIERINGA, J. J., KRESTOV, P. & KREFT, H. (2021). Source pools and disharmony of the world's island floras. *Ecography* **44**, 44–55.
- KREFT, H., JETZ, W., MUTKE, J. & BARTHOLOTT, W. (2010). Contrasting environmental and regional effects on global pteridophyte and seed plant diversity. *Ecography* **33**, 408–419.
- LENS, F., DAVIN, N., SMETS, E. & DEL ARCO, M. (2013). Insular woodiness on the Canary Islands: a remarkable case of convergent evolution. *International Journal of Plant Sciences* **174**, 992–1013.
- LÓPEZ, R., ZEHAVALI, A., CLIMENT, J. & GIL, L. (2007). Contrasting ecotypic differentiation for growth and survival in *Pinus canariensis*. *Australian Journal of Botany* **55**, 759–769.
- LOSOS, J. B. & RICKLEFS, R. E. (2009). Adaptation and diversification on islands. *Nature* **457**, 830–836.
- MACARTHUR, R. H. & WILSON, E. O. (1967). *The Theory of Island Biogeography*, First Edition. Princeton University Press, Princeton.
- MAITNER, B. S., BOYLE, B., CASLER, N., CONDIT, R., DONOGHUE, J., DURÁN, S. M., GUADERRAMA, D., HINCHLIFF, C. E., JØRGENSEN, P. M., KRAFT, N. J. B., MCGILL, B., MEROW, C., MORUETA-HOLME, N., PEET, R. K., SANDEL, B., et al. (2018). The bien r package: a tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods in Ecology and Evolution* **9**, 373–379.
- MAMMOLA, S. & CARDOSO, P. (2020). Functional diversity metrics using kernel density n-dimensional hypervolumes. *Methods in Ecology and Evolution* **11**, 986–995.
- MARX, H. E., GIBLIN, D. E., DUNWIDDIE, P. W. & TANK, D. C. (2016). Deconstructing Darwin's Naturalization Conundrum in the San Juan Islands using community phylogenetics and functional traits. *Diversity and Distributions* **22**, 318–331.
- MASON, N. W. H., MOUILLOT, D., LEE, W. G. & WILSON, J. B. (2005). Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* **111**, 112–118.
- MATTHEWS, T. J., RIGAL, F., KOUGIOMOUTZIS, K., TRIGAS, P. & TRIANTIS, K. A. (2020). Unravelling the small-island effect through phylogenetic community ecology. *Journal of Biogeography* **47**, 2341–2352.
- MEEHAN, H. J., MCCONKEY, K. R. & DRAKE, D. R. (2002). Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. *Journal of Biogeography* **29**, 695–712.
- MENCUCCHINI, M., ROSAS, T., ROWLAND, L., CHOAT, B., CORNELISSEN, H., JANSEN, S., KRAMER, K., LAPENIS, A., MANZONI, S., NIINEMETS, Ü., REICH, P., SCHRODT, F., SOUDZILOVSKAIA, N., WRIGHT, I. J. & MARTÍNEZ-VILALTA, J. (2019). Leaf economics and plant hydraulics drive leaf: wood area ratios. *New Phytologist* **224**, 1544–1556.
- MEREDITH, F. L., TINDALL, M. L., HEMMINGS, F. A. & MOLES, A. T. (2019). Prickly pairs: the proportion of spinescent species does not differ between islands and mainland. *Journal of Plant Ecology* **12**, 941–948.
- MIDWAY, S. R. & HODGE, A. M. C. (2012). Carlquist revisited: history, success, and applicability of a natural history model. *Biology and Philosophy* **27**, 497–520.
- MOLES, A. T., ACKERLY, D. D., TWEDDLE, J. C., DICKIE, J. B., SMITH, R., LEISHMAN, M. R., MAYFIELD, M. M., PITMAN, A., WOOD, J. T. & WESTOBY, M. (2007). Global patterns in seed size. *Global Ecology and Biogeography* **16**, 109–116.
- MOREIRA, X., CASTAGNEYROL, B., DE LA MATA, R., FYLLAS, N. M., GALMÁN, A., GARCÍA-VERDUGO, C., LARRINAGA, A. R. & ABDALA-ROBERTS, L. (2019). Effects of insularity on insect leaf herbivory and chemical defences in a Mediterranean oak species. *Journal of Biogeography* **46**, 1226–1233.
- MOSER, D., LENZNER, B., WEIGELT, P., DAWSON, W., KREFT, H., PERGL, J., PYŠEK, P., VAN KLEUNEN, M., WINTER, M., CAPINHA, C., CASSEY, P., DULLINGER, S., ECONOMO, E. P., GARCÍA-DÍAZ, P., GUÉNARD, B., et al. (2018). Remoteness promotes biological invasions on islands worldwide. *Proceedings of the National Academy of Sciences* **115**, 9270–9275.
- NATHAN, R. (2006). Long-distance dispersal of plants. *Science* **313**, 786–788.
- NATHAN, R., KATUL, G. G., HORN, H. S., THOMAS, S. M., OREN, R., AVISSAR, R., PACALA, S. W. & LEVIN, S. A. (2002). Mechanisms of long-distance dispersal of seeds by wind. *Nature* **418**, 409–413.
- NATHAN, R., SCHURR, F. M., SPIEGEL, O., STEINITZ, O., TRAKHTENBROT, A. & TSOAR, A. (2008). Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution* **23**, 638–647.
- NAVASCUÉS, M. & EMERSON, B. C. (2007). Natural recovery of genetic diversity by gene flow in reforested areas of the endemic Canary Island pine, *Pinus canariensis*. *Forest Ecology and Management* **244**, 122–128.
- NEGOITA, L., FRIDLEY, J. D., LOMOLINO, M. V., MITTELHAUSER, G., CRAINE, J. M. & WEIHER, E. (2016). Isolation-driven functional assembly of plant communities on islands. *Ecography* **39**, 1066–1077.
- NEUFELD, C. J., STARKO, S. & BURNS, K. C. (2017). Disturbance and diversity in a continental archipelago: a mechanistic framework linking area, height, and exposure. *Ecosphere* **8**, e01957.
- NOGALES, M., HELENO, R., TRAVESET, A. & VARGAS, P. (2012). Evidence for overlooked mechanisms of long-distance seed dispersal to and between oceanic islands. *New Phytologist* **194**, 313–317.
- NOGUÉ, S., SANTOS, A. M. C., CONNOR, S., DE BOER, E. J., DE NASCIMENTO, L., FELDE, V. A., FROYD, C. A., HABERLE, S. G., HOOGHIESTRMA, H., LJUNG, K., NORDER, S. J., PREBBLE, M., STEVENSON, J., WHITTAKER, R. J., WILLIS, K. J., et al. (2021). The human dimension of biodiversity changes on islands. *Science* **491**, 488–491.
- OLESEN, J. M., ESKILDSEN, L. I. & VENKATASAMY, S. (2002). Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. *Diversity and Distributions* **8**, 181–192.



