

Island plant functional syndromes and competition with invasive species

Kasey E. Barton¹  | Claire Fortune²

¹School of Life Sciences, University of Hawai'i at Mānoa, Honolulu, Hawai'i, USA

²AMAP (botAnique et Modélisation de l'Architecture des Plantes et des végétations), Université de Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France

Correspondence

Kasey E. Barton, 2538 McCarthy Mall, Edmondson Hall Room 216, Honolulu, Hawai'i 96822, USA.
Email: kbarton@hawaii.edu

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Abstract

Island floras are diverse with exceptionally high rates of endemism, and they are also severely threatened. Invasive plants are widespread on islands, but whether islands are particularly susceptible to invasion or island species are more vulnerable to displacement, or both, remains unclear. As part of the "island plant syndrome," it has been predicted that island plants have convergently evolved conservative resource use, slow growth rates, and weak competitive abilities in response to moderate climates and the presumed absence of competition in communities with relatively low species richness. Yet, functional trait approaches have provided mixed evidence to support this prediction, and direct tests of competition as neighbour effects on plant performance are lacking. Considering the extensive environmental heterogeneity that exists within islands and among islands, it seems more likely that diverse functional strategies, spanning conservative to acquisitive, have evolved in island plants. Furthermore, assessing island plant syndrome predictions through comparisons with invasive species, which are nonrandom subsets of continental plants, is a flawed approach. Future studies that compare functional strategies of native island versus native continental plants and direct tests for competition between native and invasive island plants within the local scale at which competition occurs, and that consider non-additivities with other simultaneous global threats, are urgently needed to conserve these biodiversity hotspots.

KEYWORDS

Darwin's naturalization hypothesis, functional diversity, functional traits, island biogeography, niche theory, plant invasions

1 | INTRODUCTION

Island biodiversity is unique, characterized by high rates of endemism, phylogenetic disharmony, and distinctive phenotypes (Carlquist, 1974; Wallace, 1881). Island biodiversity is also among the most threatened in the world, accounting for disproportionate numbers of species endangerments and extinctions (Fernández-Palacios et al., 2021). Among global threats to native island species, invasive species are particularly numerous on islands and are broadly implicated in the decline of island biodiversity (Reaser et al., 2007; Russell & Kueffer, 2019; Sax & Gaines, 2008; Schrader et al., 2021).

Whether island invasions are particularly successful because islands are more susceptible to invasion or because island species are more vulnerable to displacement, or both, remains unclear but is an urgent research priority both for insights into the evolution of island species and to conserve these biodiversity hotspots.

Considerable research has characterized island plant diversity, cataloguing species lists and describing adaptive radiations (Funk & Wagner, 1995; Romeiras et al., 2014; Weigelt et al., 2020). Stemming from classic island biogeography theory (MacArthur & Wilson, 1967), it is clear that island area and isolation play key roles in community assembly and diversification. In general, islands have fewer native

species than continents (Chown et al., 1998; Kreft et al., 2008), and low species richness is predicted to allow for high rates of invasion through the availability of empty niches (Elton, 1958; Li et al., 2018). Although global analyses have provided mixed evidence for this prediction for islands (Bingelli, 1996; D'Antonio & Dudley, 1995; Denslow, 2003; Vilà et al., 2010), a synthesis of invasions on sub-tropical islands indicate inverse relationships between native and invasive species, as native richness decreases but invasive richness increases with distance from continents (Moser et al., 2018). Whether higher numbers of invasive species on remote islands reflects greater invasion success rates, perhaps due to higher invasibility, or alternatively, greater propagule pressure and introductions associated with human activities, remains unclear and more challenging to investigate because failed introductions are often not detected or recorded (Diez et al., 2009; Sol, 2000). Nonetheless, there is strong evidence that island communities are heavily invaded, with few exceptions (Fernández-Palacios et al., 2022), and that native species are in decline, and while these patterns are often interpreted as evidence for potential underlying drivers (e.g. competition, natural enemy dynamics), they cannot provide direct evidence as they lack details about species interactions and ecological strategies. Functional traits (morphological, anatomical, physiological and phenological characteristics; Violle et al., 2007) offer a promising way forward in building a more mechanistic framework to examine interactions between island species and invasive species for a better understanding of the processes underlying native species declines on islands (Schrader et al., 2021).

