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Towards a holistic perspective on the development of island syndrome by examining its occurrence patterns in insular plants

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Abstract

The acquisition of evidence pertaining to island syndrome often relies on opportunistic observations, yet prior researchers have gradually compiled a body of examples that collectively shed light on its occurrence patterns and dynamics. Our comprehensive literature review revealed that island syndrome dominantly occurs in angiosperms on oceanic islands, with a notable abundance of taxa exhibiting high endemism and possessing functional traits associated with facultative and generalized biotic interactions. While acknowledging the influence of unequal research interest and sampling efforts on the observed patterns, deviations from prevailing sampling biases evident in global plant databases and herbarium collections lend credence to genuine differences in the occurrence of island syndrome. The disproportionate incidence of island syndrome, delineated by taxonomic groups, traits, and specific islands, can be ascribed to the distinct biogeography of oceanic islands and the presence of idiosyncratic ecological and evolutionary processes that contribute to its development. Within an evolutionary framework, our overarching hypothesis posits island syndrome as a transformative trajectory away from the diverse strategies adopted by mainland plants to the alternative strategies exhibited on islands due to their isolation and ecological simplicity. This perspective fosters a more holistic perspective, encompassing the myriad and graded responses of plants to evolutionary pressures encountered on islands. Rather than dismissing the biased occurrence patterns in the examples of island syndrome, we contend that their underlying insights hold substantial value in formulating a general, mechanistic model that enhances our understanding of the development of island syndrome and its evolutionary implications.

Highlights

- While insular plants often exhibit a suite of evolutionary transformations of morphological and physiological traits collectively known as the island syndrome, occurrence of its component traits is highly variable among taxa and islands.

- Flowering plants, particularly those with a high proportion of endemic species, such as Asteraceae, Campanulaceae, and Boraginaceae, were overrepresented in observations of the island syndrome, while gymnosperms, ferns, lycophytes, and bryophytes were rarely reported to exhibit patterns consistent with the island syndrome.

- The island syndrome appears positively associated with functional traits of sporophyte generations associated with biotic interactions, including loss of floral attractiveness, transitions from specialist to generalist pollination, and higher self-compatibility along with modifications in the size, color, and structure of stems, flowers, fruits, and seeds.

- Geographically, the examples were weighted toward oceanic islands and archipelagos (e.g., the Canary Islands and the Hawaiian Islands), followed by continental fragments such as New Zealand, with few observations from continental shelf islands.

- The overall occurrence patterns suggested that several underlying factors beyond sampling bias alone contribute to the disproportionate incidence of island syndrome, including island isolation, species richness, sensitivity to island dispersal filters, and sporophyte dominance with phenotypic modification potential.

- Island syndrome can be understood as a transition from mainland strategies to the alternative strategies that arise in response to isolation and ecological simplicity. This perspective promotes a more holistic understanding of the diverse and graded responses exhibited by plants to the evolutionary pressures encountered on islands.

Introduction

Insular plants often exhibit anomalous phenotypic traits compared to their ancestral mainland counterparts, including the loss of floral attractiveness in otherwise showy flowering plants (Carlquist 1974, Inoue and Amano 1986, Abe 2006), promiscuous pollination in plants formerly dependent on a single pollinator (Barrett 1996), development of secondary woodiness in herbaceous plants (Carlquist 1974, Lens et al. 2013), loss of defensive structures and chemicals in ancestrally herbivore-resistant plants (Bryant et al. 1989, Bowen and Vuren 1997, Vourc'h et al. 2001, Baeckens and Damme 2020), loss of refractory bark in fire-resistant plants, loss of fire-adapted cones/fruits in serotinous plants (Briand et al. 2015, Baeckens and Damme 2020), selfing in formerly self-incompatible plants (Igic et al. 2008, Grossenbacher et al. 2017), transition to dimorphic sexual expressions such as dioecy, androdioecy, and gynodioecy (Carlquist 1966d, 1974), transition to anemophily (Carlquist 1974), and loss of dispersibility in descendants of long-distance colonizing plants (Carlquist 1966a,b,c, Cody and Overton 1996, Kudoh et al. 2013). In addition, insular plants can exhibit both gigantism and dwarfism in diaspores and growth form (Burns et al. 2012, Burns 2016, Cox and Burns 2017, Biddick et al. 2019). These evolutionary transformations of morphological and physiological traits often repeatedly occur across lineages and island systems, giving rise to the concept of the island syndrome at the individual level (Carlquist 1966a).