- OLESEN, J. M. & VALIDO, A. (2003). Lizards as pollinators and seed dispersers: an island phenomenon. *Trends in Ecology & Evolution* **18**, 177–181.
- ONSTEIN, R. E., BAKER, W. J., COUVREUR, T. L. P., FAURBY, S., SVENNING, J. C. & KISSLING, W. D. (2017). Frugivory-related traits promote speciation of tropical palms. *Nature Ecology & Evolution* **1**, 1903–1911.
- OTTAVIANI, G., KEPPEL, G., GÖTZENBERGER, L., HARRISON, S., OPEDAL, Ø. H., CONTI, L., LIANCOURT, P., KLIME, J., SILVEIRA, F. A. O., JIMÉNEZ-ALFARO, B., NEGOITA, L., HÁJEK, M., IBÁÑEZ, T., MÉNDEZ-CASTRO, F. E. & CHYTRÝ, M. (2020). Linking plant functional ecology to island biogeography. *Trends in Plant Science* **25**, 329–339.
- PATÍÑO, J., WHITTAKER, R. J., BORGES, P. A. V., FERNÁNDEZ-PALACIOS, J. M., AH-PENG, C., ARAÚJO, M. B., ÁVILA, S. P., CARDOSO, P., CORNUAULT, J., DE BOER, E. J., DE NASCIMENTO, L., GIL, A., GONZÁLEZ-CASTRO, A., GRUNER, D. S., HELENO, R., et al. (2017). A roadmap for island biology: 50 fundamental questions after 50 years of The Theory of Island Biogeography. *Journal of Biogeography* **44**, 963–983.
- POORTER, H., JAGODZINSKI, A. M., RUIZ-PEINADO, R., KUYAH, S., LUO, Y., OLEKSYN, J., USOLTSEV, V. A., BUCKLEY, T. N., REICH, P. B. & SACK, L. (2015). How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytologist* **208**, 736–749.
- POORTER, L., ROZENDAAL, D. M. A., BONGERS, F., DE ALMEIDA-CORTEZ, J. S., ALMEYDA ZAMBRANO, A. M., ÁLVAREZ, F. S., ANDRADE, J. L., VILLA, L. F. A., BALVANERA, P., BECKNELL, J. M., BENTOS, T. V., BHASKAR, R., BOUKILI, V., BRANCALION, P. H. S., BROADBENT, E. N., et al. (2019). Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. *Nature Ecology & Evolution* **3**, 928–934.
- PYSEK, P., PERGL, J., ESSL, F., LENZNER, B., DAWSON, W., KREFT, H., WEIGELT, P., WINTER, M., KARTESZ, J., NISHINO, M., ANTONOVA, L. A., BARCELONA, J. F., CABEZAS, F. J., CÁRDENAS, D., CÁRDENAS-TORO, J., et al. (2017). Naturalized alien flora of the world: species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. *Preslia* **89**, 203–274.
- RAZANAJATOVO, M., DAWSON, W., WINTER, M., VAN KLEUNEN, M., KREFT, H., ESSL, F., PERGL, J., PYSEK, P. & WEIGELT, P. (2019). Autofertility and self-compatibility moderately benefit island colonization of plants. *Global Ecology and Biogeography* **28**, 341–352.
- REICH, P. B. (2014). The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**, 275–301.
- RENNER, S. (2004). Plant dispersal across the tropical Atlantic by wind and sea currents. *International Journal of Plant Sciences* **165**, 23–33.
- SAKAI, A. K., WAGNER, W. L. & MEHRHOFF, L. A. (2002). Patterns of endangerment in the Hawaiian flora. *Systematic Biology* **51**, 276–302.
- SALCES-CASTELLANO, A., PATÍÑO, J., ÁLVAREZ, N., ANDÚJAR, C., ARRIBAS, P., BRAOJOS-RUIZ, J. J., DEL ARCO-AGUILAR, M., GARCÍA-OLIVARES, V., KARGER, D. N., LÓPEZ, H., MANOLOPOULOU, I., OROMÍ, P., PÉREZ-DELGADO, A. J., PETERMAN, W. E., RIJSDIJK, K. F., et al. (2020). Climate drives community-wide divergence within species over a limited spatial scale: evidence from an oceanic island. *Ecology Letters* **23**, 305–315.
- SAUQUET, H. (2019). A database for recording morphological data and fossil calibrations. Version 1.27. <http://eflower.myspecies.info/proteus>.