Plant traits and functional diversity on islands are thought to be distinct from continental floras due to phylogenetic disharmony and adaptation to island environments, leading to the convergent evolution of "island syndromes" (Burns, 2019; Carlquist, 1974). Some island syndrome predictions, such as high rates of woodiness and shifts in body size (e.g. island rule), relate to mild island climates with weak seasonality due to the proximity to oceans (Weigelt et al., 2013), while other island syndrome predictions, such as generalized floral morphology, lower incidence of self-incompatibility, and the prevalence of wind pollination relate to the reproductive biology of plants with small population sizes and generalized pollinators (Traveset et al., 2016, 2018). In addition, several island syndrome predictions stem from the assumption that antagonistic interactions via competition or attacks by natural enemies are weak or rare on islands, leading to poorly developed competition and defence strategies (Carlquist, 1974; Darwin, 1859). Whether invasion-driven losses in island biodiversity are directly related to island plant syndromes is widely assumed (Cronk, 1997; Simberloff, 1995), but surprisingly lacking in robust confirmatory evidence. For example, recent syntheses have found island plants to have similar levels of anti-herbivore defences as continental species (Meredith et al., 2019; Moreira et al., 2021), while direct tests of competitive ability for island versus continental plants are few (Barton & Wong, 2019). Furthermore, islands are highly variable with considerable environmental heterogeneity, sometimes comparable to continents, thereby challenging the prediction that island plant syndromes have evolved convergently.

Considering the global threat of invasive species to the conservation of island floras, careful examination of the weak island competitor prediction is urgently needed, incorporating niche theory, trait-based approaches and consideration of other simultaneous threats, for a more nuanced view of island plants and their potential to withstand invasive plant competition.

2 | COMPETITION ON ISLANDS AND DURING INVASION

Resource competition occurs when neighbours suppress plant performance through the use of shared limiting resources such as light, water, and nutrients. Competition can be measured from the perspective of the neighbours as the magnitude of suppression on focal plant performance (competition effects), or alternatively, as the capacity of focal plants to withstand neighbour effects (competition responses or tolerance) (Goldberg, 1996). These contrasting perspectives more or less align with classic theories on competition, which identify strong competitors as those species or genotypes that efficiently co-opt shared resources through vigorous or efficient resource use strategies (Grime, 1977), or as those species or genotypes that achieve positive population dynamics at lower resource availabilities than co-occurring plants (Tilman, 1982).

While competition is most precisely quantified using performance metrics such as plant survival, growth, and reproduction, such studies require time and resources, and it is increasingly common to infer competitive ability from functional traits assumed to correlate with plant fitness (Violle et al., 2007). For example, high wood density has emerged as a significant predictor of both neighbour effects and responses in forest trees (Kunstler et al., 2016). However, a trade-off between growth rate and competitive ability generally occurs as high wood density is also linked to slow growth in the absence of competition (Fortunel et al., 2016; Kunstler et al., 2016), revealing that within forests, the strongest competitors are species with slow growth rates and conservative functional strategies. Contrary to this conclusion, hypotheses about the role of competition in plant invasions often predict that vigorous, fast resource use strategies underlie the success of invasive species (Wandrag & Catford, 2020). Indeed, functional traits associated with fast growth and fast returns on investment resource use strategies (e.g. high specific leaf area, low wood density) have emerged as significant predictors of competitive advantages of invasive compared to native plants (Díaz de León Guerrero et al., 2020; Ordóñez et al., 2010), suggesting that invasive plant competition may differ from that of native plant communities, as has also been indicated by pairwise competition experiments revealing invasive competition effects are stronger than those of native species (Kuebbing & Nuñez, 2016).

Competition hypotheses that are specifically relevant to island invasions generally fall into two categories: (1) those that predict that invasives establish into empty niches in island floras, thereby avoiding competition with native species; or (2) those that predict invasives outcompete native plants through vigorous resource

use strategies (Figure 1). Although not strictly related to island plant syndromes, some relevant hypotheses further consider how human activities have altered conditions that enhance competitive-displacement by invasive species (Figure 1). Importantly, niche versus competitive ability hypotheses provide contrasting predictions for performance and functional trait differences between native and invasive species.

2.1 | Invasive islands—empty niche hypotheses

Empty niche hypotheses predict that invasives occupy distinct niches from natives, as evidenced by phylogenetic and trait dissimilarity, and that such niche partitioning results in weak competition between invasives and natives (Chesson, 2000; Rundel et al., 2014). Empty niches are expected to be particularly prevalent in island floras due to their low species richness and phylogenetic disharmony compared to continental floras, allowing continental plants to invade with relatively little biotic resistance from competition with natives, an idea formulated as Darwin's Naturalization Hypothesis (Darwin, 1859). Assuming that related species have similar niches, assessment of Darwin's Naturalization Hypothesis typically involves molecular approaches to test the prediction that phylogenetic distance will enhance invasion success because invasives with close

native relatives will encounter competitive resistance. Evidence for Darwin's Naturalization Hypothesis on islands is however mixed, with examples that invasives are phylogenetically more (Diez et al., 2009; Marx et al., 2016) and less (Schaefer et al., 2011) related to natives than expected by chance.

