Biol Invasions (2025) 27:102
https://doi.org/10.1007/s10530-025-03559-8

ALIEN FLORAS AND FAUNAS

The introduced and invasive flora of Bermuda

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Received: 22 August 2024 / Accepted: 21 February 2025 / Published online: 14 March 2025

Abstract Screening incoming plants for potentially invasive species is key to preventing new invasions on islands. Doing this effectively requires knowledge of plants already present and invasive in the country, and which pathways, donor regions and plant families have previously contributed the most invasives. As Bermuda previously lacked such a dataset, we compiled a comprehensive inventory of the native, introduced, casual, naturalized and invasive plants from historic and modern literature, herbarium records and garden centre visits. The inventory contains updated taxonomy, pathways and dates of introduction, native geographic range, life form, and naturalization status for 1587 vascular plants from 162 families. Of these, 1424 species (89.8%) are introduced to Bermuda, while 151 (9.5%) are native. Classifying stage of invasion shows 321 species (22.5% of the introduced flora) have escaped cultivation to form casual, naturalized or invasive populations. Bermuda currently has 217 naturalized plants of which 52 are considered invasive. We define invasive species as non-native to Bermuda, reproducing in the wild and recruiting offspring at multiple sites, dispersed over long distances or large areas, or excluding other plants from habitats (Methods S1). We did not directly consider impacts in our definition of invasive species. Among the invasives 25 species (48%) are trees and shrubs, mostly of Asian origin. Ornamental horticulture was the introduction pathway for 75% of invasive plants, emphasizing the need for further collaboration with the commercial horticulture sector and private gardeners to reduce invasion risk from ornamental plants.

Keywords Checklist · Invasion stage · Introduced plants · Island flora · Alien species

Introduction

Oceanic islands are often characterised by species-poor native floras due to significant natural barriers to colonization (Sterrer et al. 2004; Weigelt et al. 2015; Moser et al. 2018). Thanks to past and present global trade and transport networks, oceanic barriers no longer protect islands from invasion because human activities remove obstacles to arrival, survival and dispersal. Today island isolation is positively associated with increased richness of introduced or naturalized plant species (Pyšek et al. 2017; Moser et al. 2018; Sánchez-Ortiz et al. 2020), and oceanic islands

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-025-03559-8.

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contain more naturalized plants than continental regions of similar size (van Kleunen et al. 2015).

The islands of the wider Caribbean region have a history of habitat clearance for agriculture and natural resource exploitation as part of complex colonial trade networks (Lefroy 1879; Kairo et al. 2003; Rojas-Sandoval and Ackerman 2021; Witt 2023). The disturbed, human-dominated ecosystems on these islands have relatively low native plant species richness and high introduced plant richness, some of which are considered invasive species (Sánchez-Ortiz et al. 2020; Rojas-Sandoval and Ackerman 2021). The challenge this poses for conservation of native biodiversity and invasive species management is further exacerbated by high human population densities, increasingly large-scale tourism developments, and the continued reliance on imported commodities, all of which serve to increase propagule and colonisation pressures (Essl et al. 2019; Witt 2023). The high transport connectivity between the Caribbean and the rest of the world means that invasive species introductions represent an ongoing threat to native biodiversity in the region.

Bermuda has a 400-year long history of habitat disturbance and natural resource exploitation due to its mid-Atlantic location between the former colonial nations of Europe and their territories in the New World (Lefroy 1879; Hemsley 1884; Sterrer et al. 2004). Due to this geography, naturalized plants and animals deposited by passing ships pre-date Bermuda's settlement (Lefroy 1877, 1879; Collett 1987; Sterrer et al. 2004; Marshall et al. 2005). Bermuda had no permanent human population prior to the arrival of the British in 1609 and establishment of a colony in 1612 (Lefroy 1877; Hemsley 1884).

Until 1942 the portions of Bermuda not cleared for buildings or agriculture were densely covered in endemic Bermuda cedar *Juniperus bermudiana* forest (Harshberger 1905; Beard 1940; Challinor and Wingate 1971). Weeds inhabited roadsides, fields, and waste ground, comprising mainly accidentally introduced forbs and grasses from Europe and North America (Reade 1883; Lefroy 1884; Britton 1918). Several ornamental species had escaped cultivation, but only a few had established in the understory of the cedar forest (Harshberger 1905; Britton 1918; Beard 1940). Today, however, Bermuda's fragmented woodlands often comprise a canopy of invasive broadleaved trees over a diverse understory of naturalized or invasive shrubs, vines, herbs/forbs and grasses (Sterrer et al. 2004; Marshall et al. 2005; Wolsak et al. 2018.)

A single catastrophic event initiated the shift to woodlands dominated by introduced plants. Between 1944 and 1955 two accidentally introduced insects attacked the Bermuda cedar, killing 90% of the trees in the country within 11 years (Groves 1955). This event, known locally as the Cedar Blight, resulted in the complete loss of tree cover, devastation of local habitats, exposed homes and farmlands to wind and sea spray, and denuded the landscape as tourism was becoming a mainstay of the Bermudian economy (Groves 1955; Challinor and Wingate 1971; Sterrer et al. 2004). To replace the lost vegetation, a national reforestation programme began in 1949 (Groves 1955). Salt-tolerant, fast growing trees and shrubs were imported to provide crucial windbreaks (Challinor and Wingate 1971; Sterrer et al. 2004) and ornamental species from all over the world were imported to beautify the landscape (Whitney 1955; Groves 1955; Challinor and Wingate 1971; Sterrer et al. 2004).