- SAYRE, R., NOBLE, S., HAMANN, S., SMITH, R., WRIGHT, D., BREYER, S., BUTLER, K., VAN GRAAFEILAND, K., FRYE, C., KARAGULLE, D., HOPKINS, D., STEPHENS, D., KELLY, K., BASHER, Z., BURTON, D., et al. (2019). A new 30 meter resolution global shoreline vector and associated global islands database for the development of standardized ecological coastal units. *Journal of Operational Oceanography* **12**, 47–56.
- SCHLEUNING, M., FRÜND, J. & GARCÍA, D. (2015). Intecol special issue Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant–animal interactions. *Ecography* **38**, 380–392.
- SCHRADER, J. (2020). Plants on small islands: using taxonomic and functional diversity to unravel community assembly processes and the small-island effect. *Frontiers of Biogeography* **12**, e47361.
- SCHRADER, J., CRAVEN, D., SATTLER, C., CÁMARA-LERET, R., MOELJONO, S. & KREFT, H. (2021a). Life-history dimensions indicate non-random assembly processes in tropical island tree communities. *Ecography* **44**, 469–480.
- SCHRADER, J., KÖNIG, C., MOELJONO, S., PÄRTEL, M. & KREFT, H. (2019). Requirements of plant species are linked to area and determine species pool and richness on small islands. *Journal of Vegetation Science* **30**, 599–609.
- SCHRADER, J., KÖNIG, C., TRIANTIS, K. A., TRIGAS, P., KREFT, H. & WEIGELT, P. (2020). Species–area relationships on small islands differ among plant growth forms. *Global Ecology and Biogeography* **29**, 814–829.
- SCHRADER, J., WESTOBY, M., WRIGHT, I. J. & KREFT, H. (2021b). Disentangling direct and indirect effects of island area on plant functional trait distributions. *Journal of Biogeography* **48**(8), 2098–2110.
- SI, X., CADOTTE, M. W., ZENG, D., BASELGA, A., ZHAO, Y., LI, J., WU, Y., WANG, S. & DING, P. (2017). Functional and phylogenetic structure of island bird communities. *Journal of Animal Ecology* **86**, 532–542.
- SILVERTOWN, J. (2004). The ghost of competition past in the phylogeny of island. *Journal of Ecology* **92**, 168–173.
- ŠIMOVÁ, I., VIOLLE, C., SVENNING, J. C., KATTGE, J., ENGEMANN, K., SANDEL, B., PEET, R. K., WISER, S. K., BLONDER, B., MCGILL, B. J., BOYLE, B., MORUETA-HOLME, N., KRAFT, N. J. B., VAN BODEGM, P. M., GUTIÉRREZ, A. G., et al. (2018). Spatial patterns and climate relationships of major plant traits in the New World differ between woody and herbaceous species. *Journal of Biogeography* **45**, 895–916.
- SMITH, J. M. B. (2012). Evidence for long-distance dispersal of *Sophora microphylla* to sub-Antarctic Macquarie Island. *New Zealand Journal of Botany* **50**, 83–85.
- STODDART, D. R. (1992). Biogeography of the Tropical Pacific. *Pacific Science* **46**, 276–293.
- STRATTON, L., GOLDSTEIN, G. & MEINZER, F. C. (2000). Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest. *Plant, Cell and Environment* **23**, 99–106.
- STUESSY, T. F., JAKUBOWSKY, G., GÓMEZ, R. S., PFOSSER, M., SCHLÜTER, P. M., FER, T., SUN, B. Y. & KATO, H. (2006). Anagenetic evolution in island plants. *Journal of Biogeography* **33**, 1259–1265.
- TAYLOR, A., WEIGELT, P., KÖNIG, C., ZOTZ, G. & KREFT, H. (2019). Island disharmony revisited using orchids as a model group. *New Phytologist* **223**, 597–606.
- THOMSON, F. J., MOLES, A. T., AULD, T. D. & KINGSFORD, R. T. (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology* **99**, 1299–1307.
- TRAVERSE, A., HELENO, R., CHAMORRO, S., VARGAS, P., MCMULLEN, C. K., CASTRO-URGAL, R., NOGALES, M., HERRERA, H. W. & OLESEN, J. M. (2013). Invaders of pollination networks in the Galápagos Islands: emergence of novel communities. *Proceedings of the Royal Society B: Biological Sciences* **280**, 1–9.