The lack of consensus for Darwin's Naturalization Hypothesis has generated considerable discussion, highlighting factors that can explain the variable results, including the importance of phylogenetic resolution (Thuiller et al., 2010), spatial scale at which native-invasive associations are examined (Carboni et al., 2013; Procheş et al., 2008), and the importance of considering failed invasions (Diez et al., 2009). Furthermore, it has been emphasized that competition alone does not determine invasion success, and pre-adaptation to the abiotic environment might favour invasives that are closely related to natives if they share similar tolerances for climate and soil conditions (Diez et al., 2008). Perhaps the most important limitation of phylogenetic approaches for investigating empty niche hypotheses is that phylogenetic relationships do not necessarily predict niche similarities among related native and invasive species. Assuming that phylogenetic relatedness directly corresponds to ecological similarity requires that relevant niche dimensions are conserved within lineages and that convergent evolution across different lineages is limited, but such niche conservatism is not necessarily common (Losos, 2008; Pearman et al., 2008), and convergent evolution for

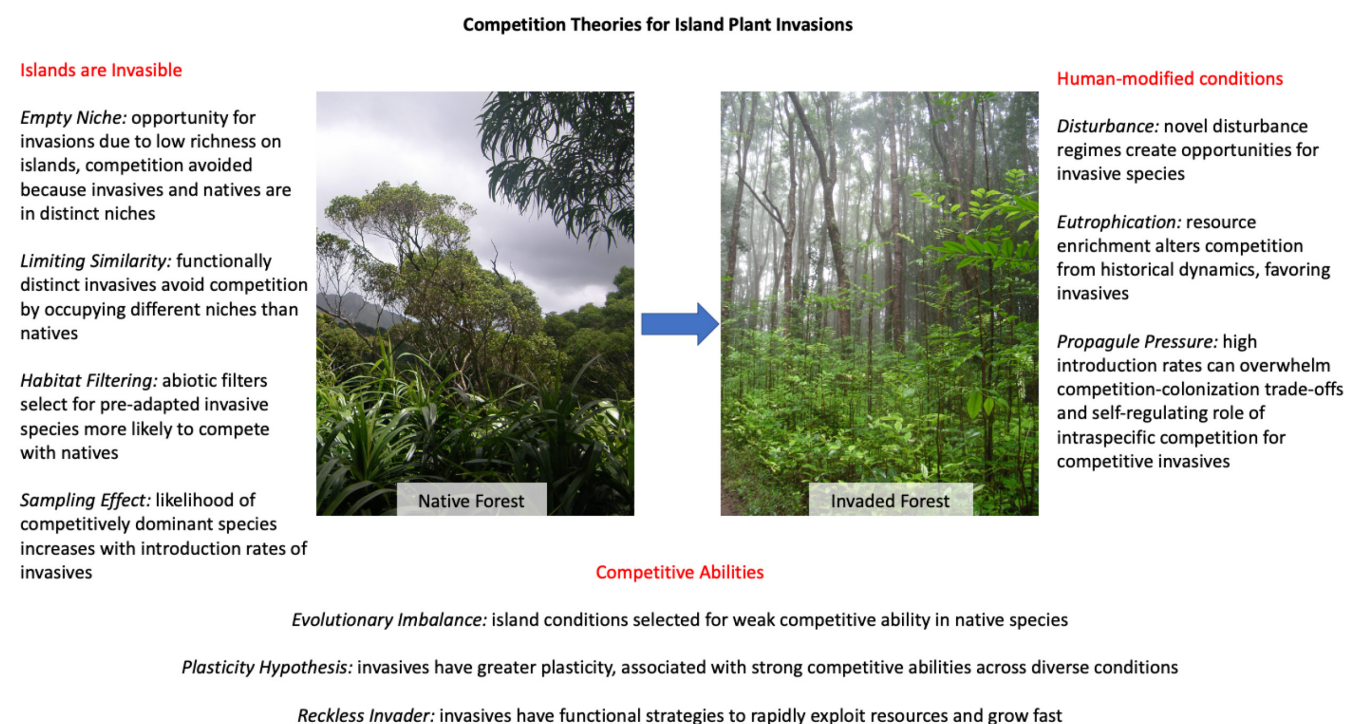


FIGURE 1 Hypotheses for role of competition in plant invasions with direct links to island plant syndrome predictions. Hypotheses related to the availability of niches and invasive species establishment include the empty niche (Chesson, 2000; Rundel et al., 2014), limiting similarity (Darwin, 1859; MacArthur & Levins, 1967), habitat filtering (Darwin, 1859), and sampling effect (Alpert, 2006). Hypotheses about inherent differences in competitive abilities of invasive vs. native species include the evolutionary imbalance (Fridley & Sax, 2014), plasticity (Richards et al., 2006), and reckless invader (Alpert, 2006; Simberloff & Gibbons, 2004). Hypotheses incorporating anthropogenic effects on invasion competition include those that consider the roles of disturbance and eutrophication (Davis et al., 2000), and propagule pressure (Catford et al., 2018). Native and invasive forest images taken in Hawaii.

key ecological strategies does occur (Sanchez-Martinez et al., 2020). For island floras that include rapid evolution and phenotypic diversification associated with adaptive radiations (Funk & Wagner, 1995; Romeiras et al., 2014; Weigelt et al., 2020), the assumption of phylogenetic niche conservatism seems particularly problematic and warrants examination.