This phenomenon is often interpreted as a response to islands' ecological simplicity and their distinct evolutionary pressures, which lead to reductions in traits otherwise adapted for long-distance dispersal, interspecific competition, and herbivory (Whittaker and Fernández-Palacios 2007, Lomolino et al. 2017). Isolated islands tend to have depauperate and disharmonic communities developed by long-distance dispersal. These features of the island syndrome at the assemblage level then cascade down to species and individual levels through ecological and demographic release. Insular plants may also exhibit novel phenotypic changes through phenotypic plasticity, anagenesis, or adaptive radiation when they persist sufficiently long in isolation and under the distinctive selective regimes of islands (Whittaker and Fernández-Palacios 2007, Losos and Ricklefs 2009, Stroud and Losos 2016, Lomolino et al. 2017, Herrmann et al. 2021). The relatively stable climates afforded by many oceanic islands may further facilitate this process by providing more extended periods to maintain or enhance these phenotypic modifications without climatic constraints and disturbances (Whittaker and Fernández-Palacios 2007, Baeckens and Damme 2020).

The diverse array of examples showcasing island syndrome provides a rich source of information to gain fresh insights and comprehend the preconditions and drivers that give rise to this phenomenon.

However, we must acknowledge that most prior studies of island syndrome may have sampling biases due to limited field survey accessibility and researchers' selections of focal taxa, traits, and islands (Lomolino et al. 2006, Lokatis and Jeschke 2018). In particular, there is a strong taxonomic bias in plant studies, with a focus primarily on flowering plants that have conspicuous, colorful, and broadly distributed flowers (Cornwell et al. 2019, Adamo et al. 2021). Unconscious biases are unavoidable, given that research is predominantly conducted by individuals and institutions based in industrialized regions with well-developed research and education infrastructures (Lokatis and Jeschke 2018, Cornwell et al. 2019, Nuñez et al. 2021). Given that sampling biases can alter our understanding of this phenomenon, identifying any potential sources of biases in the evidence of island syndrome is imperative.

Furthermore, oversimplifying the eco-evolutionary dynamics of island syndrome based on a few representative examples and explanations from specific islands or taxa can lead to a distorted understanding of this phenomenon. Ecological simplicity, which is considered a fundamental driver of island syndrome, can be modified by various geographical, geological, and climatic conditions present on different islands (Patiño et al. 2017, Ottaviani et al. 2020, Schrader et al. 2021). Factors such as island isolation, size, and age play important roles in shaping the potential size and complexity of biotas, as well as influencing the relative advantages of different competitive and reproductive strategies (MacArthur and Wilson 1967, Trøjelsgaard et al. 2013, Baeckens and Damme 2020, Schrader et al. 2021, Baker 1955, 1967). Additionally, terrestrial plant lineages exhibit diverse responses to distinct island environments due to their different evolutionary adaptations and functional traits. Several widely accepted concepts such as dispersal syndrome, floral syndromes, Baker's rule, and loss of anti-herbivory traits have been questioned and may not universally apply to all taxa (Pannell et al. 2015, García-Verdugo et al. 2017, Monroy and García-Verdugo 2019, Hetherington-Rauth and Johnson 2020, Moreira et al. 2021, Moreira & Abdala Roberts 2022). Gaining a clear understanding of the variation in the occurrence of island syndrome across islands and taxa, while accounting for sampling bias, is crucial for identifying the specific underlying drivers and conditions responsible for its development.

Here we review the available literature and examine the occurrence patterns of island syndrome in insular plants. With a critical consideration of sampling bias, we ascertain the extent to which the suggested observational patterns genuinely reflect actual occurrence patterns. Moreover, we assess the value of the observed patterns in providing insights into the underlying factors and conditions responsible for the development of island syndrome. The insights derived from our study can serve as a solid foundation for future research endeavors by enabling the development of a holistic theory and mechanistic models, beyond descriptive approaches, to explain the diverse responses of plants to the evolutionary pressures encountered on islands.