The consequence of the Cedar Blight was extreme ecosystem disturbance resulting in an unforested landscape primed for invasion. The rapid importation of a large volume of plant material, release of these plants directly onto the landscape and selection of plants with characteristics suited to the environmental conditions set the stage for nation-wide plant invasions. The appearance of the country, along with the species composition of its plant communities changed completely in the half-century following the reforestation programme (Sterrer et al 2004; Wolsak et al 2018).

Today invasive species management and the prevention of new invasions are Government priorities, as highlighted by the recent passage of the Invasive Alien Species Act 2021 (Government of Bermuda 2021). Better tools are needed to improve on-island invasive species management, and to more effectively assess invasion risk from incoming plants by identifying taxa, regions and pathways most likely to contribute new invasive species. An inventory of plants already present in Bermuda and an updated list of invasive and naturalized species is needed to facilitate better management. Bermuda's biodiversity has been well inventoried (Sterrer et al. 2004), but the information is not well reported or accessible.

In this study we compiled a comprehensive checklist of plant species reported from the Bermudian literature and other sources. Using this inventory, we then aimed to: i) update the taxonomy and examine which families and genera are most represented in the introduced flora, ii) categorise the stage in the invasion process reached by each species based on barriers overcome (Richardson et al. 2000; Blackburn et al. 2011), iii) examine the life cycles and life forms of the total introduced flora and those which have escaped cultivation, iv) explore the introduction pathways and whether introductions were intentional, and v) report the native origins of the introduced flora and Bermuda's invasive plants.

Methods

Study area

Bermuda is an oceanic archipelago in the northwestern Atlantic Ocean, located at 32.4° N and 064.8° W, and 1052 km east-southeast of Cape Hatteras, North Carolina; the closest point of continental land. The warming influence of the Gulf Stream gives the islands a frost-free, subtropical climate, despite their temperate latitude. Mean monthly air temperatures range from 18.0 in February, to 27.6 °C in August (Currie 2018). Bermuda receives 1490 mm of rainfall annually, spread almost evenly throughout the year (Currie 2012). The prevailing westerlies bring weather fronts and storms from the east coast of North America across the islands for most of the year. In late summer and autumn, periodic tropical cyclones arrive from the south or southeast. Bermuda was struck by damaging tropical storms or hurricanes about every 6 or 7 years from 1609 until the early twenty-first century, however their frequency has increased in recent years (Bermuda Weather Service 2021).

The islands form a J-shaped archipelago of 53.7 km^2, with a maximum elevation of 78 m above sea level (Copeland and Shailer 2011). Eight main islands are connected by bridges and a causeway, allowing free movement of people, plants, and animals along the length of the archipelago. An additional 193 islands and rocky islets are scattered in the bays and harbours, 56 of which are inhabited or were at one time (Copeland and Shailer 2011).

Bermuda's resident population of 63,779 (Department of Statistics 2018), gives it a population density of 1188 per km^2—one of the highest in the world. Additionally, 808,242 tourists visited Bermuda in 2019 (Bermuda Tourism Authority 2020). This density puts considerable pressure on undeveloped land, natural resources and biodiversity. The whole country is considered urban or suburban in character.

Compilation of plant names

Nathaniel Britton's *Flora of Bermuda* (1918) is considered the most comprehensive examination of Bermuda's plants and forms the basis of our dataset. We gathered 1304 plant names from this text. Other comprehensive nineteenth century publications were consulted to augment Britton's list, primarily the *Botany of the Voyage of the Challenger Expeditions* (Hemsley 1884*), Plants of the Bermudas, or Somer's Islands* (Reade 1883), and the *Botany of Bermuda* (Lefroy 1884). Other historic texts were consulted (Tables S3& 4), but many directly copied from these four lists and added little information.

After the mid-twentieth century, the literature becomes more focused on ornamental plants rather than the whole flora. Of particular note are the books published by the Garden Club of Bermuda (Whitney 1955; Wardman 1971; Ogden 2002). Unpublished checklists were available for some taxonomic groups. These were usually compiled by amateur enthusiasts or for specific projects, with the palm list of Ogden (2015) being the most comprehensive. Names of native plants were gathered from Britton's list (Britton 1918). A list of species considered invasive was compiled from GRIIS (Copeland et al. 2020) and ten other publications (Table S3).

The herbarium of the Bermuda Natural History Museum at the Bermuda Aquarium, Museum and Zoo (BAMZ) was consulted between August 2020 and January 2023. Plant species considered introduced to Bermuda are separated from native species in this collection. The introduced plants collection and the grass collection were examined and photographed in December 2022.

Two of the largest garden centres on the island were visited in December 2022 to assess the species that are presently available for sale to the public as seeds, seedlings or established plants. The garden centres contributed twenty-nine plant names that are

not found in the literature or any other sources. Some of these new taxa are artificial hybrids.

During list compilation, Plants of the World Online (POWO 2023) was used to align nineteenth century taxonomy with currently accepted names for families, genera and species. Older names found to be synonyms of other names in our list were combined into one record. All synonyms and alternate spellings, including misspellings found in the Bermudian literature were retained to allow searching and to maintain connections with the original record. Once the final list of plant species had been compiled, the names were standardized in R using the rWCVP package (Brown et al. 2023; R Core Team 2023), which added accepted binomial, family and author fields to the dataset, according to the World Checklist of Vascular Plants (Govaerts 2023).