In light of uncertainty about the assumption for phylogenetic niche conservatism, the role of empty niches in island invasions should be directly examined through characterization of species habitats and functional strategies (Rejmánek, 1996). A historical context would also shed light on the role of empty niches in island invasions because this mechanism would be most relevant during the first wave of island invasions, following human colonization. Over time, as the number of invasive species accumulated on islands, the availability of empty niches would decrease and therefore play an increasingly minor role in establishment success. To date, no test of Darwin's Naturalization Hypothesis has considered the order of species invasions on islands to incorporate this historical context.

2.2 | Weak island competitor hypotheses for island invasions

In contrast to empty niche hypotheses, which predict weak competition between native and invasive species, it has also been proposed that invasive species can successfully establish in novel habitats by out-competing native plants (Figure 1). Weak competitor hypotheses typically predict that conservative island species would be displaced by invasive species exhibiting fast resource use strategies associated with vigorous growth and fast return on investment in cheap, high turn-over tissues (Chave et al., 2009; Díaz et al., 2016; Franco & Silvertown, 1996; Wright et al., 2004). Multiple approaches can be used to test the competition abilities of native and invasive island plants, ideally via demographic assessments quantifying neighbour effects on focal plant performance (survival, growth, reproduction), using experimental tests (removal/addition at the individual or community scale), and, if limited by time and resources, via functional trait comparative analyses (Figure 2a).

Direct tests of competition using experimental and demographic approaches in island plants are relatively scarce. While pairwise competition experiments are commonly used on continental plants, and have revealed significantly stronger competition effects by invasive than native plants in general (Kuebbing & Nuñez, 2016), few of these experiments have tested island species (Barton & Wong, 2019; D'Antonio et al., 2017; Radford et al., 2009). Among those few pairwise experiments, almost all of which tested competition between native species, significantly stronger competition effects were detected on islands than continents (Barton & Wong, 2019), indicating competition plays an important role among native plants on at least some islands. Although these results contrast with weak island competitor predictions, intense native plant competition on islands may in fact be common, given the narrow range of resource availabilities, limited space and high conspecific

density that occurs in low-diversity communities (Egler, 1942; Diez et al., 2009; Russell & Kueffer, 2019). Additional research focusing on native plant competition (in the absence of invasion) would shed light on this interesting island dynamic. Moreover, given the scarcity of native-invasive pairwise competition experiments on islands, additional research is needed to quantify the strength and directionality of these interactions.

Weak island competitor hypotheses are more often examined using functional trait approaches, predicting that invasives out-compete natives through acquisitive resource use traits (Table S1). Among the 22 studies that compare resource use functional traits of native and invasive species on islands, there is approximately equal support for and against the prediction that invasives are more acquisitive than native plants (Table 1), and this pattern emerges across morphological, chemical, physiological, and architectural traits at the organ and whole-plant levels (Table S2). Moreover, while tropical islands are over-represented among the studies, both temperate and tropical islands demonstrate mixed support (Table 1). The single Subantarctic Island examined detected more acquisitive traits in invasive than native plants (Mathakutha et al., 2019), potentially highlighting the vulnerability of island plants adapted to extreme climates under invasion facilitated by climate change.

Given the lack of consensus for whether invasive plants on islands have more acquisitive resource use strategies than native plants, it is unlikely that invasive plants are generally displacing natives by outcompeting them. Thus, the role of competition in island invasions remains unclear, particularly in light of simultaneous threats that island plants face, with limited evidence to support the weak island competitor prediction. Clearly, additional research is needed to offer a more nuanced view of invasion effects on island plants, and to more directly test island plant growth and resource use in order to characterize the functional strategies and competitive abilities of island plants.

2.3 | Limitations of functional traits

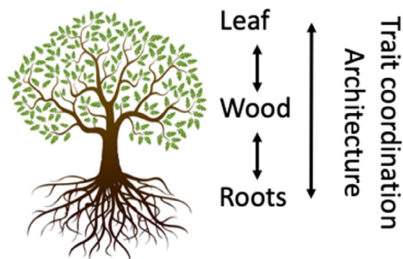
In contrast to the widespread use of functional trait approaches, there are few direct tests of island plant competition quantified as neighbour effects on plant performance, with the notable exception of removal studies illustrating the catastrophic effect of invasive grasses on native seedling recruitment in Hawaii (D'Antonio et al., 2017). A few studies combining functional traits with demographic vital rates provide some insights and have revealed that greater survival and growth of invasive than native island plants can occur even when species have similar leaf and wood economics traits (Funk, 2008; González-Rodríguez et al., 2010; Iida et al., 2019), although these studies did not consider neighbour effects, and so it is unclear whether these differences translate into competition. Conversely, more acquisitive functional traits in invasive than native island species does not necessarily correspond to greater demographic performance of invasives (Schumacher et al., 2008). As these examples illustrate, functional

