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Ornamentals lead the way: global influences on plant invasions in the Caribbean

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Abstract

Understanding the historical factors associated with the invasion success of alien species in a region may help us to identify sources, vectors, and pathways that are more likely to originate new invaders. Here, we gather data for traits related to the history of introduction (e.g., continent of origin, reason for introduction, and date of introduction) of 616 alien plant species listed as invasive on 18 island groups across the Caribbean region. We used these data to evaluate how human activity has influenced plant invasions on Caribbean islands over time and whether invasion success could be driven by traits of the introduction process. We found that significantly more invasive plants (54%) were intentionally introduced for ornamental reasons than for any other purpose. Most invaders in the Caribbean are native to Asia, South America, and Africa and the cumulative number of invasive species in this region has been steadily increasing during the last 200 years, but since 1850, this trend has been led by species introduced as ornamentals. We also found a significant association between continent of origin and reason of introduction, with more invaders than expected being ornamentals from Asia and America, and forage species from Africa. Our results show that introduced ornamentals are successfully invading all major habitats across the Caribbean, exacerbating conservation issues and threatening native biodiversity. Armed with knowledge of origins and reasons for introductions, effective biosecurity actions as well as control and management strategies can be better targeted to address the problem of invasive species in the region.

Keywords

Alien flora, horticulture, introduction pathways, invasion history, invasion success, residence time, year of introduction

Introduction

Globalization and the intensification of international trade, travel, and transport are leading to an unprecedented increase in the number of alien species translocated into new regions (Westphal et al. 2008; Hulme 2009; Early et al. 2016; Chapman et al. 2017), breaking down biogeographical barriers and homogenizing global biotas (Meyerson and Mooney 2007; Sax and Gaines 2008; Winter et al. 2010; Capinha et al. 2015; Turbelin et al. 2017). For the last few centuries, the numbers of established alien species from different taxonomic groups have increased around the world and are projected to continue in the future (Seebens et al. 2017, 2020). At the same time, changes in climate and land-use (e.g., expansion of agriculture and urban areas) are transforming and degrading natural habitats making them more susceptible to biological invasion (Mooney and Hobbs 2000; Bradley et al. 2010). Besides being a consequence of globalization, biological invasions are also major drivers of global biodiversity change, threatening the conservation of native biodiversity and human livelihoods (Pyšek et al. 2020).

Over 13,000 alien species of vascular plants have established persistent wild populations in areas outside their native range (van Kleunen et al. 2015; Pyšek et al. 2017). Most of these alien plants were originally introduced intentionally (van Kleunen et al. 2020) and a subset of them have overcome specific barriers to their survival, establishment, and dispersal and are actively spreading into new areas where they are identified as invasive species (Blackburn et al. 2011). Among the factors contributing to successful naturalization and invasion of alien species are propagule pressure, residence time, disturbance, biogeographic, climatic and socioeconomic traits of the recipient region, and intrinsic attributes of introduced species (Daehler 2003; Wilson et al. 2007; Lockwood et al. 2009; Moravcová et al. 2015; Essl et al. 2019). Consequently, the pool of alien species in a given region often depends on historical factors related to the type, intensity, and frequency of human activities in the area (Lambdon et al. 2008; Zenni 2014; van Kleunen et al. 2020). Historically, activities such as agriculture, forestry, and horticulture are well-known for the common practice of moving plant species well beyond their native distribution ranges (Inderjit 2005; Hulme 2009; Richardson and Rejmánek 2011). There is also robust evidence in the literature showing that planting practices affect invasion success and disproportionately more invaders are recruited from species introduced through horticulture than other means (Reichard and White 2001; Dehnen-Schmutz et al. 2007; Hulme et al. 2018; van Kleunen et al. 2018). Within this context, studies attempting to identify means of introduction and the historical and geographical determinants driving invasion success are crucial to help us identify regions, vectors, and pathways more likely to originate potential new invaders as well as to design science-based strategies for the prevention and control of current and future invasions.

Globally, islands are hotspots of naturalized alien species richness across multiple taxonomic groups (Dawson et al. 2017) and insular regions with high per capita GDP, high human population densities, and high levels of anthropogenic disturbance are supporting the most invasive alien species (Kueffer et al. 2010; Essl et al. 2019). While these drivers are strong, different archipelagos have unique properties associated with biological invasions that are not necessarily shared globally (Kueffer et al. 2010). The Caribbean region, comprising the Bahamas, Greater and Lesser Antilles, and islands off the coast of northern South America, is considered a global biodiversity hotspot with high priority for conservation due to its biological richness and high levels of endemism (Myers et al. 2000; Maunder et al. 2008). These islands share a complex geological and biogeographical history that has resulted in a unique distribution of their biodiversity (Santiago-Valentin and Olmstead 2004; Roncal et al. 2020). They also share an intricate human, political, and socio-economic history that has led to high levels of anthropogenic disturbance, multiple introductions of alien species over centuries, and extensive deforestation resulting in habitat-loss and degradation of biodiversity (Maunder et al. 2008; Rojas-Sandoval et al. 2017, 2020). Currently, the expansion of urban areas, massive tourism developments, and high human population densities are accelerating social-ecological changes and generating unprecedented pressure on Caribbean natural resources (Dixon et al. 2001; Grandoit 2005). Owing to the combination of these unique circumstances, Caribbean islands are an excellent model to assess the link between introductions of alien species and human activities and the potential role of historical and geographical factors driving invasion success. On the other hand, assessments of the history of plant invasions are still limited for the Caribbean region, highlighting gaps in knowledge that need to be addressed.

