Biol Invasions (2024) 26:2237–2249
https://doi.org/10.1007/s10530-024-03307-4

ORIGINAL PAPER

Habitat affiliation of non-native plant species across their introduced ranges on Caribbean islands

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Received: 18 January 2024 / Accepted: 26 March 2024 / Published online: 12 April 2024

Abstract Investigating the ability of non-native species to establish and invade different habitats is one of the most important approaches in the analysis of biological invasion mechanisms. In this study, we used a regional dataset of non-native plant species compiled for Caribbean islands to estimate the level of invasion of major habitat types in this region. Our results show that although non-native species are successfully invading all habitat types evaluated, they are exhibiting considerably higher affinity toward human-made habitats. Across these islands, highly anthropogenically altered habitats such as ruderal sites, pastures, and cultivated lands are the habitats showing higher levels of invasion compared to natural habitats with low levels of disturbance. We found a significant association between geographical origin and habitat invaded, with species originating from Asia, South America, and Africa overrepresented as invaders in the Caribbean. Additionally, a significant association between life-form and habitat invaded was detected, with more trees and herbaceous species than expected successfully invading ruderal habitats, and more trees and vines than expected invading natural forests. In general, non-native species invading habitats across Caribbean islands seem to be adapted to a broad range of successional stages ranging from highly disturbed human-made habitats to least disturbed natural forests. Our results highlight how complex interactions among human activity, geographical origin, plant life-form, and habitat affinity can determine patterns of invasions across broad landscapes.

Keywords Biological invasions · Habitat invasion · Habitat preferences · Level of invasion · Naturalization · Plant invasions · Tropical islands

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-024-03307-4.

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Introduction

Biological invasions represent a major component of global change and a serious threat to the conservation of global biodiversity in the era of the Anthropocene (Blackburn et al. 2011; Pyšek et al. 2020; IPBES 2023). Globalization of trade and the intensification of transport, travel, and human activities (i.e., horticulture, agriculture, and forestry) are not only facilitating a surge in the accidental and intentional translocation of species beyond their native distributions, but also promoting naturalization and range expansion within the introduced ranges (Hulme 2009; Chapman et al. 2017; van Kleunen et al. 2020). Over 13,000 species of vascular plants (representing ~ 4% of all known vascular plants) have already become naturalized in areas outside their native ranges, and this number is expected to continue increasing in the future (Van Kleunen et al. 2015; Seebens et al. 2017, 2021). A subset of these non-native plants has overcome environmental and reproductive barriers and are actively spreading into new areas and/or occupying variety a of habitats where they are recognized as invasive species (Blackburn et al. 2011). Species that become invaders are seriously threatening biodiversity, economy, agriculture, ecosystem services, and human health as they often cause issues of global significance such as the modification of ecosystem services, changes in the composition, structure and function of biomes, species extinctions, biotic homogenization, and economic losses of about US$ 1.288 trillion over the past few decades (Diagne et al. 2021; IPBES 2023).

Whether introduced non-native species become naturalized or invasive is influenced by inherent features of the species and the recipient ecosystems, as well as by factors associated with human activities (Catford et al. 2011; Gioria et al. 2023; Liu et al. 2023). Consequently, not all regions, biomes or habitats are invaded to the same extent. Invasion level is defined as the number or proportion of non-natives in a habitat and represents a measure of the extent or severity of invasion observed in a habitat that varies over time as an invasion progresses (Catford et al. 2011; Hui et al. 2023). Studies have shown that within regions, the level of invasion usually varies strongly among habitats, suggesting that some areas are more vulnerable to invasions than others (Lonsdale 1999; Stohlgren et al. 2002; Pyšek et al. 2010; Aikio et al. 2012; Rejmánek et al. 2013). Quantitative comparisons of the level of invasion between habitats have been conducted, and the role of habitat in determining the characteristics of invasions has been broadly recognized (Richardson and Pyšek 2006; Catford et al. 2012; Pyšek and Chytrý 2014), but so far studies are mostly limited to temperate regions (Chytrý et al. 2005; 2008a; 2008b; Hejda et al. 2009, 2015; Maskell et al. 2006; Vilà et al. 2007) with very few studies providing information for tropical regions (e.g., Rojas-Sandoval and Ackerman 2021; Rojas-Sandoval et al. 2017; 2022; Heymans et al. 2023).

Islands are one of those areas identified as particularly prone to biological invasions (Simberloff 1995; Lenzner et al. 2021). For example, islands are harboring six times more non-native plant species per native species than mainland regions (Essl et al. 2019) and it has been shown that on islands, invasive species are one of the main drivers of species extinctions (Bellard et al. 2016). To prevent extinctions and improve the effectiveness of strategies for the control and management of invasive species, it is essential to identify the level of invasion of different habitats. The Caribbean region is considered a biodiversity hotspot due to its biological richness and high levels of endemism (Myers et al. 2000; Maunder et al. 2008). However, despite its biodiversity richness, Caribbean islands share a complex human, political, and socio-economic history that has led to high levels of anthropogenic disturbance and habitat degradation as well as multiple introductions of non-native species over centuries that have resulted in extensive changes on their flora and fauna composition (Maunder et al. 2008; Ackerman et al. 2017; Rojas-Sandoval and Ackerman 2021; Rojas-Sandoval et al. 2017, 2020, 2022). For Caribbean islands, previous studies have shown that most non-native plant species have been intentionally introduced for ornamental purposes (Rojas-Sandoval and Ackerman 2021), and that islands with high *per capita* GDP, high human population densities, high levels of anthropogenic disturbance, as well as greater island area generally support the most invasive plant species (Rojas-Sandoval et al. 2017, 2020), but there is a lack of detailed assessments on the level of invasion across different habitat types on these islands. The lack of these assessments is limiting the opportunities of evaluating the invasion risks posed to different habitats, which is assumed to be a fundamental component of early detection. Additionally, the identification of those habitat types that are more prone to be invaded is crucial to optimize actions to prevent and control invasions (Zalba et al. 2000).

In this study we examined the occurrence of non-native plant species across different Caribbean habitats to estimate their level of invasion and to assess the relative vulnerability of those habitats to plant invasions. The main goals of this study were to: (1) provide an assessment of the composition and diversity of non-native plant species occurring in major habitat types on Caribbean islands; and (2) evaluate whether differences exist among life-forms, geographical origin, and date of introduction in terms of the habitat affinity of non-native plant species. The availability of updated and comprehensive datasets of non-native plant species for the Caribbean region (Rojas-Sandoval et al. 2017, 2019, 2020, 2021; CABI-ISC 2024) allowed us to identify what are the most common non-native species in each habitat type and which species have the broadest habitat range across the region. We hypothesized that habitats with low levels of human activities like mature natural forests would be generally less invaded than habitats subjected to intense levels of human activities such as ruderal and cultivated lands. Understanding the risk of invasion for different habitat types as well as the habitat affiliations of non-native species is crucial to prevent future invasions and to properly managing habitats before invaders severely impact their native biodiversity or the removal of invaders becomes too expensive.