Two names are not recognised as synonyms by POWO, and we could not determine from other sources which accepted names they refer to; therefore, these were removed from the list before it was used for analysis. Thirty-one names given by earlier authors that Britton (1918) has treated as erroneous, doubtful or a misidentification were also removed. Thirty-six names found in the historic literature were removed because the author states that the plant did not establish, and it is not recorded in recent sources or known from the island now. Some additional names are valid but do not fit the project aims – for example six seagrasses were removed so the dataset represents terrestrial flowering plants, ferns and fern allies. Non-vascular plants were excluded.

Introduction status classification

All plants were assigned to one of seven introduction classes based on their native or introduced status (Table 1; Tables S3 and S4). Native species were placed into one of two classes, with those only found in Bermuda classed as 'endemic' and those with wider distribution termed 'native'. Introduced species were classified on their success in escaping cultivation and overcoming barriers to survival, reproduction and dispersal. A classification framework (Methods S1) was created based on the concept that species must overcome barriers to move through the stages of invasion (Richardson et al. 2000; Blackburn et al. 2011). Following the frameworks of Richardson et al. (2000) and Blackburn et al. (2011), we used dispersal away from human habitation, and evidence of successful reproduction and recruitment to characterise most species using the first nine questions of the framework (Methods S1). To account for species which may not be widely dispersed but should be considered invasive as they dominate particular habitats and potentially exclude other plants, we included a tenth question in the framework (Methods S1). Answering question 10 in the affirmative is not a requirement for inclusion in the invasive class, and only added nine species to the invasive category. We do acknowledge that field assessments are needed and simply observing dominance of a habitat by one species and a lack of other plants does not equate to plant exclusion by an invasive species and may lead to erroneous conclusions. Classifications were based on literature and 15 years of plant observations by the first

Table 1 Species in each introduction class and component percentages of the Bermudian flora

Introduction status	Species Count	% of total Bermuda flora	% of native flora	% of introduced flora
Endemic	11	0.7	7.3	–
Native	140	8.8	92.7	–
Total Native Species	151	9.5	100	–
Introduced (not escaped)	1103	69.5	–	77.4
Casual	104	6.6	–	7.3
Naturalized	165	10.4	–	11.6
Invasive	52	3.3	–	3.7
Total Introduced Species	1424	89.8	–	100
Cryptogenic	12	0.7	–	–
Total Bermuda flora	1587	100	–	–

author while employed by the Bermuda Department of Environment and Natural Resources. Any species which could not be classified due to conflicting accounts of its native or introduced status were classified as cryptogenic species of undetermined origin (Table S3). The resulting seven status classes were: cryptogenic, endemic, native, introduced, casual, naturalized, and invasive.

Life cycle and life form

We obtained life form data from the Global Inventory of Floras and Traits (GIFT: Weigelt et al. 2020), using the trait 1.2.2 'Growth Form', for 1432 Bermudian species and the trait 2.1.1 'Lifecycle', for 1455 Bermudian species. We identified the modal life form and life cycle category for each species and used this single category thereafter. We also downloaded life form and life cycle descriptions from the World Checklist of Vascular Plants (WCVP: Govaerts 2023) for 1462 species. Life form and life cycle were then determined by cross referencing GIFT and WCVP data. For 506 species there was good agreement between GIFT and WCVP resulting in a life form based on both sources. Life forms for an additional 642 species appeared just in GIFT, and 213 were determined just from WCVP. For species that did not appear in either trait database, we determined their life form from Britton (1918) or various websites (Tables S3 and S4). For 72 species no information was available, so a life form was assigned from field observations or following an internet image search.

For 137 species the life form was assigned based on the family. All epiphytic and ground dwelling species in the family Bromeliaceae were assigned the life form 'bromeliad'. The life form 'graminoid' was given to grasses, sedges and rushes in the families Typhaceae, Poaceae, Cyperaceae and Juncaceae. All species in Arecaceae were given the life form 'palm'. The life form 'fern' was assigned to ferns and fern allies in the families Aspleniaceae, Pteridaceae, Polypodiaceae, Osmundaceae, Dennstaedtiaceae and Psilotaceae. The life form 'cycad' was assigned to all members of Cycadaceae and Zamiaceae. The eleven possible categories for life form were: aquatic, bromeliad, cycad, fern, forb, graminoid, palm, shrub, succulent, tree, and vine/climber.

A life cycle for 480 species was determined from agreement between GIFT and WCVP. Life cycle for an additional 919 species were determined just from GIFT, and 71 were determined just from WCVP, while those that did not appear in either database were determine from Britton (1918) or various websites (Tables S3 and S4). For 86 species no information was available, so a life cycle remained undetermined. The six possible data values for life cycle are: annual, annual or biennial, biennial, biennial or perennial, annual or perennial and perennial.

Dates and pathways of introduction

All casual, naturalized, or invasive species were assigned to an introduction pathway category and subcategory from the Convention on Biological Diversity's categorization of pathways for the introduction of invasive species (CBD 2014; Table S5). Pathways were mostly determined from the literature, otherwise the most likely scenario was assigned based on previous observations and communication with Bermudian habitat managers. We added a category with value 0 named 'unknown' if the pathway could not be determined from the literature, communication with experts or our observations. All non-escaped introduced species were assigned the value 'cultivated' for pathway (Fig. 4b) and given an appropriate sub pathway (Fig. 4c). Following categorization of the pathway, each species was also assigned one of six categories under the variable called 'intentional': accidental, probably accidental, intentional, probably intentional, unaided, or unknown (Table S5).