- TRAVERSE, A. & RIERA, N. (2005). Disruption of a plant–lizard seed dispersal system and its ecological effects on a threatened endemic plant in the Balearic Islands. *Conservation Biology* **19**, 421–431.
- TRØJELSGAARD, K., BÁEZ, M., ESPADALER, X., NOGALES, M., OROMÍ, P., LA ROCHE, F. & OLESEN, J. M. (2013). Island biogeography of mutualistic interaction networks. *Journal of Biogeography* **40**, 2020–2031.
- VARGAS, P., ARJONA, Y., NOGALES, M. & HELENO, R. H. (2015). Long-distance dispersal to oceanic islands: success of plants with multiple diaspore specializations. *AoB Plants* **7**, 1–9.
- VARGAS, P., HELENO, R., TRAVESET, A. & NOGALES, M. (2012). Colonization of the Galápagos Islands by plants with no specific syndromes for long-distance dispersal: a new perspective. *Ecography* **35**, 33–43.
- VARGAS, P., NOGALES, M., JARAMILLO, P., OLESEN, J. M., TRAVESET, A. & HELENO, R. (2014). Plant colonization across the Galápagos Islands: success of the sea dispersal syndrome. *Botanical Journal of the Linnean Society* **174**, 349–358.
- VIANA, D. S., GANGOSO, L., BOUTEN, W. & FIGUEROLA, J. (2016). Overseas seed dispersal by migratory birds. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20152406.
- VIOLLE, C., REICH, P. B., PACALA, S. W., ENQUIST, B. J. & KATTGE, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences* **111**, 13690–13696.
- WALLACE, A. R. (1880). *Island Life*. MacMillan and Co., London.
- WEIGELT, P., DANIEL KISSLING, W., KISEL, Y., FRITZ, S. A., KARGER, D. N., KESSLER, M., LEHTONEN, S., SVENNING, J.-C. & KREFT, H. (2015). Global patterns and drivers of phylogenetic structure in island floras. *Scientific Reports* **5**, 12213.
- WEIGELT, P., JETZ, W. & KREFT, H. (2013). Bioclimatic and physical characterization of the world's islands. *Proceedings of the National Academy of Sciences* **110**, 15307–15312.
- WEIGELT, P., KÖNIG, C. & KREFT, H. (2020). GIFT – a global inventory of floras and traits for macroecology and biogeography. *Journal of Biogeography* **47**, 16–43.
- WEIGELT, P. & KREFT, H. (2013). Quantifying island isolation - insights from global patterns of insular plant species richness. *Ecography* **36**, 417–429.
- WESTERBAND, C. A., KNIGHT, T. M. & BARTON, K. E. (2021). Intraspecific trait variation and reversals of trait strategies across key climate gradients in native Hawaiian plants and non-native invaders. *Annals of Botany* **127**, 553–564.
- WESTOBY, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**, 213–227.
- WESTOBY, M., FALSTER, D. S., MOLES, A. T., VESK, P. A. & WRIGHT, I. J. (2002). Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* **33**, 125–159.
- WHEELWRIGHT, N. T. (1985). Fruit size, gape width and the diets of fruit-eating birds. *Ecology* **66**, 808–818.
- WHITTAKER, R. J., BUSH, M. B. & RICHARDS, K. (1989). Plant recolonization and vegetation succession on the Krakatau Islands, Indonesia. *Ecological Monographs* **59**, 59–123.
- WHITTAKER, R. J. & FERNÁNDEZ-PALACIOS, J.-M. (2007). *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford University Press, Oxford.
- WHITTAKER, R. J., FERNÁNDEZ-PALACIOS, J. M., MATTHEWS, T. J., BORREGAARD, M. K. & TRIANTIS, K. A. (2017). Island biogeography: taking the long view of nature's laboratories. *Science* **357**, eaam8326.