(a) Approaches to Examine Island Plant Competition

1. Experiments – field, greenhouse, lab



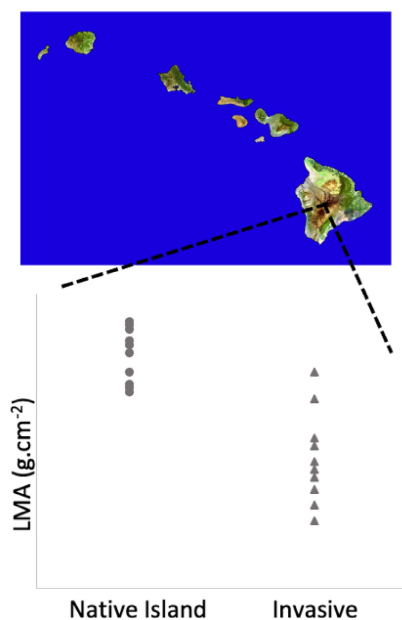
3. Functional Trait Analyses



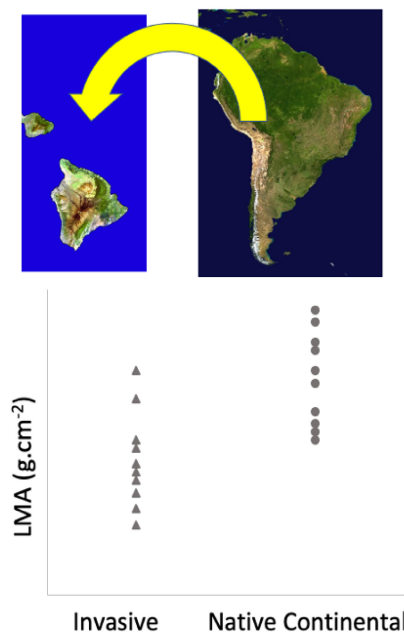
2. Demographic Models

(b) Changing the Species Comparison

1) The Common Approach



2) The Problem



3) The Solution



FIGURE 2 Competition is ideally tested (a) using experimental paired or removal approaches to assess neighbour effects on plant performance (survival, growth, reproduction), or as neighbour effects on demographic vital rates under field conditions, and increasingly, competition is inferred from functional trait analyses which offer considerable time and labour savings. For example, high leaf mass per area is a commonly sampled trait due to its role in leaf carbon economics (Wright et al., 2004) and because it correlates strongly with multivariate axes of plant functional strategies (Díaz et al., 2016). The weak island competitor prediction is commonly tested within-island through trait comparisons of native versus invasive species (b1). It is predicted that native island plants have higher LMA values than invasive continental plants, and moreover, that island plant functional diversity is lower than that of continental plants, depicted by reduced LMA variability among native species means. However, invasive species on islands are not a random subset of continental species and so present a biased representation of continental trait values. Invasive species tend to be more acquisitive than native species in general (Ordóñez et al., 2010), and so the common approach confounds invasion with origin (b2). The solution (b3) is to compare traits of native island vs. native continental species, thereby providing the most robust test of whether functional strategies have evolved to be different on islands vs. continents. Common garden and experimental seedling photos taken in Hawaii.

traits can be poor predictors of plant performance (Bauman et al., 2022; Paine et al., 2015), emphasizing the importance of careful trait selection with particular focus on the specific resource limitation most likely to be driving competition at a particular site (Laughlin et al., 2020; Rüger et al., 2018). Considering the lack of

island studies characterizing trait-demography relationships or quantifying competition via performance effects, we lack basic information about island plant resource use strategies, which limits our understanding of how competition influences species dynamics.

	Archipelago/ island	Plant form	NAT	INV	ITV	Support prediction
<i>Subantarctic</i>						
Mathakutha et al. (2019)	Prince Edward	VAR	13	7	No	Yes/mixed
<i>Temperate</i>						
Marx et al. (2016)	San Juan	VAR	265	150	No	No/mixed
Shouman et al. (2020)	New Zealand	W	8	2	No	Yes
McAlpine et al. (2008)	New Zealand	W	4	1	Yes	No
Heberling and Mason (2018)	New Zealand	W	16	3	Yes	No
<i>Subtropics/tropics</i>						
Baruch and Goldstein (1999)	Hawaii	VAR	34	30	No	Yes
Funk (2008)	Hawaii	VAR	5	5	Yes	No
Funk and Vitousek (2007)	Hawaii	VAR	19	19	No	Yes/mixed
Funk and Throop (2010)	Hawaii	VAR	19	19	No	Yes
Creese et al. (2011)	Hawaii	F	237	36	No	No
Durand and Goldstein (2001)	Hawaii	F	4	1	Yes	Yes/mixed
Kühn et al. (2021)	Canary	H	5	6	Yes	No
González-Rodríguez et al. (2010)	Canary	G	3	1	Yes	No
Cordell et al. (2002)	Hawaii	W	3	2	No	No
Peñuelas et al. (2010)	Hawaii	W	41	47	No	Yes
Stratton and Goldstein (2001)	Hawaii	W	6	1	No	Yes/mixed
Westerband, Knight, et al. (2021)	Hawaii	W	60	31	Yes	Yes/mixed
Craven et al. (2021)	Hawaii	W	42	22	No	No
Iida et al. (2019)	Ogasawara	W	20	2	No	No
Schumacher et al. (2008)	Seychelles	W	7	6	No	Yes