For early intentional introductions, we were often able to find an introduction year, but for recent introductions this information is often not reported (Tables S3 & S5). For accidental introductions, we could report the year of earliest mention in the literature. In total introduction dates are reported for 285 species and inferred from first mentions in literature or first appearance in herbaria for 1142 species. Species accumulation counts (Fig. 4) assume that following first record the species continues to persist in Bermuda and is therefore added to the cumulative number over time. This of course is not always true, as species are introduced multiple times and some fail to survive one or all introduction attempts.

Geographic origin

We obtained the geographic origins of Bermuda's plants using the World Checklist of Vascular Plants (WCVP: Govaerts 2023), accessed through the R package 'rWCVP' (Brown et al. 2023). Species origins at the scale of botanical continents (corresponding to Taxonomic Database Working Group—TDWG Level 1, Brummitt 2001), were extracted (August 2023). We re-coded the data so that '1' represents the native range and '0' the introduced range (Tables S3 and S4).

Results

The total Bermudian flora

The inventory of Bermuda's flora contains 1883 plant names. We removed 296 names from the dataset used for analysis, including 250 taxa with doubtful presence on the island. This left 1587 species which reflects the current state of the Bermudian flora. These 1587 plant species represent 162 plant families. The most species-rich families are Asteraceae (108 species), Fabaceae (100), Poaceae (90), Arecaceae (69) and Lamiaceae (55) (Fig. 1). The 1587 species come from 886 genera, with 570 genera represented by only one species. The most common genus is *Euphorbia* with 23 species, followed by *Ficus* (15 spp.), *Agave* (12 spp.) and *Ipomoea* (12 spp.).

Introduction status

Of Bermuda's 1587 plant species, 1424 (89.8%) are introduced non-natives, while 151 (9.5%) are native and 12 (0.7%) are cryptogenic species of unknown origin (Table 1). Species were classified as cryptogenic when conflicting records of its introduced or native status were found in the literature, with no consensus between authors (Table S3). The native flora is composed of 11 species which are considered island endemics, and 140 native species shared with North and South America and the Caribbean (Table S4).

The majority (77.4%) of the 1424 plants introduced to Bermuda have not escaped cultivation, and remain present only in gardens, farmlands and landscaped situations. These 1103 species were classified as 'introduced' (Table S3). Additionally, 104 species are considered casual, because they have escaped cultivation but do not appear to reproduce effectively, so there is little or no recruitment, and their populations are not self-sustaining. There are 165 species which have naturalized in Bermuda to form self-sustaining populations outside of cultivation. A further 52 species were classified as invasive representing 3.7% of the introduced plants and 3.3% of Bermuda's total flora (Table 2). These invasive species are introduced non-natives which have escaped cultivation and have formed self-sustaining and actively spreading populations (Methods S1; Table S3). They have overcome all barriers to reproduction, recruitment and dispersal (Richardson et al. 2000; Blackburn et al. 2011) and are found at multiple sites often in several habitats (Sterrer et al. 2004; Marshall et al. 2005; Wolsak et al. 2018).

Of the 1424 plants introduced to Bermuda, 321 species (22.5% of the introduced flora) have escaped cultivation and are considered casual, naturalized, or invasive. These will be referred to collectively as the 'escaped species'.