Methods

Data extraction

Data on non-native plant species occurring on Caribbean islands were obtained for the CABI Invasive Species Compendium (hereafter CABI-ISC, www.cabi.org/isc). The CABI-ISC is an open access database that provides detailed datasheets on invasive species globally, including their native and non-native ranges, invasion status, introduction pathways, habitat occurrences, impacts, and management and control recommendations. Since 2012, CABI in collaboration with the Animal and Plant Inspection Service (APHIS) of the United States Department of Agriculture (USDA) have been compiling datasheets on invasive and potentially invasive species for Caribbean islands as part of the Caribbean Invasive Species Project (Rojas-Sandoval et al. 2019; Diaz-Soltero 2022) generating the most updated and comprehensive databases of non-native invasive plant species for the Caribbean region.

In this study, we focused on a subset of 26 groups of islands or geopolitical units comprising more than 95 individual islands in the Caribbean region covering the Bahamas, Greater and Lesser Antilles, and Trinidad and Tobago (Table 1 contains the complete list of island groups included in this study). For this subset of 26 island groups (hereafter "islands"), we performed an online search in the CABI-ISC selecting all the datasheets for plant species (only vascular plants were included) regarded as the following

Table 1 List of islands, territories, and islands groups included in this study and the total number of non-native plant species recorded

Island	Number of non-natives
Cuba	552
Puerto Rico	550
Dominican Republic	488
Haiti	401
Jamaica	399
Virgin Islands (US and British islands)	336
Martinique	314
Guadeloupe	283
St Lucia	280
Trinidad and Tobago	259
Barbados	246
Bahamas	230
Dominica	212
Antigua and Barbuda	199
Grenada	191
Montserrat	172
Anguilla	169
Cayman Islands	154
St Kitts and Nevis	146
Netherlands Antilles (Saba and Saint Eustatius)	144
St Vincent and The Grenadines	138
St Martin (French and Dutch territories)	89
Bonaire	87
Curacao	85
Aruba	64
Turks and Caicos Islands	25

classification: alien, non-native, exotic, naturalized, established, and invasive. This resulted in a set of 711 species datasheets after removing duplicates, synonyms, and uncertain records (Table S1 in the Supplementary Materials). Species names were standardized using the taxonomic name resolution service website https://tnrs.biendata.org/ (Boyle et al. 2013) according to the World Flora Online (https://www.worldfloraonline.org/).

Species datasheets were then used to extract information to generate the following descriptive parameters: (1) taxonomic classification: scientific name and plant family; (2) continent of origin: classified as Africa, Asia, Australia-Pacific, Europe, North America, or South America (including Central America and the Caribbean); (3) life-form: aquatic herbs, grasses (including grass and sedge), herbs, shrubs, trees (including palms), succulents or vines (including climbers and lianas); (4) life history: classified as perennial, biennial, or annual; (5) habitat affinity; and (6) date of introduction. For the habitat affinity classification, CABI-ISC contemplates 39 different alternatives including natural and semi-natural habitats as well as human-made habitats. To simplify this classification and ensure an adequate number of species in each habitat type for statistical analyses, we developed a new classification with just 11 habitat types (Table 2) that could be consistently applied across the initial classification to transform the data into the new 11 habitat types. For many species, CABI datasheets do not contain information regarding the date of introduction in the Caribbean region. We gathered this information by searching online herbarium records on GBIF (https://www.gbif.org/) and extracting the date of "the earliest available record" for each species on islands in the Caribbean region and used it as a surrogate for its "date of introduction." We recognize that this is a proxy approach, but it allows us to have an estimation of the possible date when each non-native species could have arrived in the Caribbean region. Finally, it is important to consider that for some of the parameters used, categories

Table 2 Definitions and descriptions of the 11 habitat types used in this study. Modified from the CABI Invasive Species Compendium (2023)

Habitat type	Description	Level of anthropogenic disturbance
Human-made habitats		
Cultivated lands	Habitats created and managed by humans including agricultural lands, orchards, plantations, and intensive production systems	High
Pastures	Open areas created by humans and dominated by graminoid herbs and often used for grazing of livestock (including both active and abandoned pastures)	High
Ruderal habitats	Habitats created and managed by humans including disturbed areas, roadsides, and urban and peri-urban areas	High
Natural and semi-natural habitats		
Forest	Land dominated by trees with low levels of disturbance and characterized by closed canopy cover > 50%	Low
Open forest	Forested area with canopy openings created by disturbance	Moderate to high
Shrublands	Areas characterized by a vegetation layer (< 3 m height) of shrubs, herbaceous plants, and low trees	Moderate
Drylands	Areas characterized by pronounced seasonality in rainfall distribution, including dry forest, deserts, arid and semiarid areas	Moderate
Coastal forest	Areas along coastal plains, coastal dunes, and beaches where vegetation is often subjected to wind and salt-spray	Moderate
Riparian forest	Vegetation along riverbanks or adjacent to a body of water including streams, ponds, lakes, or reservoirs	Low to moderate
Aquatic	Submerged and floating vegetation in freshwater ponds, lakes, rivers, streams, and reservoirs	Low to moderate
Wetlands	Areas in areas seasonally flooded with seawater and/or brackish water including swamps, mangroves, estuaries, intertidal zones, and salt marshes	Low to moderate

are not mutually exclusive, and one species could be assigned to multiple categories. For example, species can occur in more than one habitat type or be native to multiple continents. In these cases, species were assigned to as many categories as appropriately applicable.

Data analysis

We used the data extracted and the new habitat classification to create a matrix of species and habitat types with binary (0/1) affiliations of species to particular habitats and then estimate the number of non-native species affiliated to each habitat type. Differences in the observed and expected numbers of species affiliated to each habitat type were analyzed using Chi-square goodness of fit test. For these comparisons, the expected number of species in each habitat type was evaluated as the mean number of species from all the habitat types. The same approach was used to compare differences in the observed and expected number of non-native species when considering continent of origin and life-form. To evaluate whether the occurrence of non-native plant species in each habitat type (habitat affinity) could be related to factors associated with their geographical origin or growth strategies, we constructed the following three interaction matrices: (1) continent of origin × habitat type, (2) life-form × habitat type, (3) life history × habitat type. Then, matrices were analyzed as contingency tables using generalized linear models (GLM) with log-link function and Poisson error terms (Crawley 2007). For fitting models, we used the *glm* function in the R package *stats*. To evaluate temporal variation in the affiliation of species to habitat types, the cumulative number of species in each habitat type was regressed and plotted against the date of introduction. All statistical analyses were performed in R version 3.6.2 (R Development Core Team 2020).