Note: Plant forms include woody (W, trees, shrubs), graminoids (G), herbs (H), ferns (F), various (VAR, including multiple groups in community surveys). Whether the overall trait comparisons support the prediction that invasive species have more acquisitive resource use strategies is reported. In studies reporting mixed support among traits, the most common pattern is reported in addition to “mixed” (yes/mixed, no/mixed). Full results for individual traits are reported in Table S2.

3 | NEW DIRECTIONS IN ISLAND PLANT FUNCTIONAL SYNDROMES

New insights into island plant functional strategies and predicted syndromes differentiating island from continental plants will emerge through the application of evolutionary ecology perspectives and a change in biogeographical approach. Considerable progress has been made using macroecological perspectives, but because species interactions occur at the local scale, new approaches are needed to bridge processes at the local scale (e.g. microevolutionary processes, genetic variation, phenotypic plasticity, ecophysiology, genomics and transcriptomics) with those that operate at the regional and global scales (e.g. propagule pressure, climate change, habitat alterations, historical biases associated with colonialism) (Swenson et al., 2020). Further integration of additional global threats common to islands

TABLE 1 Summary of studies comparing functional traits of native and invasive plants on islands. For each study, the reference, archipelago or island examined, plant forms and number of native (NAT) and invasive (INV) species for which traits were sampled, whether intraspecific trait variation was reported (ITV) are detailed

will reveal whether competition emerges as the primary mechanism driving native plant declines on islands, or reveal the degree to which competition is exacerbated by other factors. Consideration of these complexities should guide future research directions to provide a mechanistic understanding of island plant functional syndromes needed for the conservation of island biodiversity.

3.1 | Insights from evolutionary ecology

Island plant syndromes are predicted to arise through convergent evolution across islands. However, there is surprisingly little research investigating the evolutionary ecology of island plant resource use and competition. Evolution hinges on genetic variation in traits, yet studies quantifying intraspecific variation in island plant traits relevant to



resource use and competition are not common (Table 1). Non-heritable trait variation is also relevant and generally lacking. Incorporation of phenotypic plasticity is particularly warranted given its importance in plant invasion success (Davidson et al., 2011; Funk, 2008; Richards et al., 2006) and competition (Burns & Strauss, 2012). Intraspecific variation as plants develop through ontogeny may also provide new insights as shifts in resource use strategies during the seedling to sapling to adult transitions can vary among species (Fortunel et al., 2020), and how these developmental trajectories influence growth and competition outcomes between native and invasive species is underexplored (Chang-Yang et al., 2021), particularly on islands. Moreover, although weak competition is predicted to have evolved in response to supposedly generic island features, such as low species richness, mild climatic seasonality, and low disturbance frequencies, the magnitude of selection pressure for competitive ability has not been examined in island plants. Considering that islands harbour considerable heterogeneity in climate, elevation, size, age and substrate (Weigelt et al., 2013), it remains unclear whether features are similar enough across islands to have selected for convergent island plant syndromes (Sauer, 1969). Filling these knowledge gaps would provide a more rigorous assessment of whether convergent evolution for weak competition has occurred in island plants.

An evolutionary ecology framework can also help select the appropriate comparison to test island plant syndromes. The weak island competitor prediction arose from observations of invasive plants on islands (Denslow, 2003; Simberloff, 1995; Wallace, 1881). As a result, most of the studies investigating this component of island plant syndromes have focused on native versus invasive comparisons on islands. However, island plant syndromes are expected to include phenotypes distinct from continental plants broadly (Burns, 2019), and because invasive species do not represent a random subset of continental plants (Pyšek et al., 2017; van Kleunen et al., 2010), they are not the most appropriate test of island plant syndromes. Another complication with using invasive species naturalized on islands as a comparison is that these are no longer continental plants. Island populations of invasive continental species are likely to include novel evolutionary changes due to genetic drift during introduction and subsequent adaptation to novel abiotic and biotic conditions in the island habitat (Colautti et al., 2017; Felker-Quinn et al., 2013; Mooney & Cleland, 2001). A better test of island plant syndromes is to compare native island species sampled on islands to related native continental species growing in continental habitats (Figure 2b). These comparisons are complicated by environmental differences between island and continental conditions under which plants would be sampled, and yet, that is the very crux of island plant syndromes—that traits have evolved convergently on islands due to their distinct environments compared to continents.