Materials & Methods

We conducted a comprehensive literature survey through Web of Science and Google Scholar, using identifiers containing "island syndrome" in combination with "plant" and taxonomic terms, such as "bryophytes", "pteridophytes/non-seed plants", "tracheophytes/vascular plants", and "spermatophytes/seed plants". Between 1888 and 2022, 228 island syndrome-related studies were identified, of which 110 were considered primary research with field observations (Table S1). We carefully extracted information pertaining to study taxa, islands, and traits from these primary papers and compiled them to illustrate the occurrence patterns of island syndrome in insular plants. To determine whether biased-occurrence patterns arise primarily from sampling biases, we first compared the observational biases in island syndrome studies with those commonly encountered in herbarium collections and global plant diversity databases, such as the Global Biodiversity Information Facility, TRY, and GenBank. After discounting these sampling biases, we proceeded to investigate potential sources of the biased occurrence pattern, considering both island characteristics and plant traits.

Results

Taxa

Island syndrome dominantly occurred in angiosperms (92.3%), followed by gymnosperms (6.4%), bryophytes (0.9%), and ferns (0.4%). No observations occurred in lycophytes (Fig. 1A and Fig. 2). Within angiosperms, Asteraceae was particularly overrepresented (20% of angiosperms), while only a few observations were made from 109 other families, including Campanulaceae (5%), Boraginaceae (4%), Arecaceae (4%), and Rutaceae (4%). Gymnosperm observations were mainly from two families: Pinaceae (73% of gymnosperms) and Cupressaceae. Bryophytes showed only one instance of island syndrome in a single study testing Baker's rule which included four families (Lembophyllaceae, Leptodontaceae, Leucodontaceae, and Orthotrichaceae). Ferns showed a similarly low proportion of island syndrome observations (0.4%) with three families showing changes in spore size (Blechnaceae, Dicksoniaceae, and Schizaeaceae), and one family exhibiting loss of protective mutualism (Dennstaedtiaceae), all on the Hawaiian Islands.
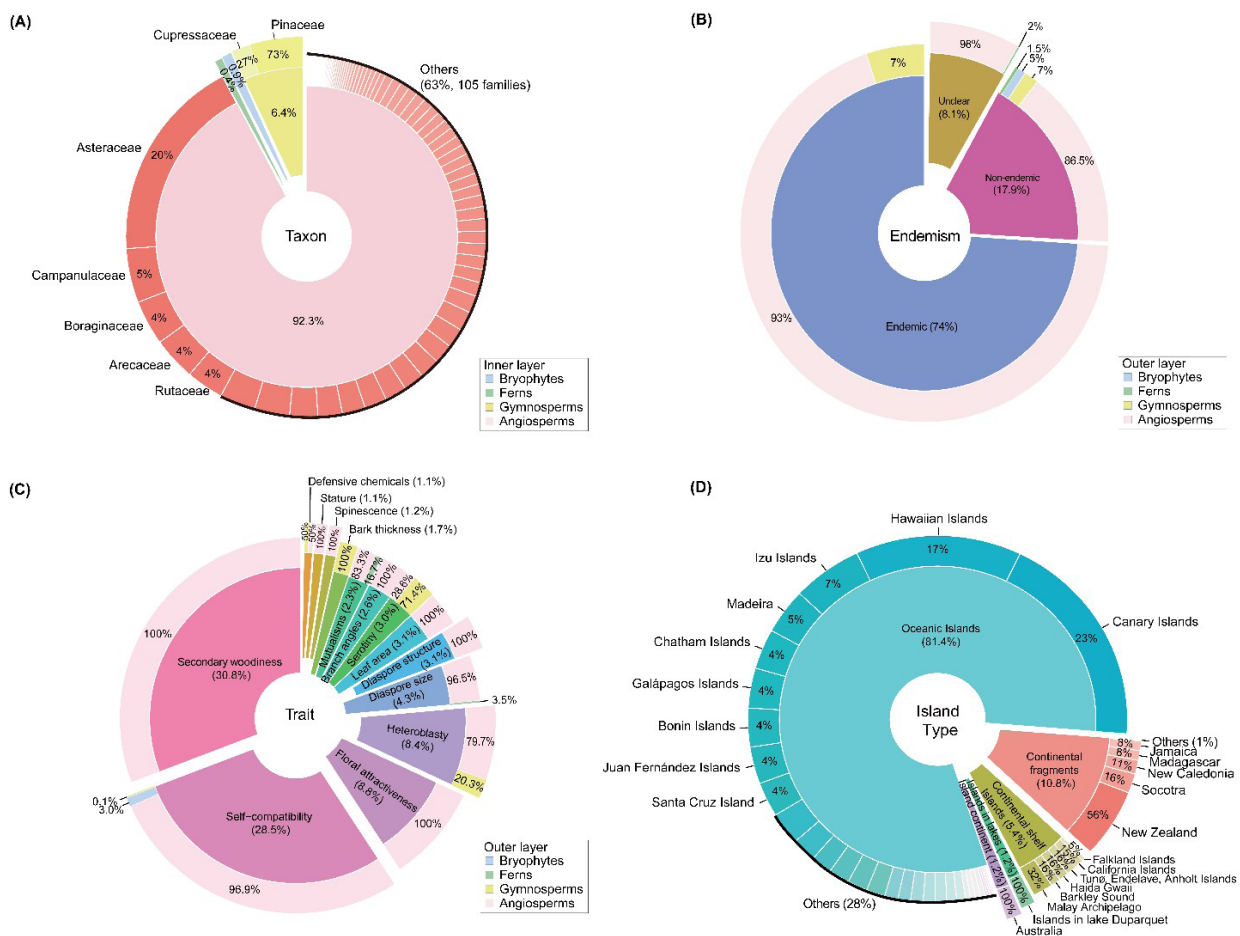