Results

The dataset of non-native plant species compiled for the Caribbean region showed extensive variation in species diversity among islands, with the lowest number of non-native species occurring in Turks and Caicos (25 species) and the highest number in Cuba (552 species, Table 1). Considerable variation in the frequency distribution of non-native species across islands was also detected, but in general the distribution is right-skewed with the higher frequency of species occurring on just one (74 species, 10%) or few islands (308 species, 43% on 5 islands or less), and few species occurring broadly on several islands (Fig. 1). Indeed, only six species (*Cocos nucifera, Gliricidia sepium, Gossypium barbadense, Leucaena leucocephala, Mangifera indica* and *Psidium guajava)* occur widely distributed on the 26 islands covered in this study (Table S1).

Origin and life form

In terms of geographical origin, we found that non-native species on Caribbean islands originated from all continents assessed, but the number of species native to each of these continents varied significantly ($\chi^2 = 366.68$, df = 5, $P < 0.001$). We detected that more species than expected are native to Asia (359 species, 32%), Africa (240 species, 22%) and South America (235 species, 21%), and fewer species than expected are native to Europe (74 species, 7%). The Australia-Pacific region and North America contributed 127 species (11%) and 93 species (8%) respectively (Table S1).

The number of species within each life-form category differed significantly ($\chi^2 = 229.3$, df = 6, $P < 0.0001$; Table S1) with a prevalence of herbs (183 species, 26%) and trees (175 species, 25%), followed by shrubs (135 species, 19%), grasses (106 species, 15%), vines (78 species, 11%), succulents (21 species, 3%) and aquatic herbs (13 species, 2%). Fewer species than expected are aquatic herbs and more species than expected are herbs and trees. Regarding life history, 79% of non-native species are perennials and the remaining 21% are short-lived plants.

Habitat affinity

Non-native plant species are occurring in all habitat types (Fig. 2), but there is more than a 40-fold difference in the occurrence of species (level of invasion) between the most invaded (ruderal habitats, 526 species) and the least invaded habitat (aquatic habitat, 12 species). The three human-made habitats analyzed in this study (ruderal, pastures and cultivated lands) are those with the highest level of invasion (highest number of non-native species) while natural habitats such

Fig. 1 Frequency distribution for the occurrence of non-native plant species across Caribbean islands. The yellow line and the right y-axis represent the percentage relative to the 711 non-native plant species combined for all islands

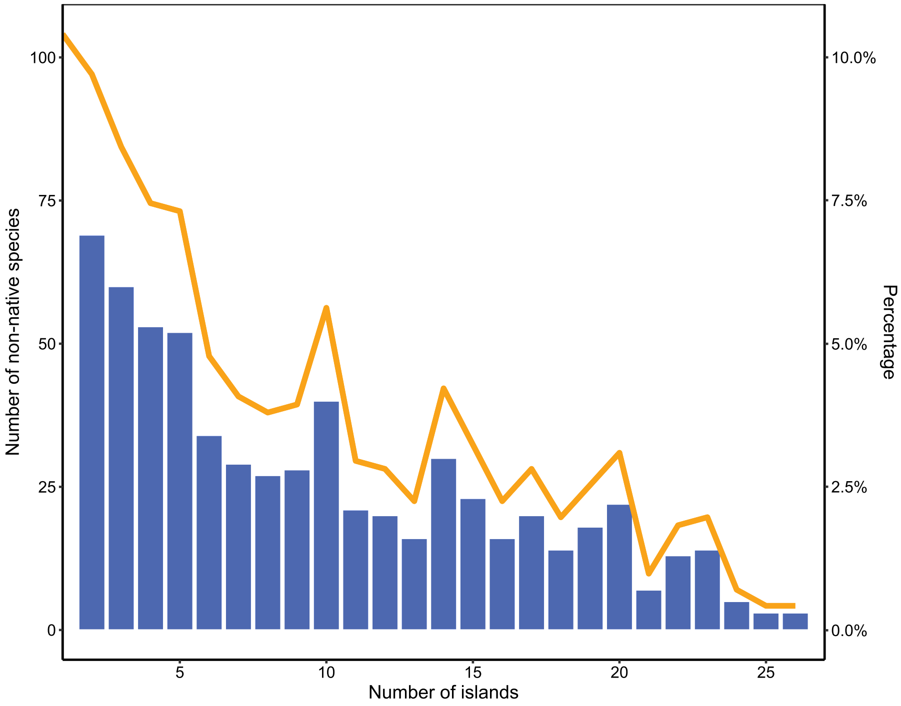
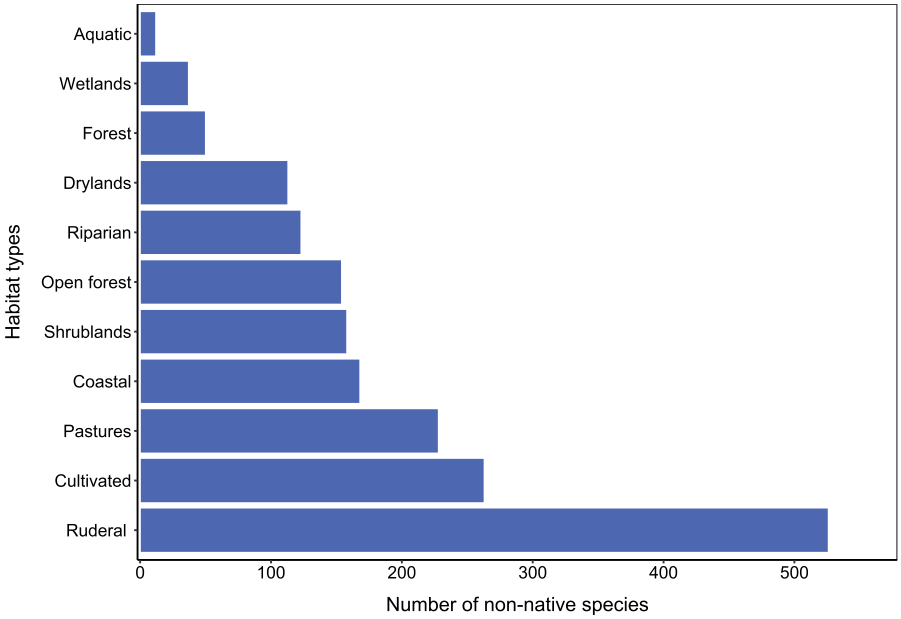


Fig. 2 Number of non-native plant species affiliated with each habitat type evaluated