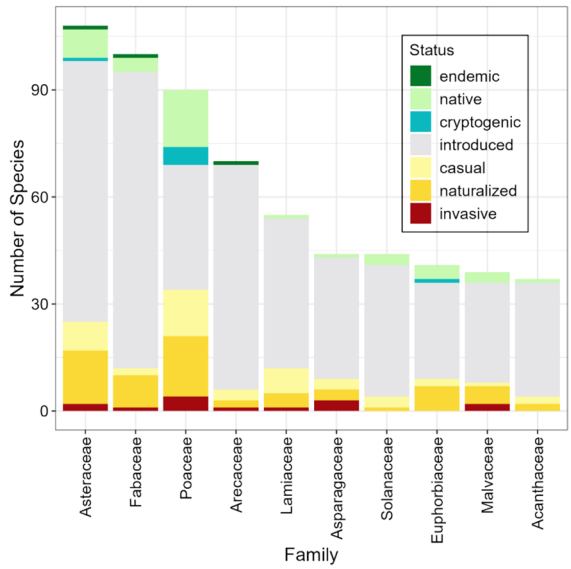

Fig. 1 The top ten most species-rich families in the Bermudian flora

Table 2 Bermuda's 52 invasive plant species as assessed by our framework

	Species	Local Name	Earliest Record	Invasive Alien Species Act 2021
1	*Abutilon grandifolium*	Hairy Mallow	2019	Not listed
2	*Abutilon theophrasti*	Indian Mallow, Velvetleaf	1909	Schedule 2—Restricted 'Category A' Invasive Species
3	*Ageratina riparia*	Mistflower, Small White Eupatorium	1911	Not listed
4	*Ardisia elliptica*	Shoebutton Ardisia	1873	Schedule 2—Restricted 'Category A' Invasive Species- whole genus
5	*Arundo donax*	Cow Cane, Giant Reed	1881	Schedule 2—Restricted 'Category A' Invasive Species
6	*Asparagus densiflorus*	Asparagus Fern	1914	Schedule 2—Restricted 'Category A' Invasive Species- whole genus
7	*Asparagus falcatus*	Longleaf Asparagus Fern	1933	Schedule 2—Restricted 'Category A' Invasive Species- whole genus
8	*Asparagus setaceus*	Wedding Fern	1912	Schedule 2—Restricted 'Category A' Invasive Species- whole genus
9	*Buddleja madagascariensis*	Madagascar Buddleia, Snuff Plant	1873	Schedule 2—Restricted 'Category A' Invasive Species
10	*Cardiospermum grandiflorum*	Large Flowered Balloon Vine	1913	Not listed
11	*Cardiospermum halicacabum*	Large Fruited Balloon Vine	1883	Schedule 2—Restricted 'Category A' Invasive Species
12	*Casuarina equisetifolia*	Australian Whistling Pine	1881	Schedule 2—Restricted 'Category A' Invasive Species- whole genus
13	*Cenchrus purpureus*	Napier Grass, Elephant Grass	1918	Schedule 3—Restricted 'Category B' Invasive Species
14	*Cenchrus setaceus*	Fountain Grass	1918	Schedule 2—Restricted 'Category A' Invasive Species
15	*Citharexylum spinosum*	Fiddlewood	1830	Not listed
16	*Clematis flammula*	Sweet Clematis	1881	Not listed
17	*Clematis terniflora*	Autumn Clematis	2011	Not listed
18	*Clematis vitalba*	Traveller's Joy	1971	Not listed
19	*Cyrtomium falcatum*	Holly Fern	1971	Schedule 2—Restricted 'Category A' Invasive Species
20	*Elaeagnus pungens*	Thorny Elaeagnus, Thorny Olive	1971	Schedule 2—Restricted 'Category A' Invasive Species
21	*Epipremnum aureum*	Golden Pothos, Elephant's Ear	1933	Schedule 2—Restricted 'Category A' Invasive Species (as *E. pinnatum*)
22	*Eriobotrya japonica*	Loquat	1850	Not listed
23	*Eugenia uniflora*	Surinam Cherry	1840	Not listed
24	*Ficus microcarpa*	Indian Laurel	1933	Schedule 2—Restricted 'Category A' Invasive Species
25	*Heptapleurum actinophyllum*	Queensland Umbrella Tree	1961	Schedule 2—Restricted 'Category A' Invasive Species (as *Schefflera actinophylla*)
26	*Heptapleurum arboricola*	Dwarf Umbrella Plant	2016	Schedule 2—Restricted 'Category A' Invasive Species
27	*Jasminum simplicifolium subsp. australiense*	Simple-leaved Jasmine, Australian Wax Jasmine	1840	Not listed
28	*Leucaena leucocephala*	Jumbie Bean	1863	Schedule 2—Restricted 'Category A' Invasive Species
29	*Livistona chinensis*	Chinese Fan Palm	1877	Schedule 2—Restricted 'Category A' Invasive Species

Table 2 (continued)

	Species	Local Name	Earliest Record	Invasive Alien Species Act 2021
30	*Lophospermum erubescens*	Climbing Gloxinia	1881	Not listed
31	*Macrothelypteris torresiana*	Mariana Maiden Fern	1958	Not listed
32	*Megathyrsus maximus*	Guinea Grass	1883	Not listed
33	*Momordica charantia*	Bitter Melon	2008	Not listed
34	*Murraya paniculata*	Mock Orange	1881	Not listed
35	*Nephrolepis cordifolia*	Tuberous Sword Fern, Fishbone Fern	1900	Not listed
36	*Noronhia emarginata*	Madagascar Olive	2003	Not listed
37	*Phymatosorus scolopendria*	Wart Fern, Creeping Fern	1971	Schedule 2—Restricted 'Category A' Invasive Species
38	*Pimenta dioica*	Allspice, Spice Tree	1881	Not listed
39	*Pittosporum tobira*	Japanese Pittosporum	1914	Not listed
40	*Pittosporum viridiflorum*	Cape Pittosporum	1971	Not listed
41	*Podocarpus macrophyllus*	Japanese Yew	1913	Not listed
42	*Pontederia crassipes*	Water Hyacinth	1905	Schedule 3—Restricted 'Category B' Invasive Species as *Eichhornia crassipes*
43	*Psidium guajava*	Guava	1671	Not listed
44	*Pteris longifolia*	Long-leaved Brake	1875	Not listed
45	*Rivina humilis*	Rouge Plant, Rougeberry	1914	Not listed
46	*Salvinia auriculata*	Water Fern	1903	Not listed
47	*Scaevola taccada*	Beach Naupaka	1998	Schedule 2—Restricted 'Category A' Invasive Species
48	*Schinus terebinthifolia*	Brazil Pepper	1933	Schedule 2—Restricted 'Category A' Invasive Species
49	*Sphagneticola trilobata*	Seaside Creeping Daisy	1881	Schedule 2—Restricted 'Category A' Invasive Species
50	*Tabebuia pallida*	White Cedar	1860	Not listed
51	*Trichostigma octandrum*	Hoop Vine	2007	Schedule 2—Restricted 'Category A' Invasive Species
52	*Volkameria glabra*	Stinky Clerodendron	1918	Schedule 2—Restricted 'Category A' Invasive Species

Introduced families and genera

The introduced flora of Bermuda contains 1424 species from 152 families, with 34 families represented by a single species (Table S2). The most common introduced families are Asteraceae (98 spp.), Fabaceae (95 spp.), Poaceae (69 spp.), Arecaceae (69 spp.) and Lamiaceae (54 spp.) (Fig. 1).