Figure 1. Observations of island syndromes in insular plants. (A) by plant group, (B) by endemism, (C) by trait, and (D) by island type. The percentage of the outer layer corresponds to the total of its adjacent inner layer. The proportion for each metric was calculated by weighting the values inversely to the number of taxa reported in each study to reduce the impact of studies reporting a relatively large number of taxa. Pie charts were generated using the r package *webr* v.0.1.5 (Moon 2020).
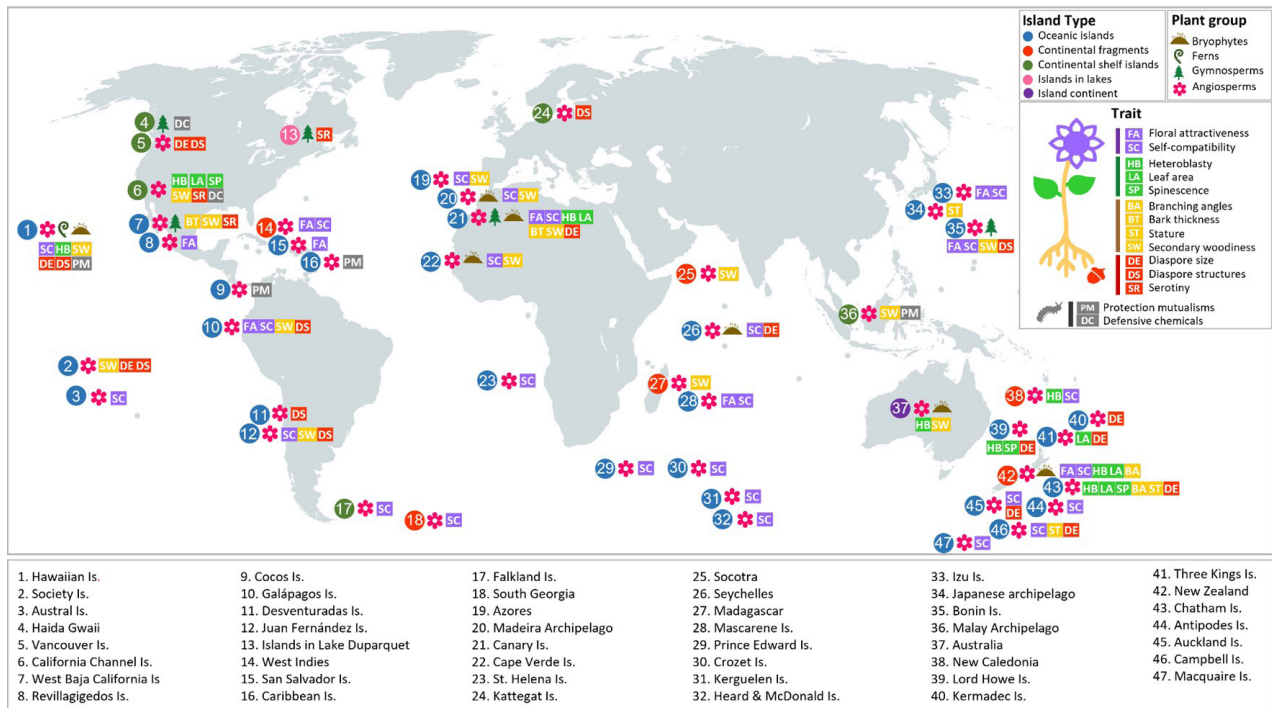
Figure 2. Global distribution of observations of plant island syndrome, based on compiled island syndrome research listed in Table S1. The map background was obtained from MapChart (https://www.mapchart.net/world-advanced.html). The classification of island origin is followed by Zizka et al. (2022).