3.2 | Scaling from island species to community dynamics and assembly

The predicted evolution of island functional syndromes and their potential role in island invasibility offer compelling opportunities to

investigate community assembly and dynamics. Modern coexistence theory highlights that both niche and fitness differences play a role in shaping local communities: niche differences contribute to stable coexistence via density-dependent mechanisms, while fitness differences hamper coexistence through the dominance of superior competitors (Chesson, 2000). This framework predicts that species will stably coexist if niche differences are stronger than fitness differences. Importantly, it formalizes the need to understand the relative contribution of both dimensions in natural systems to determine the local dynamics of species. In addition, species interactions occur at local scales, are strongly context-dependent (e.g. soil fertility, disturbance intensity, herbivory pressure), and so are best informed by trait, performance and niche comparisons made at the local scale (Carboni et al., 2013; Diez et al., 2008; Procheş et al., 2008). Competition and trait differences quantified at the local scale can then be compared across environmental gradients to more fully capture niche dimensionality and competition hierarchies (Kunstler et al., 2012), thereby providing a more nuanced understanding of community assembly and competition of island plants. Reversals in relative fitness hierarchies along environmental gradients can have strong consequences for species coexistence and community dynamics (de Bello et al., 2013; Westerbands, Knight, et al., 2021). A better understanding of the spatiotemporal variation of niche and fitness differences, particularly within islands with steep environmental gradients, is key to predict the resulting population growth rates and, ultimately, community dynamics. This emphasizes the importance of studying individual performance (growth, survival and reproduction) in a diversity of contexts to disentangle the interplay between niche overlap and competitive hierarchies. Within islands, this can be achieved by quantifying resource use strategies and performance at the individual scale across environmental gradients, combined with common garden and reciprocal transplant experiments to disentangle genetic and environmental sources of intraspecific variation (Westerbands, Funk, et al., 2021). Such studies will further allow for niche breadth to be estimated in order to assess overlap and competition among species (Chesson, 2000), and will also provide the means for characterizing the resource use functional diversity within island plant communities, which remains a poorly described dimension of island biodiversity.

3.3 | Island plant trait space

The interplay between island resource availability and species resource use strategies form the basis of ideas about island invasions and the weak island competitor prediction (Denslow, 2003). To fully assess empty niche and weak island competitor hypotheses of island invasions, resource use strategies should be examined for multiple dimensionalities of plant function, across heterogeneous environments and with the goal of characterizing entire floras. To date, most island studies have sampled relatively few species (e.g. fewer than 20 each of native and invasive; Table 1) and so cannot characterize the full functional diversity of island plant resource use.

Nonetheless, among those quantifying functional diversity, trait space has been observed to be greater for natives than invasives in the Hawaiian Islands (Craven et al., 2021), Canary Islands (Kühn et al., 2021) and Prince Edward Islands (Mathakutha et al., 2019), indicating rather broad functional diversity for island plants. Yet, without greater trait coverage for entire floras, it is difficult to determine whether functional diversity of native island plants leaves some trait space vacant as predicted by empty niche invasion hypotheses.

Trait-based studies generally leverage a limited number of plant traits either because they focus on a single mechanism or because of limited time and resources to quantify more traits. As a result, most studies only use a handful of easy-to-measure traits, namely specific leaf area, wood density, seed mass, and maximum height, that together define two main functional dimensions in plants (Díaz et al., 2016). However, as these traits are typically integrative of many functions in plants (Chave et al., 2009; Reich, 2014; Wright et al., 2004), it is unlikely that they can fully capture how plants acquire and use different resources (e.g. light, water, nutrients), in different above- and below-ground organs (e.g. leaf, stem, root, seed). Recent work has shown that traits that are more directly linked to the use of specific resources do not well align with the classically measured traits (Fortunel et al., 2012, 2014; Maréchaux et al., 2020; Vleminckx et al., 2021). This calls for expanding the target trait list to better characterize the multiple dimensions of plant form and functions, in particular selecting the traits that are predicted to be mechanistically linked to specific processes. A careful characterization of the functional space of island species relative to continental species along meaningful axes linked to resource use offer a promising way forward to quantify trait differences that can play a role in competitive interactions, in terms of both niche and fitness differences (Kraft et al., 2014), and thus shape community dynamics on islands.

3.4 | Global threats alter island competition dynamics

Identifying the primary drivers of island plant diversity losses is urgent to inform mitigation strategies to conserve these biodiversity hotspots, and invasive species have emerged as key threats (Caujapé-Castells et al., 2010). Without a doubt, invasive plants have naturalized on islands at high rates (Pyšek et al., 2017), coinciding with native plant declines. However, this pattern alone does not confirm competition as the main underlying mechanism because many other threats correlate with invasive species abundances. Native birds and insects have also suffered disproportionate extinctions on islands (Fernández-Palacios et al., 2021), resulting in lost pollination and seed dispersal services to island plants (Aslan et al., 2013; Carpenter et al., 2020; Kaiser-Bunbury et al., 2010). Invasive plants can also directly interfere with pollination and seed dispersal if their proximity reduces visitation rates to native species (Morales & Traveset, 2009; Vizentin-Bugoni et al., 2019). Antagonistic interactions are also altered for island plants, with