- WHITTAKER, R. J. & JONES, S. H. (1994). The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *Journal of Biogeography* **21**, 245–258.
- WHITTAKER, R. J., JONES, S. H. & PARTOMIHARDJO, T. (1997). The rebuilding of an isolated rain forest assemblage: how disharmonic is the flora of Krakatau? *Biodiversity and Conservation* **6**, 1671–1696.
- WHITTAKER, R. J., RIGAL, F., BORGES, P. A. V., CARDOSO, P., TERZOPOULOU, S., CASANOVES, F., PLA, L., GUILHAUMON, F., LADLE, R. J. & TRIANTIS, K. A. (2014). Functional biogeography of oceanic islands and the scaling of functional diversity in the Azores. *Proceedings of the National Academy of Sciences* **111**, 13709–13714.
- WRIGHT, I. J., DONG, N., MAIRE, V., PRENTICE, I. C., WESTOBY, M., DÍAZ, S., GALLAGHER, R. V., JACOBS, B. F., KOOYMAN, R., LAW, E. A., LEISHMAN, M. R., NIINEMETS, Ü., REICH, P. B., SACK, L., VILLAR, R., et al. (2017). Global climatic drivers of leaf size. *Science* **357**, 917–921.
- WRIGHT, I. J., REICH, P. B., WESTOBY, M., ACKERLY, D. D., BARUCH, Z., BONGERS, F., CAVENDER-BARES, J., CHAPIN, T., CORNELISSEN, J. H. C., DIEMER, M., FLEXAS, J., GARNIER, E., GROOM, P. K., GULIAS, J., HIKOSAKA, K., et al. (2004). The worldwide leaf economics spectrum. *Nature* **428**, 821–827.
- WRIGHT, S. D., YONG, C. G., DAWSON, J. W., WHITTAKER, D. J. & GARDNER, R. C. (2000). Riding the ice age El Niño? Pacific biogeography and evolution of *Metrosideros* subg. *Metrosideros* (Myrtaceae) inferred from nuclear ribosomal DNA. *Proceedings of the National Academy of Sciences* **97**, 4118–4123.