On average, 74% of the observed species were considered endemic to their corresponding islands or archipelagoes, with angiosperms accounting for 93%, gymnosperms for 7%, and none for non-flowering plants (Fig. 1B). The proportion of endemic species in the examples of island syndrome was much higher than that of background endemism in hotspots (~20-30%) (Myers et al. 2000, Mace and Baillie 2007).

Traits

The most frequently observed traits in the examples of island syndrome were secondary woodiness (30.8%), followed by increased self-compatibility (28.5%), and loss of floral attractiveness (8.8%) (Fig. 1C). Heteroblasty, characterized by abrupt changes in morphology during ontogenetic development, was observed in 8.4% of cases, while modifications in diaspore size and structure associated with dispersal syndrome accounted for 4.3% and 3.1%, respectively. Additional traits observed included changes in leaf area (3.1%), serotiny (3.0%), branching angles (2.6%), spinescence (1.2%), and stature (1.1%), and loss of protective mutualisms (2.3%), decreased bark thickness (1.7%), and loss of defensive chemicals (1.1%). Other than self-compatibility, diaspore size, and heteroblasty, most traits were related to angiosperm-focused macroscopic characters.

Islands

Geographically, observations of the island syndrome mainly occurred on oceanic islands (81.4%), including several paradigmatic archipelagos such as the Canary

Islands (23% of oceanic islands) and the Hawaiian Islands (17%) (Fig. 1D). Continental fragments were the next most frequently observed (10.8%), of which New Zealand (56%), Socotra (16%), and New Caledonia (11%) were most prevalent. About 5.4% of observations occurred on continental shelf islands once connected to mainlands such as Malay Archipelago (32%). Islands in Lake Duparquet in Quebec were also investigated to assess changes in serotiny of gymnosperms (1.2%). Australia, an island continent, also had several observations of island syndrome (1.2%). Although not included in the literature survey, some observations were reported from theoretical habitat islands, such as "sky islands", in which the surrounding habitat matrix functions as a filter for dispersal like an ocean for conventional islands, and included Asteraceae, Campanulaceae, and Solanaceae in the Andes Mountains (Carlquist 1974).

Discussion

The taxonomic biases seen in island syndrome, characterized by an over-representation of angiosperms, are also observed more generally in herbarium collections and global plant databases (Kreft and Jetz 2010, Sundue et al. 2014, Schuettpelz et al. 2016, Cornwell et al. 2019). These biases suggest that its overall occurrence pattern has been influenced by the disparity in species richness and diversification rates across plant groups. To date, angiosperms represent only one of ten major land plant phyla, but account for nearly 90% of all terrestrial plant species (Niklas 2016, Hernández-Hernández and Wiens 2020).