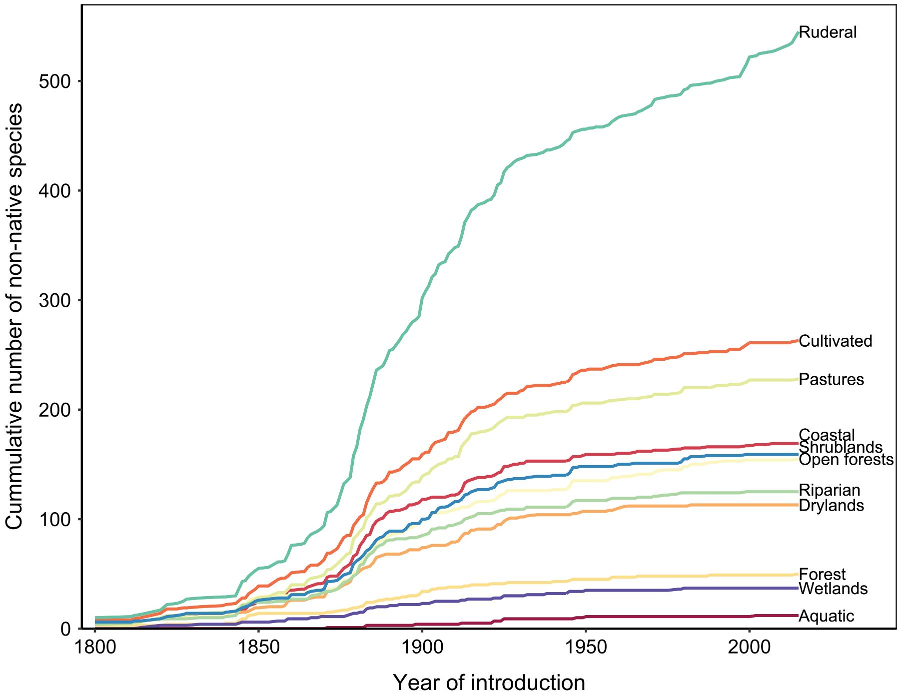
as aquatic systems, wetlands and forests are among those with the lowest level of invasion (Fig. 2). Our results show that a significant fraction of non-native plant species in this region are species successfully exploiting human-made habitats (ruderal habitats, pastures, and cultivated lands) often associated with higher levels of disturbance. About 193 species (27%) occurred exclusively in ruderal habitats. For example, species often regarded as weeds such as *Emilia coccinea, Galinsoga quadriradiata, Persicaria chinensis*, and *Youngia japonica* were always associated with ruderal heavily disturbed anthropogenic habitats. On the contrary, there are species like *Pterocarpus indicus, Odontonema cuspidatum,* and *Miconia calvescens* that show more affinity to natural and semi-natural habitats, which are areas characterized by low to moderate level of disturbance (Table 2).

There are also some species capable of adapting to a wide range of habitat types. *Achyranthes aspera, Albizia lebbeck* and *Antigonon leptopus* are the species with the broadest habitat affinity occurring in 9 out of the 11 habitat types. Other species with broad habitat affinities are *Schinus terebinthifolius* and *Spathodea campanulata* (8 habitats) and *Abrus precatorius, Leucaena leucocephala*, and *Megathyrsus maximus* (7 habitats). At the other end of the spectrum, 223 species (31%) occurred only one habitat type (Table S1), with this one habitat showing more affinity towards human-made habitats (85%) than to natural habitats (15%). A remarkable group including species such *Adenanthera pavonina, Epipremnum pinnatum, Oeceoclades maculata, Schinus terebinthifolius,* and *Syzygium jambos* are among the 50 species showing more affinity to natural habitats with low levels of human activity and are shade-tolerant species currently invading closed canopy forests across the region (Table S1). There are also species preferring particular habitat types, for example, *Melaleuca quinquenervia, Ischaemum rugosum, Fimbristylis littoralis,* and *Urochloa mutica* are species that show high affinity to wetlands while species such as *Cocos nucifera, Casuarina equisetifolia, Scaveola taccada,* and *Terminalia catappa* are occurring almost exclusively on coastal habitats (Table S1).

Temporal trends

Based on herbarium records, we found that since the 1850s there has been a steady increase in the cumulative number of non-native plant species occurring across the different habitat types (Fig. 3). We also detected that while the number of non-native species varied among habitats, the temporal trends in species accumulation suggest that the broad pattern in their level of invasion have remained consistent over the last 100 years. In general, the trend in the cumulative number of non-native species among habitats became relatively fixed by early 1900s and since then, ruderal habitats consistently have had the highest level of invasion while forest, wetlands, aquatic habitats consistently have had the lowest level of invasion, and the rank order of the other habitats have remained similar over this period. Our data also show that the introduction of non-native species with affinity to ruderal

Fig. 3 Temporal trends in the introduction of non-native plant species across 11 habitat types evaluated on Caribbean islands



habitats has accelerated since 1850 with a substantial increment observed in the last 20 years having no signs of saturation (Fig. 3).

Interaction matrices

For the different interaction matrices evaluated, we found significant differences for the association between life-form and habitat invaded ($\chi^2 = 320.66$, df = 54, $P < 0.001$; Fig. 4; see also Supplementary Materials). Species successfully invading ruderal habitats are more likely herbs and trees than other life-forms. Vines are overrepresented among species invading open forests and riparian habitats compare to other life-forms while more succulents than expected are invading drylands and shrublands. We also found that species successfully invading forests are more likely trees and vines than other life-forms (Fig. 4). Additionally, our analysis detected significant differences in the interaction between the continent of origin and habitat invaded ($\chi^2 = 129.54$, df = 50, $P < 0.001$, Fig. 5). More species than expected native to Asia, South America, and Africa are invading ruderal habitats and more species than expected native to