The 104 casual species come from 45 plant families, with the Poaceae (13 spp.), Asteraceae (8 spp.), Lamiaceae (7 spp.) and Brassicaceae (6 spp.) most represented. The 165 naturalized species come from 57 plant families; of which 25 are represented in the naturalized flora by only one species (Table S2). The families with the most naturalized species are Poaceae (17 spp.), Asteraceae (15 spp.), Fabaceae (9 spp.), and Plantaginaceae (8 spp.).

The 52 species classified as invasive come from 34 families, with 22 families represented by a single invasive species. The most represented families in Bermuda's invasive flora are Poaceae (4 spp.) Asparagaceae, Myrtaceae, Polypodiaceae, and Ranunculaceae each with three invasive species (Table S2). Among Bermuda's invasive families Petiveriaceae stands out as it does not contain any native species, and the two introduced species from this family, *Rivina humilis* and *Trichostigma octandrum*, are both invasive.

The 321 species that have escaped captivity to become casual, naturalized, or invasive, all together

represent 236 genera from 82 families. The most frequently escaped families are Poaceae (34 spp.), Asteraceae (25 spp.) and Fabaceae and Lamiaceae with 12 species each. The genus with the most escaped plants is *Euphorbia* with 7 species, followed by *Oxalis* (5 spp.) and *Erigeron, Ipomoea* and *Ranunculus* with 4 species each. The 52 invasive species represent 43 genera, with three species of *Asparagus* and *Clematis*, and two species of *Abutilon*, *Cardiospermum, Cenchrus, Heptapleurum* and *Pittosporum*.

The 1103 introduced species belong to 139 plant families. The most represented families among these cultivated species are Fabaceae (83 spp.), Asteraceae (73 spp.), Arecaceae (63 spp.), Lamiaceae (42 spp.) and Solanaceae (37 spp.). The 1103 introduced but not escaped species come from 663 genera, with 450 genera having a single introduced species. The most represented is *Ficus* with 14 species, followed by *Euphorbia* (11 spp.), *Agave* (10 spp.), *Begonia, Senna* and *Solanum* (9 spp. each), and *Salvia* (8 spp.). Comparison of the escaped flora with those remaining only in cultivation shows that Asphodelaceae, Zingiberaceae and Annonaceae are the families with the most species introduced to Bermuda but failing to naturalize, with 11, 10 and 8 species respectively. The genera that are most widely introduced but have not escaped include *Senna* and *Solanum* with 9 introduced species each, and *Clerodendrum*, *Erythrina* and *Hibiscus* with 7 species each.

Life forms

Most of the 1424 plants introduced to Bermuda are forbs (40%) followed by trees (18%), shrubs (17%), vines/climbers (7%), graminoids (5%), succulents (5%) and palms (5%). Non-woody life forms make up the majority of the escaped flora which is 53% forbs and 12% graminoids (Fig. 2). Forbs comprise 60% of casual and 63% naturalized species, followed by graminoids (12% of casual species and 13% of naturalized species). In contrast, woody life forms make up much of the invasive flora with 29% being trees and 19% shrubs. Bermuda's 52 invasive plants display eight life forms, including 2 aquatic plants, 4 forbs, 5 ferns, 4 graminoids, 11 vines, one palm, 10 shrubs and 15 trees (Fig. 2; Table S3).

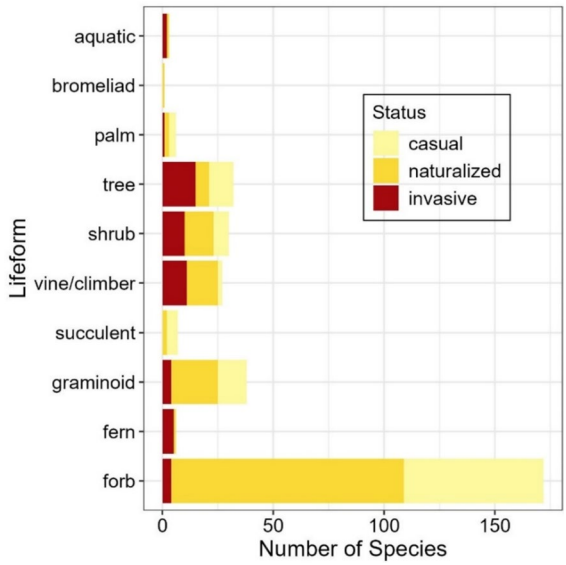

Fig. 2 The ten life forms of Bermuda's 321 casual, naturalized and invasive plant species

Life cycles

Perennial life cycles dominate the introduced flora, with 1112 perennial species (78%). Among the 321 escaped species, 25% are annuals and 55% are perennials. The remainder are some combination of annual, biennial or perennial as multiple types of life cycle were reported in the sources consulted (Table S3). Perennial life cycles are most dominant among the invasive species also. Only *Abutilon theophrasti* was classed as 'annual', while *Cardiospermum halicacabum*, *Cardiospermum grandiflorum, Momordica charantia* and *Salvinia auriculata* were classed as 'annual or perennial'. The remaining 47 invasive species (90%) were perennial.

Native range of the introduced flora

Bermuda's introduced flora contains plants from all nine continents in the Taxonomic Database Working Group (TDWG) continental scheme (Brummitt 2001; Govaerts 2023). Some species were native to five or six TDWG continents, making comparative percentages uninformative. The major sources of introduced species are Temperate Asia (352 spp.), Southern America (336 spp.), Northern America (322 spp.), Tropical Asia (282 spp.) and Africa (278

spp.). The 321 plants that have escaped cultivation also originate from all nine continents (Fig. 3; Table S3), with Temperate Asia (118 spp.), Africa (99 spp.) and Northern America (91 spp.) as the major sources. The 52 invasive species are native to eight continents, excluding Antarctica. Again, Temperate Asia is the most represented potential source, supplying 22 invasive species, followed by Tropical Asia (17 spp.) and Africa (16 spp.), Southern America (11 spp.) and Australasia (9 spp.) (Fig. 3; Table S3).

