A roadmap to plant functional island biogeography

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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, succession, 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

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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 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 (Michay & 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; Whittakers 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 (Šimůvá et al., 2018; Poorter et al., 2019), plant growth forms and height (Šimůvá 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 epizoocochorous 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) seahird dispersal, (ii) wind dispersal or (iii) ocean currents. | Island area and isolation | | Retten (2004); Gillespie et al. (2012); Alou et al. (2015); Vargas et al. (2015) |
| | O H2 | On oceanic islands, successful colonizers have traits suitable for long-distance dispersal. | Island isolation | Seed mass, propagule appendages, floating and saltwater resistance | Carlquist (1974); Gillespie et al. (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 | Carlquist (1974) |
| | O H4 | Plants specialized for dispersal by seabirds have external attachments and their prevalence in a community increases with island isolation. | Island isolation | Propagule appendages | Aoyama et al. (2012); Nogales et al. (2012) |
| 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 | | Meehan et al. (2002); Kiidling et al. (2009); Carvajal-Endara et al. (2017); Onstein et al. (2017) |
| | 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 | Schrader et al. (2012a); Burns & Neufeld (2012b); Schrader et al. (2018); Neufeld et al. (2017); Schrader et al. (2014) |
| | 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 | Whitaker et al. (1989); Burns & Neufeld (2009); Karadimou et al. (2018); Schrader et al. (2012a, 2012b, 2012c) |
| | 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 | Cordell et al. (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 |
|---------|-------------|------------------|--------|------------------------|------------|
| O 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. | Seed output, dispersal syndrome, plant height, stem density, mycorrhizal type | FG CWM | Sakai et al. (2002); Burns & Neufeld (2009); Whittaker et al. (2014) |
| P H14   | Diversity of mutualists including pollinators and animal seed dispersers decreases with increasing island isolation. | Island isolation | Mycorrhiza, pollination mode, flower morphology | FD | Bawa (1980); Givnish (2010); Hiraiwa & Ushimaru (2017); Delavaux et al. (2019); Razanaarajonarisoa et al. (2019); Taylor et al. (2019) |
| O H15   | Functional diversity of traits linked to mutualistic relationships and reproduction decreases with island isolation. | Island isolation | Flower morphology, pollination syndromes, vegetative reproduction | FG | Baker (1955); Delavaux et al. (2019); Razanaarajonarisoa et al. (2019); Taylor et al. (2019) |
| O H16   | With increasing island isolation, the proportion of species increases that (i) have generalist pollination strategies, (ii) are self-compatible or (iii) reproduce vegetatively. | Communities present | Pollination syndromes | CWM FG | Bawa (1980); Givnish (2010); Aho et al. (2015); Grossenbacher et al. (2017) |
| 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. | Diversity of animals on islands | | | |
| P H18   | Selection for dispersal within islands can favour different vectors compared to those that initially brought species to the island. | Island elevation and type | Anemochorous appendages, salt water resistance | FG CWM IMC | Carliquist (1974) |
| 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. | Seed mass, anemochorous appendages | FG CWM | Kreft et al. (2010); Keppel et al. (2016) |
| O H20   | High-elevation sites on islands have high proportion of (i) species with small seeds and (ii) propagules with anemochorous appendages. | Island elevation | | | |
| O H21   | Islands with well-developed vertebrate communities also have a high proportion of zyoochorous-dispersed plants. | Diversity of animals on islands | Fruit type and colour | NM IMC | Whittaker et al. (1997); García-Verdugo et al. (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 | | | Jørgensen & Olesen (2001); Silvertown (2004); Givnish (2010); Gillespie et al. (2012); Garcia-Verdugo et al. (2017); Biddick et al. (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 | Jørgensen & Olesen (2001); Grossenbacher et al. (2017) |
| O H24   | Propagules with anemochorous appendages, water resistance or small seeds evolve towards (i) fleshiness, (ii) loss of appendages or (iii) larger seed masses. | Island area, age and isolation | Fruit type and mass, propagule appendages, salt water resistance | FTS IMC | Cody & Overton (1996); Givnish et al. (2009); Kavanagh & Burns (2014); García-Verdugo et al. (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 et al. (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 | Carliquist (1974); Lens et al. (2013); Burns (2019) |
(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).