## X. APPENDIX A.

### METHODOLOGICAL AND STATISTICAL APPROACHES FOR FUNCTIONAL ISLAND BIOGEOGRAPHY

Empirical studies in functional island biogeography require specifically tailored statistical methods. In recent years, a plethora of such methods have been developed in functional ecology that can be applied to island studies. An important element is to account for the nested structure of island comparisons, such as islands within archipelagos, and plots within islands. Another important element is to account for differences in species richness between islands; this is a genuine biological difference and at the same time a confounding factor for comparing trait amplitudes. Here, we discuss methods that can be used in functional island biogeography in general and that can help to test our hypotheses.

#### (1) Island–mainland comparisons

Island–mainland comparisons of traits are useful to identify the nature of insularity and to test for prevalence of island syndromes or functional differences of the same species or its closest relatives between islands and/or the mainland. The distribution of single, continuous trait values of island and mainland species (intra- and interspecific) or communities (community means) can be compared. Examples of island–mainland comparisons include loss of defence mechanisms in island species in response to relaxation of herbivory, loss of dispersal potential or changes in seed mass after island colonisation (Cody & Overton, 1996; García-Verdugo *et al.*, 2017; Biddick *et al.*, 2019; Meredith *et al.*, 2019).

#### (2) Functional trait spaces

Functional trait spaces are based on the concept that a given set of individuals or species are distributed within a

multidimensional space of their functional traits (Díaz & Cabido, 2001). Trait spaces can be generated using ordination systems such as principal component analyses, non-metric multidimensional scaling or n-dimensional hypervolumes (Blonder, 2018; Mammola & Cardoso, 2020). Trait spaces can be used to compare and visualise differences within island communities, between islands and mainlands or to distinguish among traits evolved from adaptive and non-adaptive radiations (Fig. 1). The simplest form of a trait space requires at least two continuous trait variables. When more than two trait dimensions are available, categorical traits can also be included. Examples for two-dimensional trait spaces can be found in Biddick *et al.* (2019) and for multiple dimensions in Díaz *et al.* (2016) or Schrader *et al.* (2021a).