In this study, we used data for traits related to the history of introduction (e.g., continent of origin, reason for introduction, and date of introduction) of alien plant species classified as invasive on 18 island groups in the Caribbean region to: (1) assess how human activity has influenced plant invasions in the Caribbean during the last 200 years, (2) identify how many invasive species were introduced from different continents and for certain purposes and whether these patterns of introductions have changed over time, and (3) evaluate whether invasive species introduced for certain purposes are invading a wider range of habitat types. We expected plant taxa native to tropical regions to be the dominant invaders in the Caribbean following the premise that climate matching between native and introduced range is one of the few factors that consistently predicts invasion success (Thuiller et al. 2005; Hayes and Barry 2008; Bellard et al. 2016; Cabra-Rivas et al. 2016). We also expected species introduced for ornamental purposes to dominate the pool of invaders on these islands based on robust evidence in the literature indicating that from all the introduction pathways, ornamental trade is the largest source of invasive plants worldwide (Hulme et al. 2018; van Kleunen et al. 2018). By evaluating the introduction history of invasive alien species on these islands and the potential associations among continent of origin, reason of introduction, and preferred habitats invaded, we attempt to identify whether there are specific regions (sources) or reasons for introduction (specific economic and/or environmental uses) related to invasion success. These analyses would enable one to target management strategies linked to those sources and uses that represent higher invasion risk.

Methods

Data collection

To compile our dataset, we searched for relevant literature on Scopus, Google Scholar, and CAB Direct. Searches were performed in English, French, and Spanish with no restriction on publication year, using the following keywords: invasive, exotic, alien, non-native, naturalized AND plant, vegetation, and flora AND West Indies, Caribbean, Lesser and Greater Antilles. Additional references were identified using specialized invasive databases and by manually scanning the reference lists from the retrieved publications. The final dataset included only alien spermatophyte species that were listed as invasive in the original source consulted and are spreading beyond the point of introduction (Suppl. material 1: Appendix S1 contains the list of all sources consulted). Species occurring exclusively in captivity or under cultivation, hybrids, and unreliable records were excluded. The resulting dataset comprised invasive plant species from 18 Caribbean island groups including Anguilla, Aruba, the Bahamas, Bonaire, Cuba, Curacao, Dominican Republic, Guadeloupe, Jamaica, Martinique, Puerto Rico, St. Barthélemy, St. Eustatius, St. Lucia, St. Martin (including the Dutch and French parts of the island), Saba, Trinidad and Tobago and the Virgin Islands (including the British and U.S. Virgin Islands).

Our dataset includes the taxonomic family of each invasive plant species and the following descriptive parameters:

1. Continent (or region) of origin: Each species was classified with respect to where it is native (Africa, Asia, South America, North America, Australia-Pacific region, Europe, and West Indies). For each continent, species were also classified as "tropical origin" (species whose region of origin occurs entirely within the tropics or includes either the tropics of Cancer or Capricorn) and "temperate origin" (species whose region of origin occurs exclusively in temperate regions at latitudes >35°).
2. Life form: We classified species as either aquatic herbs, grasses, herbs, shrubs, trees (including palms), succulents or vines. In addition, herbaceous and woody habits were distinguished.
3. Reason for introduction: For each species we categorized the main reason for introduction as follows: (i) agroforestry, (ii) agriculture/food (species introduced for human consumption), (iii) forage (including forage and fodder for domestic animal food), (iv) ornamental, (v) soil conservation (including species introduced for erosion control and dune stabilization), and (iv) timber production.
4. Habitat type: Each species was classified according to the natural habitat that they have invaded on Caribbean islands. The habitat types evaluated are: (i) drylands (including dry forest, cactus thickets and Caribbean semiarid shrublands), (ii) moist forest, (iii) rainforest (including wet forest, high montane forest, and rainforest), and (iv) wetlands (including swamps, mangroves and seasonal flooded coastal forest).

Some of these categories are not mutually exclusive and one species could be assigned to multiple categories. For example, species introduced for multiple purposes were assigned to each of them. Similarly, if the native distribution range of one species covers more than one continent or if the species is invading more than one habitat, it was assigned to each of them. Species complementary data were obtained from the National Plant Germplasm System (GRIN-Global) and other local and international sources and websites (Suppl. material 1: Appendix S2 for a complete list of the sources consulted).

We also determined the date of introduction for each plant species in our dataset. However, for Caribbean islands obtaining data on the exact dates of introduction of alien species is very difficult due to the lack of detailed historical records. Thus, we decided to use the "minimum residence time" as a conservative approach to have an estimate of the latest possible date when each species could have entered the Caribbean region. For this, we searched online herbarium records of the U.S. National Herbarium (US) and the New York Botanical Garden (NY), two herbaria with extensive collections from the Caribbean region. From these herbarium collections we extracted the date of "the earliest available record" for each species on a Caribbean island and used it as a surrogate for its "date of introduction".

Data analyses

Descriptive statistics and contingency table analyses were used to describe the profile of invasive plant species. We used χ^2 tests to evaluate differences in the observed and expected numbers of invasive species introduced from different regions (continents of origin) and for different purposes. For these comparisons, the expected number of invasive species in each category was evaluated as the mean number of species from all the categories. To evaluate whether the invasion success of alien plant species could be related to factors associated with their history of introduction, we used our dataset to construct the following interaction matrices: (1) continent of origin × reason of introduction, (2) continent of origin × habitats invaded, (3) life-form × habitat invaded, (4) reason for introduction × habitats invaded and (5) reason for introduction × habit. Then, matrices were analyzed as contingency tables using generalized linear models with log-link function and Poisson distribution of errors (Crawley 2007). To evaluate temporal variation in the number of invasive species the cumulative number of species was regressed against the date of introduction. We also evaluated temporal variation in the cumulative number of invasive plant species introduced from each continent and by the different reasons of introduction. We performed all statistical analyses in *R* version 3.6.2 (R Development Core Team 2020) using the *MASS* package (Venables and Ripley 2002) and the *Circlize* package (Gu et al. 2014) to generate visualizations of the flows of invasive species.