Propagate 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 island size as seabirds feed and 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, 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 (Chiarrucci 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; Abos 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 (Wheelewright, 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 (Carquist, 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 local 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 extinctions 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 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 & Partomiharjo, 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 DISPERAL

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 & Venkatasaamy, 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; Schleunning, 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 zoo-
chorous 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 vec-
tors that have reached the island. Quantified frequencies of
dispersal traits comparing both between islands and between
habitats within islands (H19 & H20) can measure the conse-
quences of these different effects.

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

Oceanic island floras are renowned for their spectacular evo-
olutionary radiations which considerably contribute to diver-
sity 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 mainland species 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 com-
petition. 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 col-
oniser 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 spe-
cies differentiating their traits when in sympathy to reduce
competition for resources (Emerson, 2002; Losos & Ricklef,
2009). However, the prevalence of character dis-
placement 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 competi-
tion 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) flesh-
iness, (ii) loss of appendages or (iii) larger seed masses.
H25. Insularity causes trait convergence, i.e. large spe-
cies or organs become smaller and small species or
organisms become larger.
H26. On oceanic islands, herbaceous species tend to
evolve secondary woodinesse.
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 colo-
nisation 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 pre-
vailing abiotic and biotic factors (adaptive radiation) or ran-
dom, 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 lobelias (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 monocarp, developmental heterophyll, 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 Garcia-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; Grossenbacher 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 & Elmquist, 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 Marquette 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., Eriech, D., Eideksen, P. B., Solstad, H., Westergaard, K. B., Schönswetter, P., Tibrisch, A., Birkeland, S., Elven, R. &
Heinen, J. H., Harter, D. E. V., James, S. A., Kreft, H., & Gray, A., Heleno, R., König, C., 2019. Ectric-driven changes in frugivorous communities on oceanic islands. *Ecography* 42, 1254–1255.

Heleno, R., Blake, S., Jaramillo, P., Travest, A., Vargas, P. & Nogales, M., 2018. Seed dispersal networks in the Galápagos and the consequences of alien plant invasions. *Proceedings of the Royal Society B: Biological Sciences* 285, 1–9.

Heleno, R. H., Vargas, P., 2018. How do islands become green? *Global Ecology and Biogeography* 27, 526–532.

Hirakawa, M. K. & Ushirmaru, A., 2017. Low functional diversity promotes niche changes in natural island pollinator communities. *Proceedings of the Royal Society B: Biological Sciences* 284, 20172218.

Hoyle, F. & Smith, J. W., 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.

Jørgensen, T. H. & Olesen, J. M., 2001. Adaptive radiation of island plants: evidence from the flora of the Canary Islands. Perspectives in Plant Ecology, Evolution and Systematics 4, 29–42.

Karadimo, E., Kalimani, A. S., Tsipriou, I., Raux, T., Bergmeier, E. & Dimopoulos, P., 2018. Functional diversity changes over 100 yr of primary succession on a volcanic island: insights into assembly processes. *Ecography* 41, e02374.

Karger, D. N., Van Loon, E. E., Beierkuhnlein, C., Jetz, W., Froyd, C. A., Condon, R., Donoghue, J. D., McAuley, B., Casler, N., Meredith, F. L., Ens, W. G., Kallimanis, A. S., Moreira, X., Pernis, R., Leusch, M. R., Wilson, J. B., Auld, J. R., Gill, L., 2007. Contrasting ecotypic differentiation of growth and survival in Pinus species. *Australian Journal of Botany* 55, 759–769.

Lemos, 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. Princeton University Press, Princeton.

Maitner, B. S., Boyle, B., Casler, N., Condit, R., Donoghue, J., Durán, S. M., Guaderrama, D., Hinchliff, C. E., Jürgens, P. M., Kraft, N. J. B., McGill, B., Merow, C., Morueta-Holme, N., Peet, R. K., Sandel, B., et al., 2016. The bcr package: a tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods in Ecology and Evolution* 7, 880–886.