Net diversification rate, which reflects the rate of new species formation and extinction, is substantially higher in this comparatively young lineage, leading to the substantial accumulation of phenotypic modifications (Hernández-Hernández and Wiens 2020). Accordingly, morphological diversity and disparity have greatly increased within angiosperms relative to other lineages, which may subsequently increase the number of observations of island syndrome. Certain groups within the angiosperm lineage, such as Asteraceae, have much higher species richness and speciation rates, which are commensurate with their representation in island syndrome studies.

The observed trait biases in the island syndrome observations were likely linked to the aforementioned taxonomic biases, as most cases studied were based on angiosperms. In addition, common sampling biases that prioritize conspicuous traits, including floral structure and secondary woodiness, appear to contribute to the underrepresentation of certain taxonomic groups and their traits. In particular, non-flowering plants lacked representation due to the inherent challenges in detecting and visualizing their microscopic diagnostic characters. For example, vascular but seedless ferns and lycophytes possess distinctive but simple microscopic traits, such as sporangia, indusia, sori, and strobili, which limit both their range of morphological variation and the opportunities for their observation. Similarly, bryophytes typically have simple structures, such as thalli, capsules, and gemmae that are too small to be effectively observed during field surveys. This argument finds support in the underrepresentation of microscopic traits even in angiosperm examples, as sub-cellular, anatomical, and physiological traits including stomata and wood vessel characters have not been observed in previous island syndrome studies, despite their frequent documentation in broader plant trait databases. Furthermore, the frequency of island syndrome observations may also be influenced by a selection bias towards specific traits of interest to researchers. For example, self-compatibility has attracted interest due to the desire to assess Baker's rule.

Observations of island syndrome have primarily focused on oceanic islands, with notable examples found in paradigmatic archipelagos such as the Canary Islands and the Hawaiian Islands. Studies of island syndrome have often been driven by specific emblematic cases, such as the secondary woodiness and seed gigantism of *Argyroxiphium* (Asteraceae) on the Hawaiian Islands. Similarly, the presence of model organisms including *Echium* (Boraginaceae) on the Canary Islands and *Coprosma* (Rubiaceae) on New Zealand may contribute to the geographical bias in island syndrome research. Such bias toward specific islands may be further exacerbated by factors such as accessibility of field surveys and availability of preexisting information on biotas and island characteristics (Yang et al. 2013). These potential sampling biases in taxa, traits, and islands can result in an incomplete understanding of the occurrence patterns of island syndrome and may limit our ability to generalize findings across plant lineages.

However, the occurrence patterns observed in island syndrome studies exhibited distinct characteristics that cannot be solely attributable to general sampling biases. For instance, several large families other than Asteraceae, including Orchidaceae, Fabaceae, and Rubiaceae, were underrepresented compared to their expected representation in island syndrome studies. Moreover, globally well-sampled families, such as Poaceae, Pinaceae, Solanaceae, and Moraceae, were underrepresented relative to their global species richness. While pteridophytes are generally underrepresented, their case may be interpreted differently considering their typically high abundance on islands. Their high dispersal and gene flow, combined with their low sensitivity to island filters, may limit in-situ speciation and endemicity, thereby reducing the evolutionary pressure that results in island syndrome. Although unequal research interest and sampling efforts undoubtedly contributed to the biased pattern, the extent of these discrepancies nonetheless support that the biases seen in island syndrome examples likely reflect genuine differences in their occurrences. The occurrence of island syndrome can be attributed to the distinct biogeography of specific oceanic islands, as well as the presence of unique ecological and evolutionary processes that contribute to its development.

Isolation has been proposed as a key factor in the emergence of island syndrome (Burns 2019). By interrupting gene flow and generating distinct biotic and abiotic conditions, isolation directly contributes to the main drivers of island syndrome: island impoverishment and disharmony. Distance decay effects predict that more distant islands tend to have more depauperate and disharmonic assemblages due to their remoteness. Isolation itself reduces gene flow between islands and the mainland, which further promotes the formation of insular endemics. Therefore, the geographic bias in which island syndrome has mostly been observed on oceanic islands could be fundamentally explained by the biogeographic variable of isolation. For example, the Canary Islands and Hawaiian Islands, which are hotspots of island syndrome, have sufficient remoteness to intensify in-situ and inter-island speciation, thereby gradually amplifying the disharmonic nature of their biological communities (Barton et al. 2021). In contrast, the lack of observations of island syndrome on continental islands may be attributed to the limited geographic and genetic isolation among their populations (Carlquist 1966a).