Results

We found 616 alien plant species from 402 genera and 102 families that are classified as invaders on at least one of the islands included in this study (Suppl. material 1: Fig. S1). Plant families with the largest number of invasive species are Fabaceae, Poaceae, and Asteraceae and these accounted for 37% of all invaders (Fig. 1a). The number of invasive species within each life-form category differed significantly ($\chi^2 = 229.3$, df = 6, $p < 0.0001$) with a prevalence of herbs (29%) and trees (21%) followed by shrubs (17%), grasses (14%), vines (13%), succulents (3%) and aquatic herbs (3%). Fewer invasive species than expected were aquatic herbs and more species than expected were herbs (Fig. 1b). Regarding habit, 55% of all invasive species are herbaceous and 45% are woody species. For the continent of origin, we found that invasive plants in the West Indies originated from all continents, but the number of species introduced from each region varied significantly ($\chi^2 = 253.5$, df = 6, $p < 0.0001$, Fig. 2). Asia, South America, and Africa contributed significantly more invasive species than expected while fewer than expected invasive species came from Europe. As expected, most invaders on Caribbean islands originated from tropical regions across the different continents but the group is dominated by species coming from tropical regions in Asia, South America, and Africa (Suppl. material 1: Fig. S2). For example, 85% of the total number of invasive species introduced from Asia (281 species) has its origin (native distribution range) in tropical regions of Asia. Similar results were identified for most continents including the other two major donors of invasive species, South America (82% species with tropical origin) and Africa (78% species with tropical origin) (Suppl. material 1: Fig. S2).

We were able to determine the pathway of introduction for 605 out of 616 invasive species in our dataset. We found that 111 species were unintentional introductions (18%) and 494 species were intentionally introduced (82%). Of the latter, we detected clear significant differences for the reasons of introduction ($\chi^2 = 528.7$, df = 5, $p < 0.0001$, Fig. 3a), with considerably more species being introduced as ornamentals than by any of the other purposes. Species introduced as ornamentals accounted for 54% of all invaders followed by species introduced for forage (17%), agriculture/food (13%) and agroforestry (9%). Species introduced for soil conservation and timber production only contributed 5% and 2%, respectively. Our results also showed that across the Caribbean islands, invaders occurred in all the habitat types (Suppl. material 1: Fig. S3), but when we normalized each habitat type by habitat area (considering all the islands included in the study), we found that the number of invasive species per unit area is slightly higher in drylands compared to moist forests and rainforests (Fig. 3b). Wetlands are the habitats with the lowest number of invasive species per unit area.

Of the 616 species included in our dataset, we found herbarium records for 523 species that had been collected from Caribbean islands. We used those records to evaluate the temporal variation in species introductions. These data showed that there has been a steady increase in the cumulative number of invasive species introduced into the Caribbean in the last 200 years (Fig. 4a) with the most rapid increase occurring between 1850 and 1925. We also found that more than 79% of all invasive species are long-term residents in the Caribbean and have minimum residence times of more than 100 years (Fig. 4b). There is also a steady increase in the cumulative number of species being introduced for different purposes (Fig. 4c) but this increase has been led