the introduction of novel herbivores and pathogens causing high rates of damage and mortality (Donlan et al., 2002; Mortenson et al., 2016), and invasive plants can act as reservoirs of novel pathogens contributing to native plant disease rates (Stewart et al., 2018). Invasive plants on islands are also associated with elevated abiotic threats to native plants. Fire-promoting, invasive grasses have altered fire regimes on islands, directly and indirectly reducing native plant abundances via cascading negative effects on native plant regeneration (D'Antonio et al., 2011; Newman et al., 2018). Some island invaders alter ecosystem processes such as ecohydraulics, nutrient and light availability (Jager et al., 2009; Takahashi et al., 2011; Zhang et al., 2020). As ecosystem engineers, invasives may thus interfere with native plant performance via non-competitive dynamics of resource use.

Anthropogenic modification of the environment may further contribute to native plant declines, often enhancing invasive plant performance via eutrophication, habitat alteration or loss, and intentional introduction and spreading of invasives (Caujapé-Castells et al., 2010). Some competition theories of island invasion explicitly incorporate anthropogenic factors (Figure 1), although these have not been examined in combination with direct measures of competition or functional traits of island plants to date. Considering the decline in available habitat for native island plants as a consequence of human modification of landscapes, island species are likely to be even more vulnerable to other threats, including invasive competition, but also climate change, disturbance and natural enemies, than they would have been historically. Habitat losses are particularly detrimental to species with limited distributions and small population sizes, including those classified as micro-endemics, which are common in island floras (Birkeland et al., 2017; Sakai et al., 2002).

The synchrony and common non-additivities among multiple global threats to island plants (Barton et al., 2021; Barton & Shiels, 2020; Macinnis-Ng et al., 2021) challenge identification of the primary drivers of biodiversity losses. Predicting that invasive plants displace native plants by out-competing them could be an important mechanism, but it is also likely that simultaneous losses in pollination, seed dispersal, reduced population sizes, and climate change contribute directly to the competition dynamics. Disentangling these various factors should be a research priority for a more nuanced understanding of island plants that moves beyond the simplistic prediction that island plants are declining because they are weak competitors.

4 | ACHIEVING A GLOBAL SYNTHESIS OF ISLAND PLANTS

With limited time and resources to conduct competition experiments of native versus continental plants, a global synthesis of island plant resource use strategies continues to elude us as a consequence of data and inclusion gaps. While a few archipelagos are very well studied, specifically Hawaii, Canary Islands, New Zealand and the Galapagos, even those have only a few resource-use functional traits sampled for representative numbers of species (Table 1).

Sampling resource use traits, including traits directly quantifying plant physiology and anatomy, for more species on more islands is a major research need before we can robustly assess whether the weak island competitor syndrome has evolved. Complementary approaches including genomics and transcriptomics would shed light on underlying expression of island plant functional strategies. To meet these data needs will be challenging and will benefit from global scientific collaboration and in particular, participation of local island scientists, including Indigenous peoples, in order to avoid “parachute science” and biases and to foster equity and inclusion in the biological sciences (Asase et al., 2022; Haelewaters et al., 2021; Trisos et al., 2021). From first contact to colonial times and contemporary globalization, waves of human settlements and socioeconomic transformations over centuries have led to extensive habitat loss, ecosystem disruption, and biodiversity losses on islands (Russell & Kueffer, 2019; Wood et al., 2017), and it is possible that colonial biases from European and American cultures have contributed to misperceptions of island species, such as their depiction as “fragile” or “weak” (Crosby, 2004; Nunn, 2004). Expanding our understanding of island plant functional strategies will thus best be achieved through global collaborative networks that leverage resources and expertise from experienced trait-based scientists with local and Indigenous scientists with unique ecological knowledge of island plants (Aitken et al., 2021; Winter et al., 2018). Previous network science projects provide examples for developing equitable opportunities and training, resulting in repeated protocols used across diverse sites and led by local scientists (Bradford et al., 2021; Davies et al., 2021; Malhi et al., 2021). Establishing an island plant functional trait network to collect new resource use trait data would be a promising step towards a global understanding of island plant functional diversity.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Kasey E. Barton  <https://orcid.org/0000-0002-4549-4150>

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BIOSKETCH

Kasey E. Barton is a professor in the School of Life Sciences at the University of Hawaii at Mānoa. Her research examines the functional ecology of island plants and ontogenetic variation in plant form and function.

Claire Fortunel is a Research Scientist at IRD (Institut de Recherche pour le Développement) based at AMAP lab (botanique et Modélisation de l'Architecture des Plantes et des végétations) in Montpellier, France. She studies the ecological and evolutionary mechanisms shaping community structure and dynamics, and the consequences for ecosystem processes, in particular in plant systems (<https://cfortunel.wordpress.com>).

Author contributions: KEB conceived the project and developed the framework with contributions from CF. Both authors wrote and edited the manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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