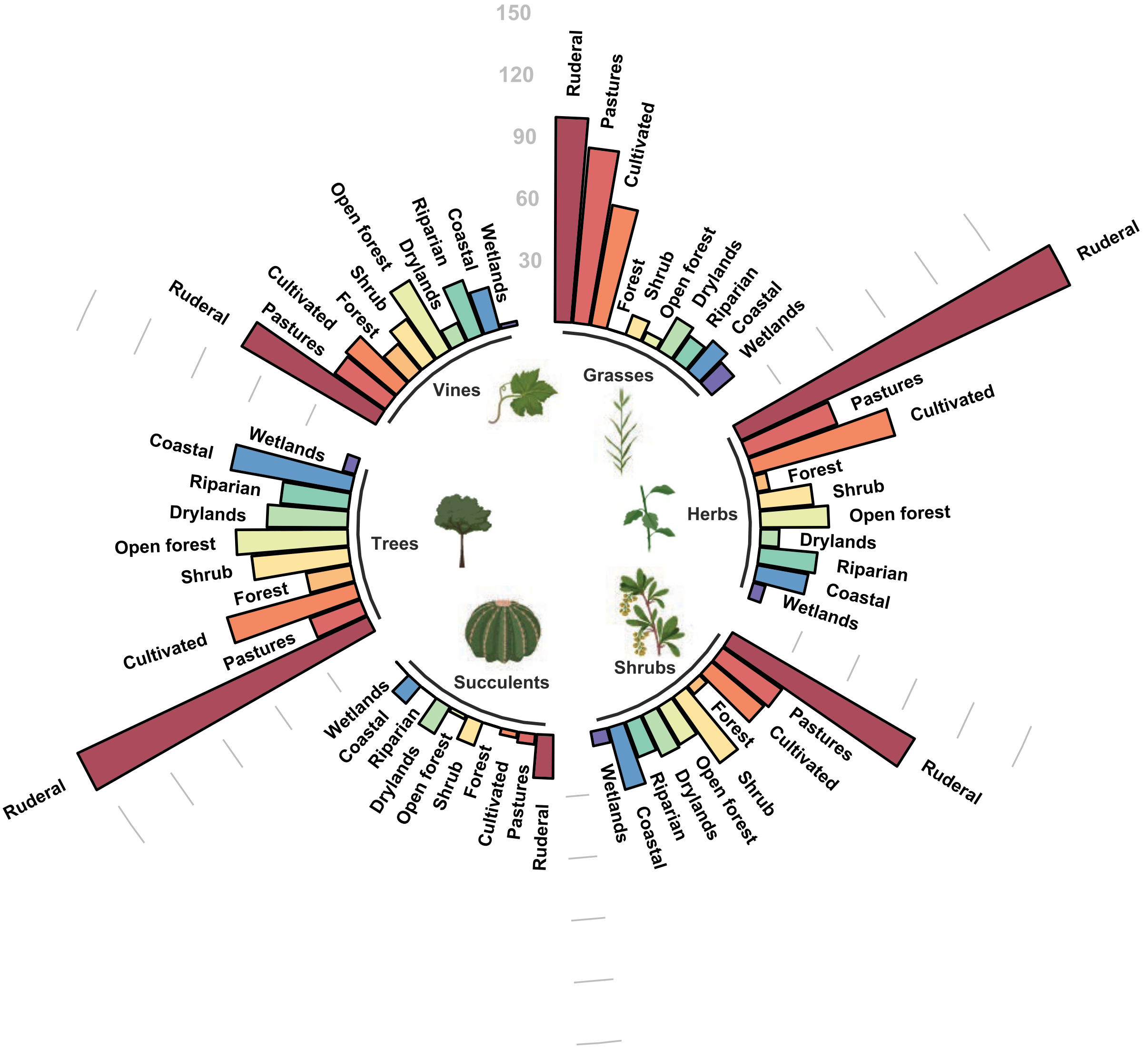


Fig. 4 Non-native plant species grouped by life-form and the frequency of occurrence of these life-forms within each habitat type

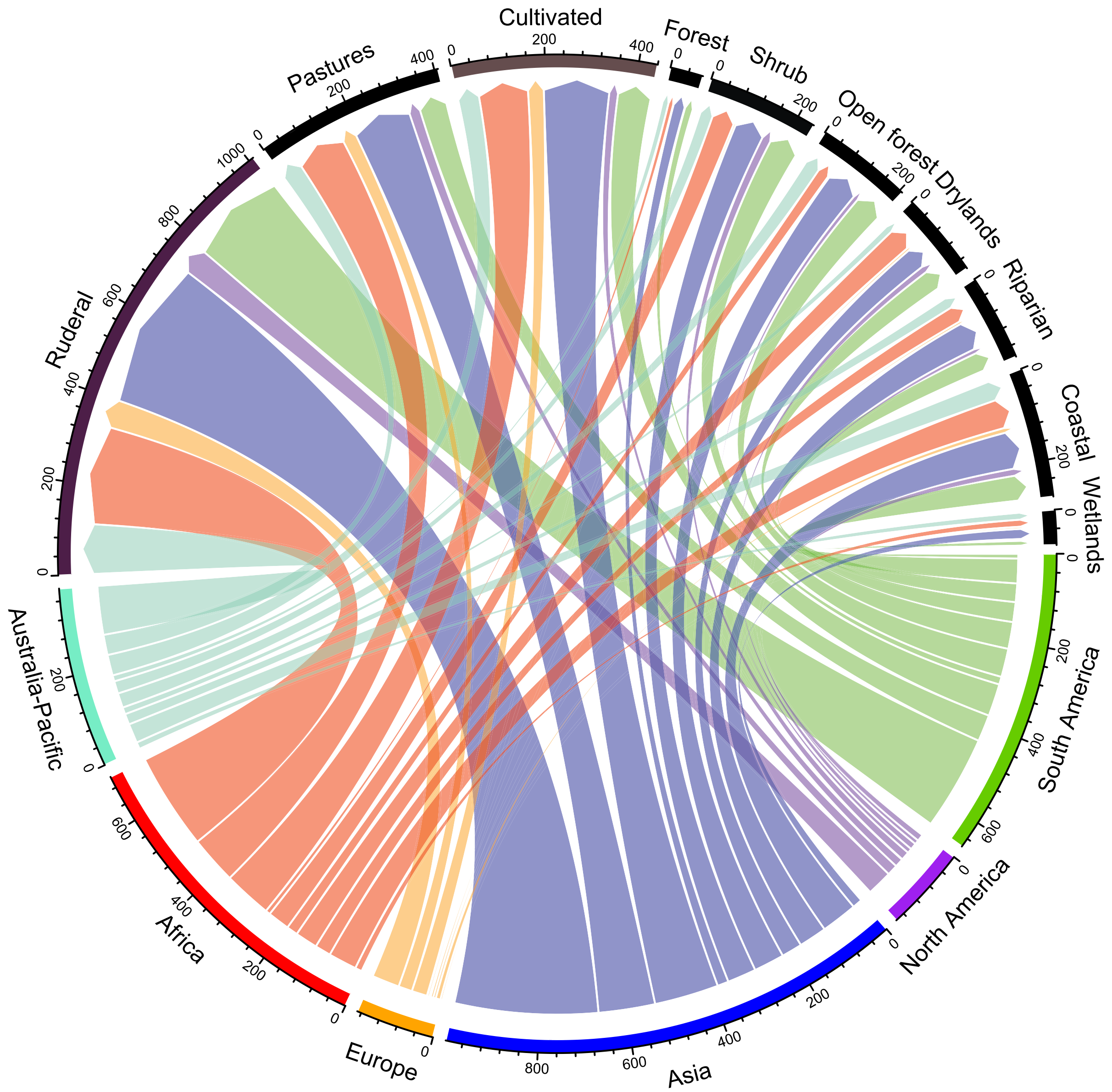


Fig. 5 Flows of non-native plant species native to each continent and their affiliation with each habitat type across Caribbean islands

Australia-Pacific are invading wetlands. For the interaction matrix between life history and habitat invaded no significant association was detected ($P > 0.05$).