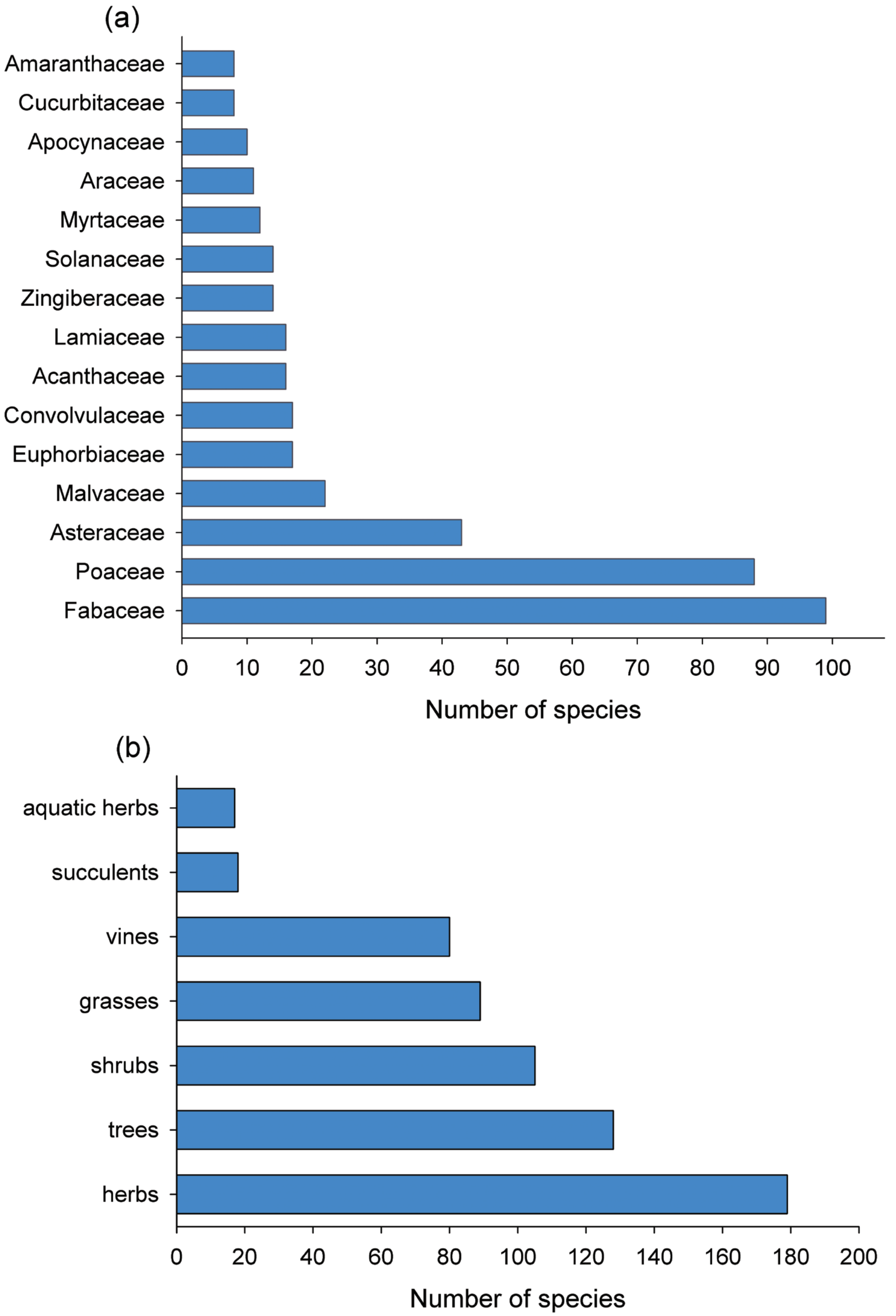

Figure 1. Number of invasive plant species on Caribbean Islands grouped by **a** plant families with the largest numbers of invasive species and **b** primary life-forms.

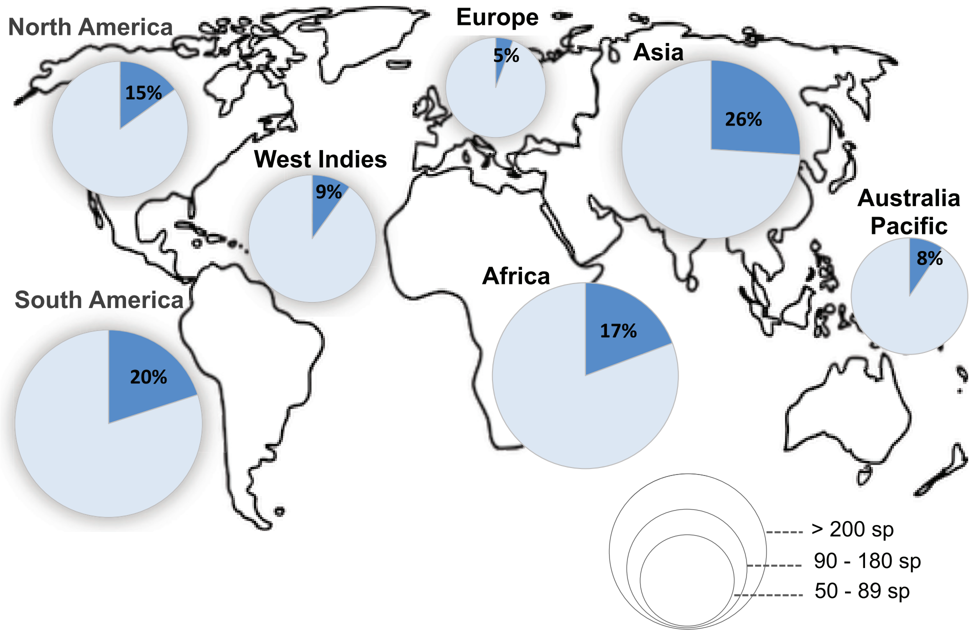

Figure 2. Continent of origin of invasive plant species on Caribbean islands. The size of the circle indicates the number of invasive species originating from each continent and the percentage in the circle represents the contribution of each continent to the total pool of invasive plant species on Caribbean islands. In this map, North America comprises Canada, USA and Mexico, and South America includes the Central and South America countries.

by species introduced for ornamental reasons. Our data showed that ornamental introductions have been increasing steeply since 1850 and remain at high levels (Fig. 4c). For the continent of origin, we did not detect a real sequence of introductions from one continent or another. Species introduced from Asia, America, and Africa have been gradually increasing since 1880 while species introduced from the remaining regions have nearly ceased since the mid-20th century (Fig. 4d). We assume any effect of local collecting bias would be minimal and not affect general outcomes as our data have broad spatial (18 islands) and temporal (>200 yrs) coverage.

For the different interaction matrices evaluated, we found significant differences for the association between continent of origin and reason for introduction (χ^2=134.7, df=25, p<0.0001, Fig. 5). Our combined results showed that more species than expected were ornamentals introduced from Asia and America, and more species than expected were introduced from Africa to be cultivated as forage. We also detected significant differences for the interaction between reason for introduction and habitat invaded (χ^2=28.2, df=15, p=0.02, Fig. 6), with more habitats invaded by species introduced as ornamentals than for any other purpose. For the other interaction matrices analyzed we found no significant associations (p>0.05 in all cases, Suppl. material 1: Figs S4, S5).