We grouped the nine TDWG botanical continents into broader areas that species were native to, giving five combinations of continental origins (Table 3). We examined the conversion rate of total species in all introduced classes to invasive species. Oceania (includes Australasia, Antarctica, and Pacific) had the highest conversion rate (10.2%) despite the fewest introductions originating from this part of the world. Asia (Temperate Asia and Tropical Asia) and Africa had rates roughly half as high, with 6.1% and 5.7% respectively. The Americas (Northern and Southern America) had a low conversion rate despite a large number of introductions from this region (Table 3). European species had the lowest conversion rate with only 1% of introductions becoming invasive.

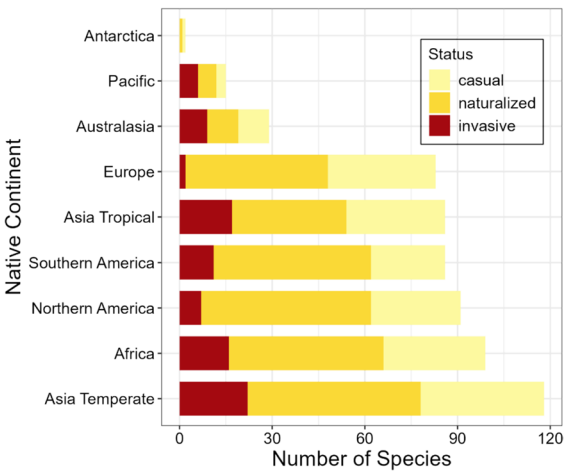

Fig. 3 Continents of origin of Bermuda's introduced plant species. NB. The sum of species across continents is greater than the total number of introduced species because most species are native to more than one continent

Table 3 Conversion rates of introduced species into invasive species by grouped continents of origin

Native Origin	Invasive in Bermuda	All Introduced to Bermuda	Conversion Rate (%)
Oceania	15	148	10.2
Asia	39	636	6.1
Africa	16	279	5.7
Americas	18	658	2.7
Europe	2	199	1.0

Introduction pathways of casual, naturalized and invasive flora

The majority of Bermuda's 1424 introduced plants were brought to the island intentionally (88%), while

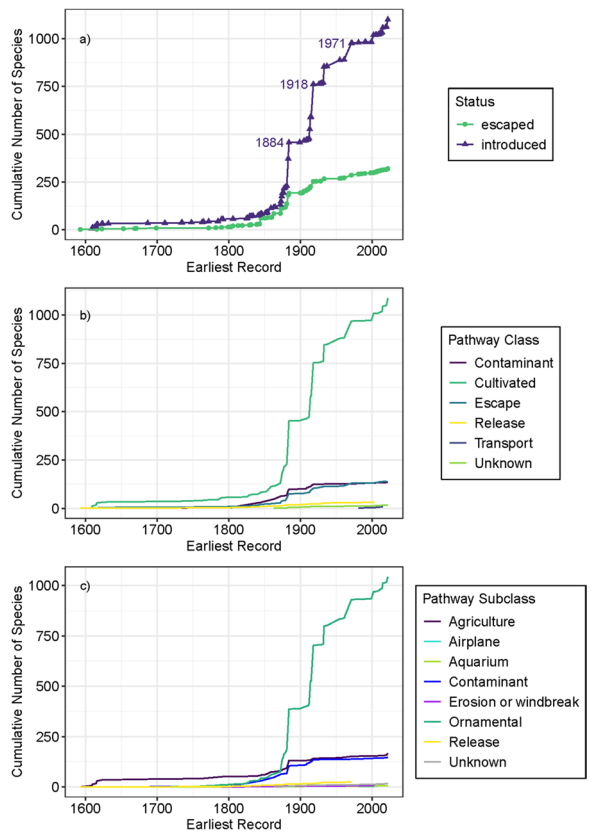

Fig. 4 **a** The cumulative number of introduced plant species (triangles) and casual, naturalized or invasive species (circles) present on Bermuda from 1593 to 2022. Publication dates of major botanical works are indicated **b** the cumulative number of species introduced by six pathways **c** cumulative the number of species introduced by eight sub pathways

11% were accidental introductions, and for 1% the introduction type could not be determined from the literature. For the 321 species in the escaped flora, 54% were intentional introductions, while 45% were accidental and 1% were unknown (Table S5). Among invasive species, 94% were intentionally introduced, while 6% were accidentally introduced.

The majority of casual and naturalized plants arrived as contaminants in imported goods prior to 1918. These historic contaminated imports account for 46% of casual species and 41% of naturalized species introductions (Table S5). The introduction of plants as contaminants is probably under-represented by these figures, as the true number of plants that arrived but did not establish, or were not reported, cannot be known.

Escape from cultivation of plants imported for ornamental purposes accounted for 31% of casual species and 33% of naturalized species. Plants imported for agriculture, particularly fodder grasses, account for 8.5% of naturalized species introductions.

Of Bermuda's 52 invasive species, 45 species (87%) have escaped from cultivation, with six imported for agriculture including three fruit trees. The remaining 39 species (75% of the invasive flora) for imported ornamental purposes, including one aquatic species the water hyacinth *Pontederia crassipes*. The three trees with edible fruits are the Surinam cherry *Eugenia uniflora*, loquat *Eriobotrya japonica* and guava *Psidium guajava*.