March, H. E., Giblin, D. E., Dunwiddie, P. W. & Tank, D. C., 2016. Deconstructing Darwin’s Naturalization Conundrum in the San Juan Islands using gene flow in reforested areas of the endemic Canary Island pine, *Pinus canariensis*. *Proceedings of the Royal Society B: Biological Sciences* 283, 20152352.

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.

Meneguetti, M., Rossa, T., Rowland, L., Chot, B., Cornelissen, H., Lassen, N., Nokher, K., Lapenis, A., Manzoni, S., Ninedets, U., Reich, P., Schmidt, F., Soudzilovskaya, N., Wright, I. J. & Martínez-Vilalta, J., 2019. Leaf economics and plant productivity drive leaf: wood area ratios. *New Phytologist* 224, 1544–1556.

Mentred, F. L., Tondali, M. L., Hemmings, A. F. & Miles, A. T. (2019). Pinky pairs: the proportion of space-ties species does not differ between islands and mainland. *Journal of Plant Ecology* 12, 941–948.

Midway, S. R. & Hodge, A. M. C., 2012. Carlgquist revisited: history, success, and applicability of a natural history model. *Biological and Philosophy* 27, 497–502.

Moles, T. A., Ackerly, D. D., Dickie, J. B., Smith, J. F., 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., Cantagnor, B., de la Mata, R., Fyllas, N. M., Gálma, A., Verdiu, C., Larraig, A. R. & Armada-Robert, L., 2019. Effects of insularity on insect leaf herbivory and chemical defences in a Mediterranean oak species. *Journal of Biogeography* 46, 1226–1233.

Mosier, D., Lenzner, R., Weigelt, P., Dawson, W., Kreft, H., Perge, J., Pekel, V., van Kleeun, W., Winter, M., Capinha, C., Cassey, P., Duling, S., Economio, E. P., García-Díaz, P., Guénard, B., et al., 2018. Promotess promotes biogeographic insights on islands worldwide. *Proceeding of the National Academy of Sciences* 115, 9270–9275.

Nathan, R. (2006). Long-distance dispersal of plants. *Science* 313, 786–788.

Nathan, R., Ratev, G. G., Horne, S. H., Thomas, S. M., Oren, R., Avisar, N., Pacala, S. W. & Levin, S. A., 2002. Mechanisms of long-distance dispersal of seeds by wind. *Nature* 418, 869–874.

Nathan, R., Schurr, F. M., Spiegel, O., Steinz, O., Trakhtenbrot, A. & Tsoar, A., 2008. Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution* 23, 638–647.

Navasán, 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.

Negotta, I., Freidle, J. D., Lomolino, M. V., Mettelhauser, G., Crane, J. M. & Wiether, 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. *Ecography* 40, e01957.

Nogales, M., Heleno, R., Travest, A. & Vargas, P., 2012. Evidence for overlocked mechanisms of long-distance seed dispersal to and between oceanic islands. *New Phytologist* 194, 313–317.

Nogues, S., Santos, J. A. C., Connor, S., de Boer, E. J., De Nascimento, L., Felde, V. A., Froyd, C. A., Haberer, S. G., Hooghiemstra, H., Ljung, K., Norder, S. J., Preble, M., Stevenson, J., Whittaker, R. J., Willin, K. J., et al., 2014. The human dimension of biodiversity changes on islands. *Science* 348, 481–491.

Olesen, J. M., Ekböll, I. S. & Venkataramy, S., 2002. Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. *Diversity and Distributions* 8, 101–102.
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 & Kreft, 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; Travestet 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) 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). 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 (Cutt et al., 2021).

The Botanical Information and Ecology Network (Maitner et al., 2018; www.bien.nceas.ucsb.edu) and sPlot (Bruelheide et al., 2019; 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 (Sales-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.earth.data.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). 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). 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)