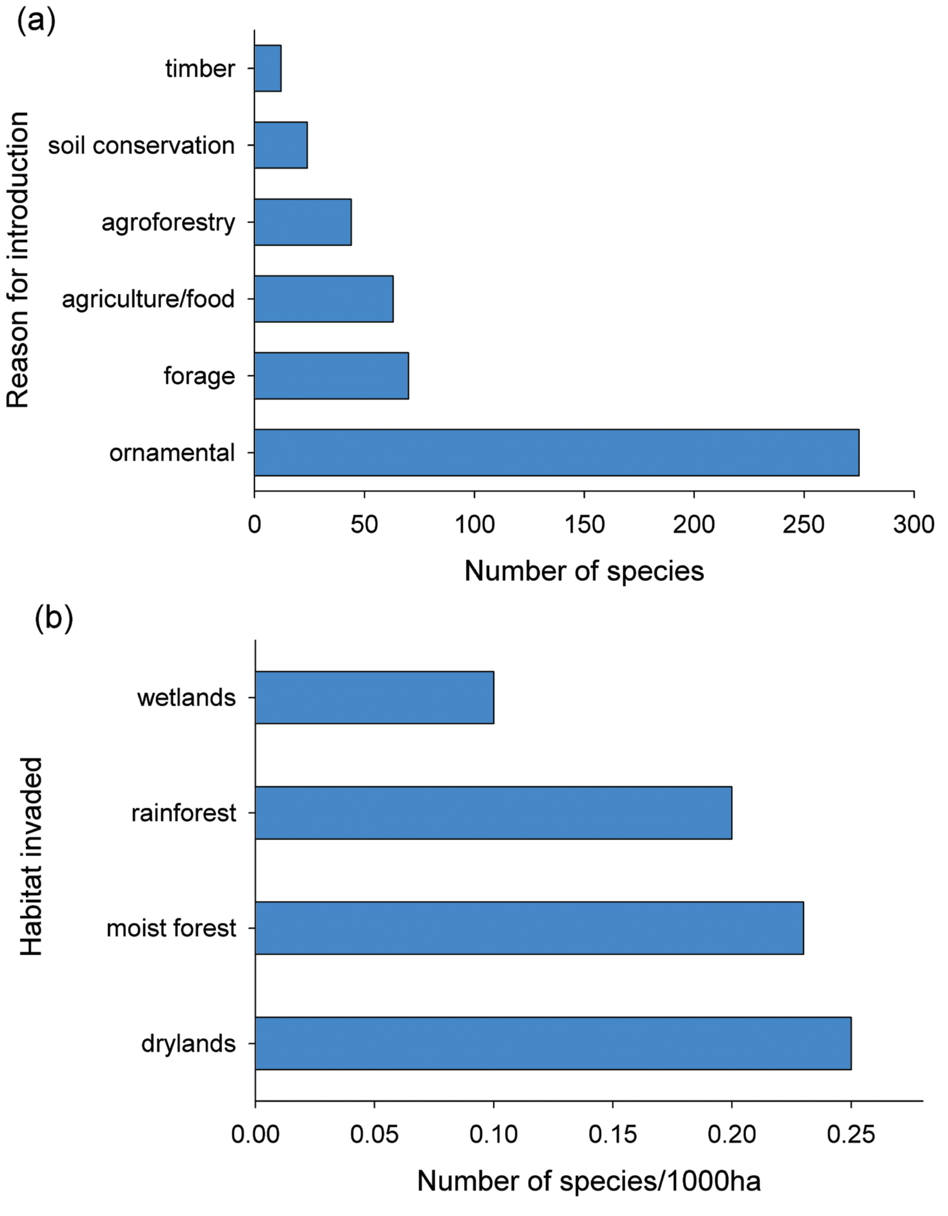

Figure 3. Number of invasive plant species on Caribbean islands considering **a** the reason of introduction and **b** the habitat types that they are invaded normalized by the total area cover by each habitat type.

Discussion

By analyzing the reason of introduction and the geographical origin of invasive species in the Caribbean, we show that while many species were unintentional introductions or deliberately introduced for practical reasons related to land management,

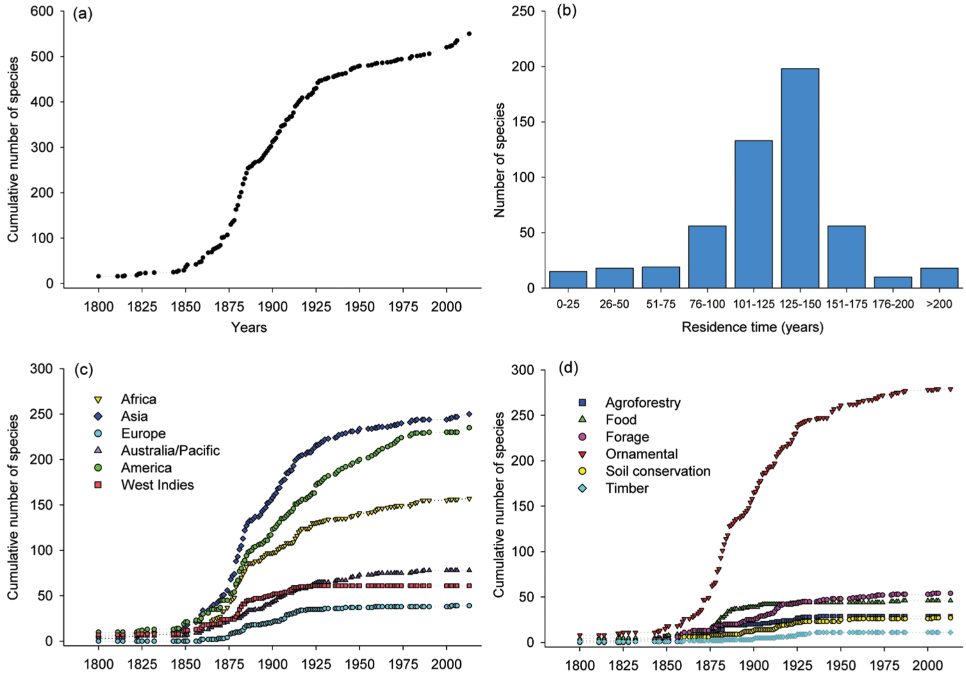

Figure 4. Temporal patterns of introduction of invasive alien species on Caribbean islands considering **a** the cumulative number of species that have become invasive plotted again the year of introduction **b** minimum residence time (invasive species are grouped by the number of years that they have been present on Caribbean islands) **c** cumulative number of species origination from each continent and **d** cumulative number of species introduced for different purposes.

food and forest products, most plant invaders in this region are species that were intentionally introduced for esthetic purposes as ornamentals. Indeed, we found that ornamental introductions have been leading the cumulative number of invasive species in the Caribbean over the last 200 years. Our results also showed that invasive species largely came from tropical and subtropical regions of Asia, South America, and Africa. The findings of this study highlight the role of introduction history attributes to explain invasion patterns and show that ornamental trade is the primary activity that has been facilitating the introduction and dissemination of invasive alien species in the region (see below).