#### (3) Community (weighted) means

Community (weighted) means summarise values for continuous traits at the level of an island community or assemblage. Community means are useful in many statistical frameworks such as regression or path analysis and describe how trait values change along geo-environmental gradients, such as island area, isolation or elevation. In their abundance-weighted form, community means express differences in what traits are predominant in communities. Community trait means in island biogeography could indicate scaling relationships of dispersal and successional traits along island area or isolation. However, community trait means have been used rarely in island studies to date (but see Negoita *et al.*, 2016; Schrader *et al.*, 2021b).

#### (4) Functional diversity

Functional diversity describes the diversity of functional traits at any given organisational level (e.g. individual, population, community) and can be linked directly to ecosystem functioning, productivity or resilience (Díaz & Cabido, 2001; Mason *et al.*, 2005). Functional diversity has received much attention in recent years, including development of functional diversity–area relationships (Whittaker *et al.*, 2014). Different indices have been developed to describe functional diversity, such as functional richness, divergence and dispersion and species abundances can be included (Mason *et al.*, 2005). Most indices, however, are highly sensitive to species richness and cannot clearly discern whether functional diversity–area relationships are a by-product of increasing species richness with island area or are directly affected by island area (Si *et al.*, 2017; Schrader *et al.*, 2021a).

#### (5) Null models

Null models can be used to detect non-random patterns in communities by comparing observed diversity (e.g. species richness, community weighted means, functional diversity) against randomly created diversity from the species pool. Null models can thus account for differences in species richness or abundance between samples or islands. For example,

whether the functional diversity–area relationship is affected directly by island area or indirectly by increasing species richness or habitat diversity with island area can be tested using null models (Si *et al.*, 2017; Schrader *et al.*, 2021a). Null models can also reveal filtering or other non-random assembly processes by testing whether an observed community is less diverse (e.g. as result of filters) or more diverse (e.g. as result of niche differentiation or competition) than expected by chance (Götzenberger *et al.*, 2016; Schrader *et al.*, 2021a).

## (6) Functional groups

Functional groups categorise species according to the same or similar ecological strategies, such as growth forms or pollination or dispersal vectors. In contrast to continuous traits, functional groups are categories and can be represented by a frequency distribution, such as per cent of flora using wind dispersal. These can also be abundance weighted. Categorical traits often have better global coverage than continuous traits (Weigelt, König & Kref, 2020). For functional groups, biodiversity indices such as species richness, abundances or functional diversity can be calculated and used for diversity–environment relationships. Examples for islands include species–area relationships calculated for herb, shrub and tree species richness (Schrader *et al.*, 2020), global compositions of plant growth forms (König *et al.*, 2019) or tree lines on islands (Karger *et al.*, 2019).

## (7) Species-interaction networks

Species-interaction networks indicate the complexity and number of links among co-occurring species of an island or community (Trøjelsgaard *et al.*, 2013). Linked to functional trait values or constructed for specific species groupings based on their traits, interaction networks can inform on the level of mutualistic relationships, pollination and dispersal agents or predominant herbivores (Heleno *et al.*, 2013; Traveset *et al.*, 2013). As such, interaction networks are useful to understand plant strategies at the community level or when managing environmental threats (Heleno *et al.*, 2011).

## (8) Molecular-phylogenetic approaches

Molecular-phylogenetic approaches can be used to infer ancestral traits of, for example, island founder populations or character displacement (Emerson, 2002). When compared to species trait dissimilarities, phylogenetic distances between species can reveal whether traits or common ancestry drive invasion success on islands (Marx *et al.*, 2016). In addition, in the absence of traits, phylogenetic relatedness can be used as proxy for trait similarity and can indicate filtering processes on islands (Matthews *et al.*, 2020).