Discussion

Our study highlighted the wide-ranging occurrence of non-native plant species across various habitats on Caribbean islands. We found that although different habitats have different levels of invasion, in general, invasion success on these islands seems to be associated with a strong disturbance regime. Notably, human-made habitats such as ruderal sites, pastures, and cultivated lands exhibited the highest levels of invasion emphasizing the role of anthropogenic activities in facilitating the spread of non-native species. Similar results have been described for both temperate and tropical locations (Chytrý et al. 2008b; Clotet et al. 2016; Heberling et al. 2017; Rojas-Sandoval et al. 2017) where disturbance has been identified as one of the main factors facilitating plant invasions mostly as a result of higher propagule pressure (human-mediated dispersal) and higher availability of light, water, and nutrients in open areas (Davis et al. 2000; Daehler 2003; Vilà et al. 2007; Chytrý et al. 2008a, b; Gasso et al. 2012; Haeuser et al. 2017). In general, our results indicate that disturbed habitats throughout Caribbean islands are subject to the same ecological processes that drive plant invasions worldwide and that involves species of high colonizing ability, fast growth rates, and high tolerance of disturbance regimes associated with human activities (Fridley 2008). Indeed, some of the most widespread species across the islands such as *Cocos nucifera, Gliricidia sepium, Leucaena leucocephala, Mangifera indica,* and *Megathyrsus maximus*, are commonly found in areas associated with human activities, often exhibiting elevated levels of disturbance (current study).

The identification of an important number of non-native species showing affinity to natural habitats with low level of disturbance and that are successfully invading closed-canopy forests, highlights the adaptability of certain non-native species. A recent paper by Fridley et al. (2023) shows that some of the most impactful invaders worldwide are woody species invading closed-canopy forests. We also detected that more trees and vines than expected are successfully invading forests on Caribbean islands. Understanding the preferences and behaviors of non-native species with different adaptative strategies can contribute to more targeted conservation efforts in sensitive ecosystems like islands that are areas particularly prone to biological invasions and where invasive species are one of the main drivers of species extinctions (Simberloff 1995; Bellard et al. 2016; Lenzner et al. 2020).

In terms of the temporal patterns of introduction of non-native species, our results indicate that despite variations among habitats, there is a consistent pattern in the levels of invasion for the different habitats over the last century. Ruderal habitats consistently showed the highest level of invasion, while forests, wetlands, and aquatic habitats consistently exhibited the lowest levels. Our data also show an accelerated introduction of non-native species with ruderal habitat affinity since 1850, with sustained high rates of introduction and an observable increment in the last two decades (Fig. 3). These findings suggest that for Caribbean islands, habitat type seems to have a much larger effect on invasion success than year of introduction as the minimum residence time is not having a major effect on the temporal trends and basically for the different habitat types the patterns have remained much the same for the last century. Because sampling effort varies in space and time, these temporal patterns prompt further exploration into the underlying factors influencing the long-term dynamics of non-native species within specific Caribbean habitats. Variation in propagule pressure and, to a lesser extent, sampling effort in space and time can significantly mask the intrinsic vulnerability of different habitats to plant invasions (Aikio et al. 2012). We also recognize the importance of considering variations in the area covered by each habitat type for a more comprehensive study, but unfortunately, such information is currently unavailable for this region. However, a previous study by Ackerman et al. (2017) showed that only 11% of the variation in the number of invasive species in municipalities of Puerto Rico could be attributed to area differences, suggesting that, in this context, variations in area may not significantly influence the observed patterns of invasive species.

The distribution of non-native species from different continents highlights the role of historical trade routes, human migration, and climate patterns in shaping plant invasions. Asia with at least one third of the species is the major single donor of non-native species for Caribbean islands. Previous studies for this region have also highlighted the contribution of Asian species to the pool of non-natives species (Rojas-Sandoval et al. 2017; Rojas-Sandoval and Ackerman 2021). Similarly, other studies have also shown that Asian species are often overrepresented as donors of naturalized plants worldwide and that they are most likely to become naturalized in other continents due to an intrinsic "higher innate naturalization potential" compared to plants from other regions (Van Kluenen et al. 2020; Gioria et al. 2023). Species with intrinsically high naturalization potential make them highly competitive and thus capable of invading elsewhere (Fridley and Sax 2014).

One of the most interesting findings of this study is the interaction between habitat invaded and different life-forms. This result suggests that different plant traits are filtered out in some habitats but not in others. For example, herbs and trees are overrepresented in ruderal habitats, while vines and trees are overrepresented in forests. Similar interactions have been recognized for different systems (Giorgis et al. 2016; Marcora et al. 2018; Rojas-Sandoval and Ackerman 2021) highlighting that within the recipient locations, the level of invasion and habitat invasibility may be highly dependent of the life-form of the non-native species introduced. Additionally, the overall prevalence of herbs and trees across the different habitats analyzed here underscores the adaptability of these life-forms to novel environments. These findings reinforce the importance of considering life-form and the interaction with habitat when evaluating and managing biological invasions.

In conclusion, our study contributes to the understanding of habitat preferences of non-natives species and provides a basis for informed conservation and management strategies at local and regional scale. We recognize that our dataset does not have the level of resolution needed to answer the question of why some habitats are more invaded than others. For this, one must consider habitat invasibility including the effects of specific habitat properties and factors such as functional diversity, propagule pressure and climate (Chytrý et al. 2005, 2008b; Richardson and Pyšek 2006; Rejmánek et al. 2013; Renault et al. 2022). Nonetheless, since management actions are often focused on habitat types rather than species (Fazey et al. 2005), our findings have important implications for conservation and management strategies. Recognizing the specific habitats prone to high levels of invasion allows for more effective allocation of resources. In this case, our results suggest that the best defense against non-native invaders is to reduce the levels of disturbance in human-made habitats as well as to protect natural and seminatural areas from disturbance to prevent the spread of non-natives into forests and other habitats with low levels of human activity to slow down the pace of plant invasions on these islands (Ackerman et al. 2017). It is known that the rate of spread of non-native invaders is affected by many factors that differ along spatial and temporal scales, making generalization difficult. Therefore, future studies should include factors such as climate, vegetation structure, resource availability, native species richness and abundance, propagule pressure and associated ecosystem processes such as competition and adaptation.

Acknowledgements This research was funded by the U.S. Department of Agriculture through the Cooperative Agreement number AP21OA00000C008. We thank Anna Page and IT personnel at CABI for technical support preparing and handling the dataset. Logistic support for this research was provided by Eduardo Ventosa at Effective Environmental Restoration Inc., the Institute of the Environment, and the University of Connecticut.

Author contributions JRS conceived the study and compiled the data. JRS designed and performed the analyses with inputs from JDA. JRS led the writing and all authors contributed critically to the manuscript and gave final approval for publication.