Patterns in taxonomy and geographical origin

The taxonomic composition of the invasive flora in the Caribbean is quite diverse, but it is dominated by species belonging to large species-rich families such as Fabaceae, Poaceae, and Asteraceae, which as expected, are also highly diverse families across tropical regions (Stevens 2017). This result can be evaluated from multiple perspectives. One possibility could be that this outcome simply reflects a numeric response. These three plant families

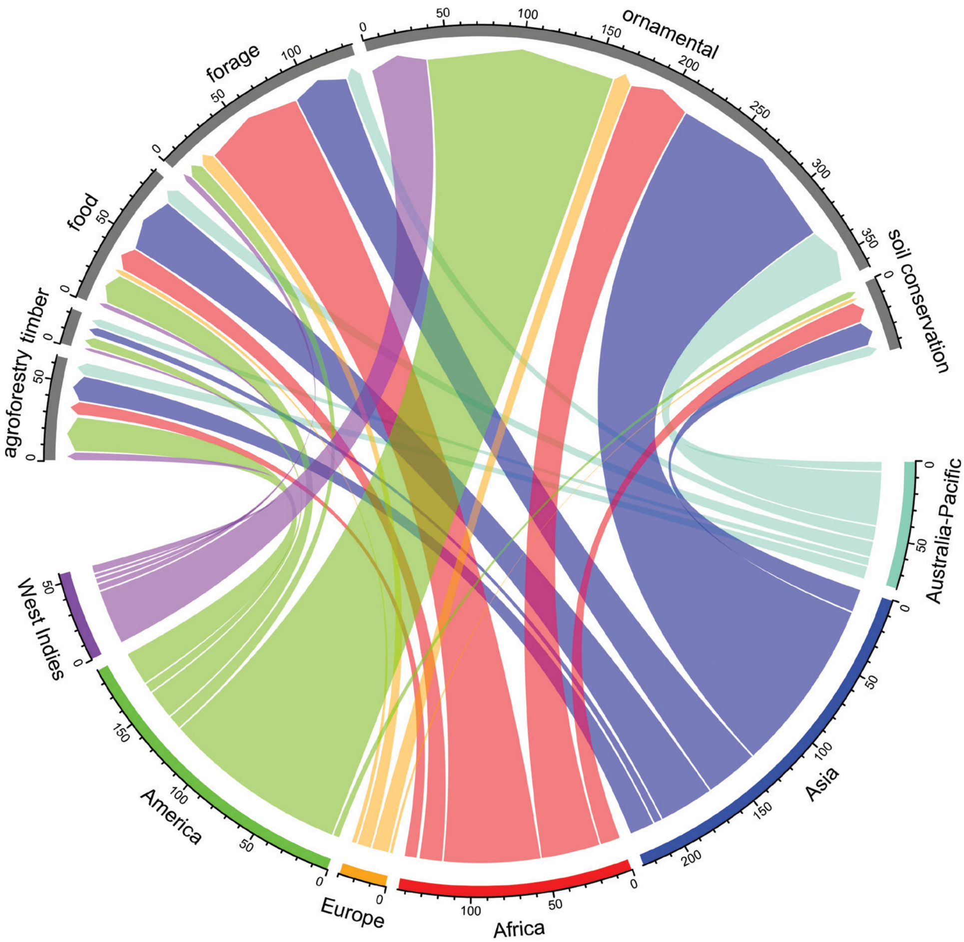

Figure 5. Flows of invasive species between continent of origin and reason of introduction. This chord diagram shows the number of invasive alien species received on Caribbean islands from each continent by the different reasons of introduction. Colored outer sections indicate the number of species originating from each continent and the width of a chord represents the number of species that have been introduced for each different purpose.

are known for contributing disproportionately most to the global naturalized alien flora (Pyšek et al. 2017). However, a recent study has shown that across angiosperm plant families naturalization success is positively associated with their evolutionary history, implying that for families with high diversification rates and large geographic ranges the likelihood of becoming naturalized increases (Lenzner et al. 2020). Another possibility could be related to specific traits of members of these families that may result in higher adaptation to the new habitats (Pyšek and Richardson 2008; Kueffer et al. 2013; Otto 2018). For example, it is well known that species in the Poaceae and Asteraceae are well adapted to highly disturbed and ruderal environments, a life-history strategy known to promote the naturalization of alien plants (Guo et al. 2018). Similarly, members of the