## (9) Data and resources for functional island biogeography

In functional island biogeography, many insights into processes and outcomes have been generated by field studies, but it is time to validate this knowledge across islands at

macroecological scales. Recent years have seen an increase in the availability of plant functional trait data, mostly driven by large global data initiatives. Other databases have assembled global species occurrences at plot and regional scales including island data. Integration of data from different domains and scales to island studies could help to bridge the gap between trait patterns at local and macroecological scales (König *et al.*, 2019). Some initiatives are especially valuable in the context of functional island biogeography.

The Global Inventory of Floras and Traits database (GIFT; [www.gift.uni-goettingen.de](http://www.gift.uni-goettingen.de)) holds occurrence information for *ca.* 315,000 species in *ca.* 2900 geographic entities worldwide including 1845 islands and 1048 mainland regions and nature reserves (Weigelt *et al.*, 2020). In addition, GIFT contains information for 83 functional traits with high coverage of categorical traits such as species growth forms or woodiness. Trait data from GIFT is extracted from originally published resources or integrated from other databases. GIFT has great potential to answer questions in functional island biogeography at macroecological scales (e.g. König *et al.*, 2019, 2021; Taylor *et al.*, 2019; Schrader *et al.*, 2020).

The TRY database is the world's largest repository for plant functional traits at the level of individual species including both mainland and island species (Kattge *et al.*, 2020; [www.try-db.org](http://www.try-db.org)). Data can be extracted upon request and can help to fill gaps in field-collected data or for global comparisons of island and mainland communities (Cutts *et al.*, 2021).

The Botanical Information and Ecology Network (Maitner *et al.*, 2018; [www.bien.nceas.ucsb.edu](http://www.bien.nceas.ucsb.edu)) and sPlot (Bruehlheide *et al.*, 2019; [www.idiv.de/de/splot](http://www.idiv.de/de/splot)) databases hold species occurrence and community data at the level of plots. Most plot data from these databases were sampled on the mainland. They can often provide mainland comparisons for island plots.

In addition, many global trait comparisons have been published in recent years. While most of these publications did not specifically target island species or assemblages, they can be used as null model (or mainland comparison) for island studies. Examples include global patterns for leaf traits (Wright *et al.*, 2004, 2017; Butler *et al.*, 2017), plant growth forms (König *et al.*, 2019), biomass allocation (Poorter *et al.*, 2015), plant hydraulics (Mencuccini *et al.*, 2019) or floral traits (Sauquet, 2019).

Global environmental layers provide information on island geo-environmental factors such as island age, area, climate, soil, substrate, elevation, topography or isolation (Weigelt *et al.*, 2013). These factors are suitable to include both in macroecological and field studies in functional island biogeography. For instance, CHELSA layers (Karger *et al.*, 2017) and downscaled products (Salces-Castellano *et al.*, 2020) hold information on global climatologies including precipitation and temperature. Global, high-resolution digital elevation models exist to model island elevation, topography and habitat heterogeneity (e.g. digital elevation

at 1 arc-s from the Shuttle Radar Topography Mission; [www.earthdata.nasa.gov](http://www.earthdata.nasa.gov)). Island substrate and soil can be extracted *via* the Harmonized World Soil Database (Fischer *et al.*, 2008; [www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12](http://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12)). Recently, a global layer for all islands worldwide has been released

that can be used to extract island area and to calculate different isolation metrics (Global Island Explorer; Sayre *et al.*, 2019; [www.rmgsc.cr.usgs.gov/gie](http://www.rmgsc.cr.usgs.gov/gie)). The GIFT database summarises geo-environmental information for most islands worldwide and data is released upon request (Weigelt *et al.*, 2020).

*(Received 10 March 2021; revised 9 July 2021; accepted 12 July 2021; published online 23 August 2021)*