Species richness is another important factor to consider when examining the occurrence of island syndrome, as it can help ascertain whether taxa with high species richness are structurally more inclined to generate island syndrome. Given that island syndrome is primarily driven by the disharmonic nature of isolated communities, plant groups with high species richness, along with abundant functional traits and large gene pool size, are expected to have a greater potential to contribute to disharmonic taxonomic and functional communities. Theoretically, the number of possible community compositions on an island, and therefore the likelihood of a disharmonic community, follows a unimodal distribution dependent on differences in species numbers between the island and its source mainland.

This can explain the predominance of angiosperms in island syndrome examples, as their species richness allows for greater disparities in species composition between islands and mainlands. However, the previously mentioned underrepresentation of globally abundant families in island syndrome studies suggests that high species richness is not always a precondition for the incidence of island syndrome nor does it always lead to high representation within the island syndrome. This strengthens the notion that, although species richness is influential, the occurrence patterns of island syndrome cannot solely be attributed to sampling biases that may arise from the differences in species richness across taxa.

Given global differences in species richness among taxa, one additional underlying factor that contributes to the occurrence patterns of island syndrome is the immigration filtering process, which plays a crucial role in shaping biased species richness and composition on islands (Vargas et al. 2014). Numerous studies have demonstrated that the effects of immigration selection vary depending on taxon-specific biological attributes. These attributes include dispersal capabilities, breeding system flexibility, growth rates, tolerance of nutrient disequilibrium, disease resistance, seed or spore dormancy, and sensitivity to species interactions (Carlquist 1966c, Baker 1955, 1967, Jordan 2001, Page 2002, Burns 2005, Whittaker et al. 2008, König et al. 2017). The lack of gymnosperms and pteridophytes in the examples of island syndrome illustrates how the immigration filtering process influences the likelihood of exhibiting island syndrome. Due to the limited absolute numbers of island immigrants among gymnosperms (König et al. 2021), their probability of exhibiting island syndrome is expected to be low. This is supported by the occurrence of island syndrome in gymnosperms almost exclusively on continental islands as this would remove dispersal limitation and instead isolate these populations by vicariance. Conversely, pteridophytes can be less affected by island filters due to their high dispersal ability, reproductive capacity, and independence from biotic interactions. Subsequently, the compositions of pteridophyte populations on islands tend to resemble those on the mainland, which reduce the evolutionary pressures to develop island syndrome.

The overall patterns of trait bias suggest that island syndrome primarily arises from the modification of traits associated with biotic interactions. While some traits, such as diaspore size and structure, may be more closely related to dispersal, the overall pattern can be summarized as a reduction in resource and reproductive competition strategies. This reduction can be understood as a loss of costly traits in depauperate island communities, in which such traits are less advantageous or unnecessary. It also means that island syndrome predominantly manifests in phenotypic characters associated with facultative and generalized biotic interactions in which their character states tend to be more easily lost or gained. For example, branching angles, stature, leaf area, as well as secondary woodiness and heteroblasty, can be altered with only limited genetic modification in a few generations.

Traits such as spinescence and defensive chemicals that evolved in response to plant-animal interactions are generally not species-specific, and their loss would have minimal impact on fitness in the absence of herbivores on islands. Similarly, loss of floral attractiveness, transitions from specialist to generalist pollination, and higher self-compatibility all reflect adaptations to the more depauperate pollinator communities typically found on islands. In contrast, loss of traits associated with obligate and specialized interactions can easily be precluded because species or individuals undergoing such changes are unlikely to establish successfully on islands. Theoretically, one could expect to find modifications in more cryptic traits related to simpler ecological interactions on islands, such as weakened immunity to parasites and diseases, as well as loss of characteristics associated with mutualisms, but this should be verified in future studies.