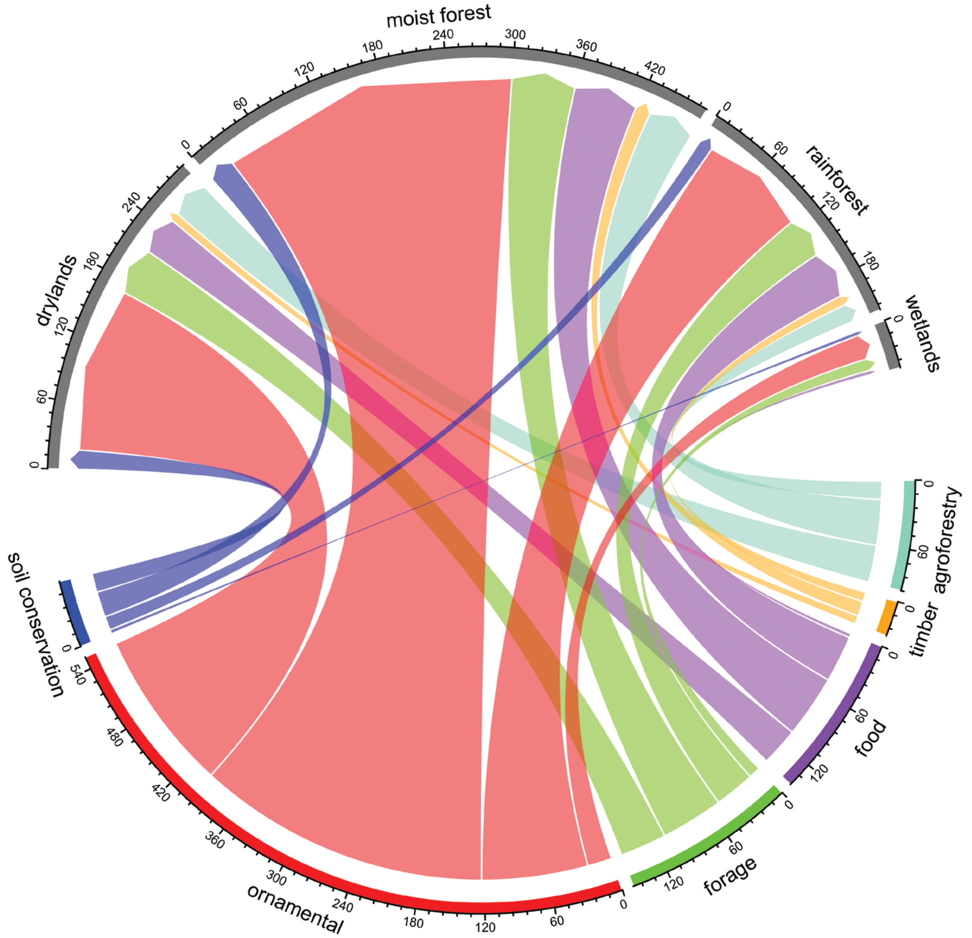

Figure 6. Flows of invasive species between reason of introduction and habitat type invaded. This chord diagram shows the number of invasive alien species established in each habitat type resulting from each reason for introduction. Colored outer sections indicate the number of species introduced for each purpose and the width of a chord represents the number of invasive species that are invading each habitat type.

Fabaceae share the ability to fix atmospheric nitrogen, a trait that give them a competitive advantage in coping with anthropogenic habitats and nutrient-poor soils in their introduced range (Sprent 2009; Le Maitre et al. 2011; Rascher et al. 2011).

As expected, we found that continents with large tropical regions (Asia, South America, and Africa) dominate the geographic origin of invasive species in the Caribbean. This is consistent with previous studies showing that climatic similarity with the native region is an essential requirement for invasion success as such species are more likely to be pre-adapted to their new environments (Thuiller et al. 2005; Hayes and Barry 2008; Bellard et al. 2016; Cabra-Rivas et al. 2016). Another plausible explanation could be related to the apparent "high naturalization potential" intrinsic of species native to geographical regions which share particular evolutionary histories that make them highly competitive and thus capable of invading elsewhere (Fridley and Sax 2014). For example, it has been recently shown that species native to Asia are overrepresented as donors of naturalized plants worldwide and that they are most likely to become naturalized in other continents probably due to a “higher innate naturalization potential” of Asian species compared to plants from other regions (van Kluenen et al. 2020). Independently of the reasons explaining why species native to Asia, South America, and Africa are overrepresented on Caribbean islands, the relevance of this result is that plants introduced from these three continents should be a priority concern given that they appear in general capable of more rapid shift to invasiveness.

Ornamentals lead the way

Our results revealed that historical factors related to the type, intensity, and frequency of introductions of alien species in the Caribbean are influencing the composition of the regional invasive floras. While all the reasons for introduction that we analyzed are contributing species to the pool of invasive species, our data clearly show that introduction for ornamental use is the major contributor of invaders. This is a pattern that have been previously reported for other regions (Reichard and White 2001; Dehnen-Schmutz et al. 2007; Lambdon et al. 2008; Zenni 2014) and a recent global comparison of the frequency of invasive plant species also showed that most invaders have originated from ornamental trade (Hulme et al. 2018). For the Caribbean region we also found that the cumulative number of invasive species has been steadily increasing during the last 200 years, but since 1850 this trend has been notably led by species introduced as ornamentals. This pattern could be explained by the increasing popularity of gardening and landscaping, both of which are associated with tourist development and the expansion of urban areas (see below). Such human activities create a demand for ornamentals and amenity species (Lambdon et al. 2008; Waugh 2009; van Kleunen et al. 2018). These results underscore the assertion that alien ornamentals are one of the major threats to the conservation of native floras and pose a significant environmental concern for the Caribbean region.

Plants commercialized as ornamentals are not randomly selected, and some of the biological traits that are desirable for the ornamental trade, such as rapid growth and establishment, production of large numbers of flowers, fruits and seeds, and easy propagation, are also traits that promote invasion (van Kleunen et al. 2018). Moreover, ornamentals have more opportunities for introduction and spread than other plant species as they are actively propagated and repeatedly planted generating high propagule pressure (Lockwood et al. 2009; Hulme et al. 2018; Gou et al. 2019; van Kleunen et al. 2020). Propagule pressure has been recognized as one of the main drivers of invasion success, and locations receiving heavy influx of propagules often have higher establishment rates and are more invaded than areas with fewer introductions (Cassey et al. 2018; Lenzner et al. 2020). For the Caribbean, long residence times and high propagule pressure appear to be key elements for the success achieved by alien ornamentals.