Data availability All data used in this study are publicly available at the CABI Invasive Species Compendium at https://www.cabidigitallibrary.org/product/QI. The dataset generated and analyzed in this study, R codes, and test results are available in the Supplementary Materials.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

References

Ackerman JD, Tremblay RL, Rojas-Sandoval J et al (2017) (2017) Biotic resistance in the tropics: patterns of seed plant invasions within an island. Biol Invasions 19:315–328. https://doi.org/10.1007/s10530-016-1281-4

Aikio S, Duncan RP, Hulme PE (2012) The vulnerability of habitats to plant invasion: disentangling the roles of propagule pressure, time and sampling effort. Glob Ecol Biogeogr 21(8):778–786. https://doi.org/10.1111/j.1466-8238.2011.00711.x

Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. Biol Lett 12:20150623. https://doi.org/10.1098/rsbl.2015.0623

Blackburn TM, Pyšek P, Bacher S et al (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26:333–339. https://doi.org/10.1016/J.TREE.2011.03.023

Boyle B, Hopkins N, Lu Z, Raygoza Garay JA, Mozzherin D, Rees T, Matasci N, Narro ML, Piel WH, Mckay SJ, Lowry S (2013) The taxonomic name resolution service: an online tool for automated standardization of plant names. BMC Bioinform 14:1–15

CABI, 2024. Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc

Catford JA, Vesk PA, White MD, Wintle BA (2011) Hotspots of plant invasion predicted by propagule pressure and ecosystem characteristics. Divers Distrib 17:1099–1110. https://doi.org/10.1111/j.1472-4642.2011.00794.x

Catford JA, Vesk PA, Richardson DM, Pyšek P (2012) Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. Glob Change Biol 18:44–62. https://doi.org/10.1111/j.1365-2486.2011.02549.x

Chapman DS, Scalone R, Štefanić E, Bullock JM (2017) Mechanistic species distribution modeling reveals a niche shift during invasion. Ecology 98:1671–1680. https://doi.org/10.1002/ecy.1835

Chytrý M, Pyšek P, Tichý L, Knollová I, Danihelka J (2005) Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. Preslia 77:339–354

Chytrý M, Maskell LC, Pino J, Pyšek P, Vilà M, Font X, Smart SM (2008a) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. J Appl Ecol 45:448–458

Chytrý M, Jarosik V, Pysek P, Hajek O, Knollová I, Tichý L, Danihelka J (2008b) Separating habitat invasibility by alien plants from the actual level of invasion. Ecology 89(6):1541–1553. https://doi.org/10.1890/07-0682.1

Clotet M, Basnou C, Bagaria G et al (2016) Contrasting historical and current land-use correlation with diverse components of current alien plant invasions in Mediterranean habitats. Biol Invasions 18:2897–2909. https://doi.org/10.1007/s10530-016-1181-7

Crawley MJ (2007) The R book. John Wiley & Sons, Hoboken

Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annu Rev Ecol Evol Syst 34:183–211. https://doi.org/10.1146/annurev.ecolsys.34.011802.132403

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88(3):528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x

Diagne C, Leroy B, Vaissière AC, Gozlan RE, Roiz D et al (2021) High and rising economic costs of biological invasions worldwide. Nature 592:571–576. https://doi.org/10.1038/s41586-021-03405-6

Diaz-Soltero H (2022) Global identification of invasive species: The CABI invasive species compendium as a resource. In: Invasive species and global climate change.CABI, GB, pp. 239–247 https://doi.org/10.1079/9781800621459.0013

Essl F, Dawson W, Kreft H et al (2019) Drivers of the relative richness of naturalized and invasive plant species on Earth. AoB Plants 11:1–13. https://doi.org/10.1093/aobpla/plz051

Fazey I, Fischer J, Lindenmayer DB (2005) Who does all the research in conservation biology? Biodivers Conserv 14:917–934. https://doi.org/10.1007/s10531-004-7849-9

Fridley JD (2008) Of Asian forests and European fields: Eastern US plant invasions in a global floristic context. PLoS ONE 3(11):e3630. https://doi.org/10.1371/journal.pone.0003630

Fridley JD, Sax DF (2014) The imbalance of nature: Revisiting a Darwinian framework for invasion biology. Glob Ecol Biogeogr 23:1157–1166. https://doi.org/10.1111/geb.12221

Fridley JD, Bellingham PJ, Closset-Kopp D, Daehler CC, Dechoum MS, Martin PH, Murphy HT, Rojas-Sandoval J, Tng D (2023) A general hypothesis of forest invasions by woody plants based on whole-plant carbon economics. J Ecol 111(1):4–22. https://doi.org/10.1111/1365-2745.14001

Gasso N, Pino J, Font X, Vila M (2012) Regional context affects native and alien plant species richness across habitat types. Appl Veg Sci 15(1):4–13. https://doi.org/10.1111/j.1654-109X.2011.01159.x

Gioria M, Hulme PE, Richardson DM, Pyšek P (2023) Why Are Invasive Plants Successful? Annu Rev Plant Biol 74:635–670. https://doi.org/10.1146/annurev-arplant-070522-071021

Giorgis MA, Cingolani AM, Tecco PA et al (2016) Testing alien plant distribution and habitat invasibility in mountain ecosystems: growth form matters. Biol Invasions 18:2017–2028. https://doi.org/10.1007/s10530-016-1148-8

Haeuser E, Dawson W, van Kleunen M (2017) The effects of climate warming and disturbance on the colonization potential of ornamental alien plant species. J Ecol 105(6):1698–1708. https://doi.org/10.1111/1365-2745.12798

Heberling JM, Jo I, Kozhevnikov A, Lee H, Fridley JD (2017) Biotic interchange in the Anthropocene: strong asymmetry in East Asian and Eastern North American plant invasions. Glob Ecol Biogeogr 26:447–458. https://doi.org/10.1111/geb.12551

Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. J Ecol 97(3):393–403. https://doi.org/10.1111/j.1365-2745.2009.01480.x

Hejda M, Chytrý M, Pergl J, Pyšek P (2015) Native-range habitats of invasive plants: are they similar to invaded-range habitats and do they differ according to the geographical direction of invasion? Divers Distrib 21:312–321. https://doi.org/10.1111/ddi.12269

Heymans L, Meyer JY, Ah-Peng C et al (2023) Do native and alien species differ in their ecological strategies? A test with woody plants in tropical rainforests on Réunion Island (Mascarene Archipelago, Indian Ocean). Plants 12(23):3990. https://doi.org/10.3390/plants12233990

Hui C, Pyšek P, Richardson DM (2023) Disentangling the relationships among abundance, invasiveness and invasibility in trait space. Npj Biodivers 2(1):13. https://doi.org/10.1038/s44185-023-00019-1