In this context, the dominance of sporophyte generations emerges as a key factor in elucidating the taxonomic and trait bias patterns observed in island syndrome. As natural selection primarily operates on persistent sporophyte generations, plants with more sporophyte-dominant life cycles should have more opportunities for evolutionary innovations. Vascular plants particularly rely on their homoihydric, long-lived, and large sporophytes to persist through drought conditions and compete for resources, which increases their susceptibility to phenotypic modification during island evolution. Alternatively, non-vascular plants like bryophytes have simple bodies and ontogenies, which maximize the poikilohydric properties of their gametophyte generations (Proctor 2000, Proctor et al. 2007). This adaptation liberates them from the unique selective pressures exerted by islands while limiting the availability of additional characters for conspicuous modification. The relatively short life span of gametophytes further reduces the likelihood of the modified phenotype persisting over time. Therefore, this hypothesis provides an explanation for the predominance of traits associated with sporophyte-dominant seed plants in island syndrome, including seeds, flowers, wood, and bark. Acquisition of heteroblasty is also more feasible within sporophyte generations characterized by extended developmental periods and multiple ontogenetic stages (Zotz et al. 2011).

Furthermore, plants with large and long-lived sporophyte generations, coupled with iteroparous reproduction (multiple reproductions over the course of a lifetime), can maximize sub-individual plasticity. Modular organization in plants allows for variation in size, shape, or texture through organ-level phenotypic modification (Endress 2000, Sobral and Sampedro 2022). This sub-individual variation enhances overall phenotypic plasticity and can be inherited through epigenetic modification (Herrera 2017, Herrera et al. 2022). Subsequently, angiosperms are likely to exhibit the greatest potential for phenotypic modification during island evolution due to their possession of multiple modifiable structures such as complex flowers, seeds, and secondary structures.

Conversely, bryophytes, ferns, and lycophytes, with their independent gametophyte generations, have more limited opportunities for phenotypic change and lower genetic potential as certain alleles may be easily lost in their haploid generations (Otto and Gerstein 2008). Future research should explore inherent differences in phenotypic plasticity among taxonomic groups to identify those more likely to exhibit island syndrome.

Conclusion

Despite the inherent opportunistic nature of collecting evidence of island syndrome, previous researchers have gradually accumulated sufficient examples to assess its overall occurrence patterns and provide insights into its dynamics and drivers. Considering the possible causes for the biased occurrence patterns of island syndrome discussed thus far, it remains challenging to conclusively attribute the dominance of specific taxonomic groups, traits, and islands solely to sampling biases. However, instead of dismissing the biased occurrence patterns, their underlying insights can be valuable in formulating a general, mechanistic model that aids in comprehending the incidence of island syndrome. As previously discussed, the prevalence of certain groups, traits, and islands in examples of island syndrome, primarily among angiosperms on oceanic islands exhibiting functional traits associated with facultative biotic interaction, can be comprehended within an evolutionary framework. Representative plant groups may have evolved competitive strategies on the mainland that are more reliant on facultative biotic interactions, leading to the emergence of a diverse array of conspicuous morphological traits, particularly in persistent sporophyte generations. The selective pressures present in depauperate and disharmonic communities on oceanic islands, with their reduced ecological complexity, are anticipated to exert a more pronounced influence on these groups. Conversely, underrepresented plant groups may have evolved strategies on the mainland that prioritize evasion of biotic interactions and instead rely heavily on dispersibility and abiotic adaptations, given their independent poikilohydric gametophyte generations. This overarching hypothesis can contribute to a more holistic understanding of the diverse and graded responses of plants to the evolutionary pressures exerted by specific islands. These studies should investigate the frequency of its occurrence in relation to lineage ages, habitat types, and geographic locations, while considering various innate biological characteristics of islands and species. Collecting detailed temporal and spatial information on each instance of island syndrome will also be crucial for gaining a deeper understanding of the ecological and evolutionary context in which it develops. Moreover, such information will facilitate investigations into graded responses and intermediate phenotypes on the evolutionary pathway to island syndrome.

Author Contributions

NH and MVL co-led the study design. NH and SY performed the literature survey. NH wrote the manuscript, followed by critical review from all authors.

Data Accessibility

The examples of island syndrome compiled for the article is shown in Supplementary Table S1.

Supplemental Material

Table S1. List of the observation of island syndrome

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