The overrepresentation of Asian and American ornamentals detected in the invasive flora of the Caribbean could be explained by the globalization of horticultural trade and the intercontinental fluxes of alien ornamental plants. The United States, the major provider of nursery products for the Caribbean region (Waugh 2009), has a nursery trade dominated by species imported from Asia and tropical America (especially Mexico, Central America and Brazil; Bradley et al. 2012), indicating how the geographical origin of ornamental nursery stocks in the US is influencing sources of naturalized and invasive plant species in recipient regions (Bradley et al. 2012; Hulme et al. 2018; van Kleunen et al. 2018). The overrepresentation of African forage species has a very different origin and could be explained by the establishment of human-maintained pasturelands to support livestock activity. Across tropical regions, the conversion of native forests to pasturelands has resulted in landscapes dominated by alien grasses which has had intense ecological and climatic consequences (D'Antonio and Vitousek 1992; Williams and Baruch 2000). The Caribbean region is not the exception. Agricultural experiment stations across the region worked together to improve primary productivity and nutritional quality of forage species. To this end, they introduced alien species, many from Africa which were presumably more resistant to grazing pressure (Sterns 1992; Fernandez-Prieto 2013).

Implications for management and conservation

Caribbean islands have undergone profound social and economic changes transitioning from an economy based largely on agriculture and exploitation of natural resources (e.g., logging and mining) to one more based on tourist development. This conversion has led to the removal and alteration of much of the original vegetation and has contributed to major changes on terrestrial habitats and a significant reduction in biodiversity (Dixon et al. 2001). While the abandonment of agriculture has led to forest regeneration, the increasing demand for tourism facilities and the expansion of commercial and residential development is contributing to the degradation and reduction of natural habitats and thus facilitating the introduction and establishment of potentially invasive species (Parés-Ramos et al. 2008; Timms et al. 2013; Walters 2016; Rojas-Sandoval et al. 2020). Due to the fragile conservation status of Caribbean natural habitats, the fact that invasive species are occurring in all the habitat types analyzed in this study represents an additional level of vulnerability. Moreover, the socio-political complexity of this region (that comprises independent nations as well as British, Dutch, French and U.S. overseas territories), with many competing units and scales of governance, hinders the implementation of effective actions to address the conservation issue of invasive species (Vaas et al. 2017).

Currently, the tourism industry (including transportation, lodging, and amenities) is the dominant economic force in the Caribbean (Palmer 2009) and is the major consumer of ornamental horticulture products throughout the region (Waugh 2009). Tourism facilities (e.g., resorts and vacation homes) often have large green areas and thus consume large quantities of gardening products, including live plants (Waugh 2009). Similarly, the current expansion of urban areas is also facilitating the naturalization and invasion of alien plants in the Caribbean region. For example, about two-thirds of the ornamentals cultivated in domestic gardens in urban areas in Puerto Rico are introduced alien species and, in agreement with our results, most of them are also alien ornamentals native to Asia and tropical America (Vila-Ruiz et al. 2014; Rojas-Sandoval and Acevedo-Rodríguez 2015; Melendez-Ackerman and Rojas-Sandoval 2021). These results are relevant because gardens often act as "reservoirs" of potential invasive species since many ornamentals have high naturalization success and thus represent a greater risk of escaping and becoming invasive (Guo et al. 2019).

Conclusions

Caribbean forests are among the most heavily utilized, disturbed, and least preserved ecosystems across the tropics. This study provides evidence that historical factors related to the type, intensity, and frequency of human-mediated introductions of alien species have been influencing the composition of invasive plant species in the Caribbean during the last 200 years. These factors are important for understanding current patterns of invasions, but they are also crucial for planning adequate management actions for the control and prevention of current and future invasions. Our results clearly identified the drivers and sources that contribute most to the pool of invasive species in the Caribbean. We also showed that introduced ornamentals are successfully invading all major habitats, exacerbating conservation issues and threatening the diverse native flora of the Caribbean. Therefore, effective biosecurity actions to regulate ornamental trade and importations from Asia, America and Africa regions should become a management priority. Due to the complexity of the problem, reducing intentional introductions of alien species through the ornamental pathway will require the cooperation of the tourism industry, landscapers, garden owners, and nursery vendors. Additionally, Caribbean states should strengthen their biosecurity protocols and implement and enforce effective management strategies to address the problem of invasive species.

Data availability statement

The databases that we used are all publicly available and the references for all the sources consulted are provided in the Supplementary Materials. The data used in this study were deposited in the FigShare Digital Repository https://figshare.com/s/36971893d1fdf9b43a77

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Supplementary material 1

Supplementary materials

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Data type: tables and figures

Explanation note: **Appendix S1.** List of sources consulted to compile the initial list of invasive alien plant species on Caribbean islands. **Appendix S2.** List of resources consulted to complement the dataset of invasive alien plant species on Caribbean Islands with information on taxonomic family, continent of origin, life-form, habit, reason of introduction, and habitats invaded. **Figure S1.** Map of the Caribbean islands included in this study showing the number of invasive alien plant species reported for each island. **Figure S2.** Continent of origin of invasive plant species on Caribbean islands showing the percentage of species with tropical and temperate origin. **Figure S3.** Number of invasive alien species occurring in each habitat type across Caribbean islands. **Figure S4.** Flows of invasive plant species among continent of origin and the habitat types invaded. **Figure S5.** Flows of invasive plant species among life-forms and the habitat types invaded.

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