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18

IPBES2023Summary for policymakers of the thematic assessment report on invasive alien species and their control of the intergovernmental science-policy platform on biodiversity and ecosystem servicesIPBES Secretariat10.5281/zenodo.7430692IPBES (2023) Summary for policymakers of the thematic assessment report on invasive alien species and their control of the intergovernmental science-policy platform on biodiversity and ecosystem services. IPBES Secretariat. https://doi.org/10.5281/zenodo.7430692

Lenzner B, Latombe G, Capinha C, Bellard C, Courchamp F, Diagne C, Dullinger S, Golivets M, Irl SD, Kühn I, Leung B (2020) What will the future bring for biological invasions on islands? An expert-based assessment. Front Ecol Evol 8:80

Lenzner B, Magallón S, Dawson W et al (2021) Role of diversification rates and evolutionary history as a driver of plant naturalization success. New Phytol 229:2998–3008. https://doi.org/10.1111/nph.17014

Liu Y, Zheng Y, Jahn LV et al (2023) Invaders responded more positively to soil biota than native or noninvasive introduced species, consistent with enemy escape. Biol Invasions 25:351–364. https://doi.org/10.1007/s10530-022-02919-y

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536. https://doi.org/10.1890/0012-9658(1999)080[1522:GPOPIA]2.0.CO;2

Marcora PI, Ferreras AE, Zeballos SR et al (2018) Context-dependent effects of fire and browsing on woody alien invasion in mountain ecosystems. Oecologia 188:479–490. https://doi.org/10.1007/s00442-018-4227-y

Maunder M, Leiva A, Santiago-Valentín E, Stevenson DW, Acevedo-Rodríguez P, Meerow AW, Mejía M, Clubbe J, Francisco-Ortega J (2008) Plant conservation in the Caribbean Island biodiversity hotspot. Bot Rev 74:197–207. https://doi.org/10.1007/s12229-008-9007-7

Maskell LC, Bullock JM, Smart SM, Thompson K, Hulme PE (2006) The distribution and habitat associations of non-native plant species in urban riparian habitats. J Veg Sci 17:499–508. https://doi.org/10.1111/j.1654-1103.2006.tb02471.x

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403(6772):853. https://doi.org/10.1038/35002501

Pyšek P, Bacher S, Chytrý M, Jarošik V, Wild J, Celesti-Grapow L, Gassó N, Kenis M, Lambdon PW, Nentwig W, Pergl J, Roques A, Sádlo J, Solarz W, Vilà M, Hulme PE (2010) Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. Glob Ecol Biogeogr 19:317–331. https://doi.org/10.1111/j.1466-8238.2009.00514.x

Pyšek P, Chytrý M (2014) Habitat invasion research: where vegetation science and invasion ecology meet. J Veg Sci 25:1181–1187. https://doi.org/10.1111/jvs.12146

Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM (2020) Scientists' warning on invasive alien species. Biol Rev 95(6):1511–1534. https://doi.org/10.1111/j.1466-8238.2009.00514.x

Rejmánek M, Richardson DM, Pyšek P (2013) Plant invasions and invasibility of plant communities. In: van der Maarel E, Franklin J (eds) Vegetation ecology. Wiley-Blackwell, Oxford, pp 387–424

Renault D, Hess MC, Braschi J, Cuthbert RN, Sperandii MG, Bazzichetto M, Chabrerie O, Thiébaut G, Buisson E, Grandjean F, Bittebiere AK (2022) Advancing biological invasion hypothesis testing using functional diversity indices. Sci Total Environ 834:155102. https://doi.org/10.1016/j.scitotenv.2022.155102

Richardson DM, Pyšek P (2006) Plant invasions—merging the concepts of species invasiveness and community invasibility. Prog Phys Geogr 30:409–431. https://doi.org/10.1191/0309133306pp490pr

Rojas-Sandoval J, Ackerman JD (2021) Ornamentals lead the way: global influences on plant invasions in the Caribbean. NeoBiota 64:177–197. https://doi.org/10.3897/neobiota.64.62939

Rojas-Sandoval J, Tremblay RL, Acevedo-Rodríguez P, Díaz-Soltero H (2017) Invasive plant species in the West Indies: geographical, ecological, and floristic insights. Ecol Evol 7:4522–4533. https://doi.org/10.1002/ece3.2984

Rojas-Sandoval J, Acevedo-Rodríguez P, Datiles M et al (2019) Invasive plants of the Caribbean: application of herbarium collections to protect a regional biodiversity hotspot. In: Veitch CR, Clout MN, Martin AR, Russell JC, West CJ (eds) Island invasives: scaling up to meet the challenge. Occasional Paper SSC no. 62. Gland, Switzerland: IUCN. pp xiv +734

Rojas-Sandoval J, Ackerman JD, Tremblay RL (2020) Island biogeography of native and alien plant species: contrasting drivers of diversity across the Lesser Antilles. Divers Distrib 26:1539–1550. https://doi.org/10.1111/ddi.13139

Rojas-Sandoval J, Ackerman JD, Marcano-Vega H, Willig MR (2022) Alien species affect the abundance and richness of native species in tropical forests: the role of adaptive strategies. Ecosphere. https://doi.org/10.1002/esc2.4291

Seebens H, Blackburn TM, Dyer EE et al (2017) No saturation in the accumulation of alien species worldwide. Nat Commun 8:14435. https://doi.org/10.1038/ncomms14435

Seebens H, Bacher S, Blackburn TM et al (2021) Projecting the continental accumulation of alien species through to 2050. Glob Chang Biol 27:970–982. https://doi.org/10.1111/gcb.15333

Simberloff D (1995) Why do introduced species appear to devastate islands more than mainland areas? Pac Sci 49:87–97

Stohlgren TJ, Chong GW, Schell LD, Rimar KA, Otsuki Y, Lee M, Kalkhan MA, Villa CA (2002) Assessing vulnerability to invasion by nonnative plant species at multiple spatial scales. Environ Manage 29:566–577. https://doi.org/10.1007/s00267-001-0006-2

van Kleunen M, Dawson W, Essl F et al (2015) Global exchange and accumulation of non-native plants. Nature 525:100–103. https://doi.org/10.1038/nature14910

van Kleunen M, Xu X, Yang Q, Maurel N, Zhang Z, Dawson W, Essl F, Kreft H, Pergl J, Pyšek P, Weigelt P (2020) Economic use of plants is key to their naturalization success. Nat Commun 11(1):3201. https://doi.org/10.1038/s41467-020-16982-3

Vilà M, Pino J, Font X (2007) Regional assessment of plant invasions across different habitat types. J Veg Sci 18(1):35–42. https://doi.org/10.1111/j.1654-1103.2007.tb02513.x

Zalba SM, Sonaglioni MI, Compagnoni CA, Belenguer CJ (2000) Using a habitat model to assess the risk of invasion by an exotic plant. Biol Cons 93(2):203–208. https://doi.org/10.1016/S0006-3207(99)00146-9