Another four invasive species were intentionally released into coastal habitats for erosion control or as windbreaks, namely the Australian whistling pine *Casuarina equisetifolia*, Madagascar olive *Noronhia emarginata*, beach naupaka *Scaevola taccada* and seaside creeping daisy *Sphagneticola trilobata.* The remaining three invasive plants originated as contaminants in historic imports.

Introduction date or earliest record

The majority of Bermuda's introduced plants arrived between about 1830 and 1930 (Fig. 4). The sharpest increase in the introduction of species that were released from, or escaped cultivation occurred between about 1880 and 1918 (Fig. 4b). Of Bermuda's 52 invasive species, 34 were already present when Dr Britton surveyed Bermuda's flora between 1905 and 1918 (Britton 1918; Table 2). From the mid-twentieth century onward the rate of introduction of escaped species flattens off, while total introductions continue to increase (Fig. 4a, b). New pathways of introduction appear in the late twentieth century, with the first records of species attributed to transport on the wheels of aircraft. For example the casual species *Buchnera floridana* and the naturalized *Imperata brasiliensis* both first appear as a herbarium specimens collected at the airfield in 1981 (Fig. 4b).

The introduction of two naturalized plants, *Carica papaya* and *Olea europaea,* predate settlement, having been recorded on the islands in 1593 (Fig. 4a; Lefroy 1884; Collett 1987; Sterrer et al. 2004). Once the British arrived in Bermuda in 1609 a low volume of plant introductions began, with little increase for 200 years (Fig. 4a). Bermuda's colonial governor from 1871 to 1877, Sir John Henry Lefroy was a keen botanist who exchanged plants with botanical gardens in the United States and Europe (Lefroy 1884; Wolsak et al. 2018) and was responsible for introducing more species to Bermuda than any other person (Marshall et al. 2005). The activities of Governor Lefroy resulted in a cluster of well-documented introductions in the 1870's (Fig. 4a; Reade 1883; Lefroy 1884; Britton 1918). Other large increases in first mentions of introduced plant species result from the publication of major botanical works in 1883, 1884, 1918, 1933 and 1971 (Reade 1883; Hemsley 1884; Lefroy 1884; Britton 1918; Baker 1933 in Jones 1986; Wardman 1971).

Discussion

The 1587 native and introduced plants reported in our inventory represent Bermuda's first checklist of accepted plant names with modern taxonomy and a standardized classification of their introduction status, life form, native range and date of first record. Our analysis of the inventory indicates that within the Bermudian flora introduced species outnumber native species 9:1, and casual, naturalized and invasive introductions outnumber native plants 2:1 (Table 1). The introduced Bermudian flora comprises 1424 species, 321 (22.5%) of which are found outside of cultivation, including 52 (3.7%) that have become invasive. Here, we discuss these findings in the context of Bermuda's economic development stages, present and historic landscapes, and we compare Bermuda

to patterns in naturalized floras globally and on other islands.

Economic development stages and plant introductions

Bermuda has passed through various stages in its socioeconomic development since the islands were permanently settled. Plants were imported at each stage through varying trade and transport links to meet various goals (Collett 1987; Sterrer et al. 2004), which influenced both introduction pathways and propagule pressure, and in turn dictated the potential for invasion (Essl et al. 2019).

The British settled Bermuda in 1609 and a permanent colony was established in 1612 (Lefroy 1877). The earliest introductions were crops and medicinal plants critical to survival of the new colony, which were sent from Europe and are well reported in the colonial records (Lefroy 1877, 1879; Collett 1987). Two naturalized species, papaya *Carica papaya* and the European olive *Olea europaea* have the earliest recorded mentions in the literature from 1593 (Fig. 4a), giving a current residence time of 431 years (Collett 1987; Sterrer et al. 2004). Lefroy (1884) reports that *Olea europaea* was already "naturalized, probably from seeds sown by the crews of Spanish vessels visiting the islands or wrecked on them in the sixteenth century" when the first colonists arrived in 1609. The next oldest naturalized species is the common fennel *Foeniculum vulgare* introduced in 1616 as seeds sent from Europe (Lefroy 1884; Collett 1987). Today fennel is naturalized on grassy hillsides and among sand dunes along the South Shore.

The earliest reported non-edible introductions are, the wild indigo *Indigofera suffruticosa* and castor oil plant *Ricinus communis* both introduced prior to 1623, and cotton *Gossypium herbaceum* introduced in 1624, all of which were imported as cash crops for export (Lefroy 1884; Hemsley 1884; Collett 1987). European colonies in the New World sought to develop all potential commercial ventures, so plants arriving at this time were intended to generate profits. Many new plants were being discovered by European explorers in the mid-seventeenth century and these were sent to the colonies for trial as commercial enterprises (Lefroy 1879, 1884; Collett 1987; Sterrer et al. 2004).

The earliest mention of a non-agricultural plant is the pasture weed *Sida acuta*. On November 10th, 1669 the Governor Sir John Heydon issued a notice to all tenants that they are to pull up the wireweed or risk forfeiting their land for neglect of it (Lefroy 1879). Governor Lefroy has made a footnote on this record, reporting *Sida acuta* was "still a great pest" over 200 years later (Lefroy 1879). From the early years of the Bermuda colony up until the 1930's hay was imported from North America to feed the island's horses (Lefroy 1884; Sterrer et al 2004) providing an important pathway for weeds to enter as contaminants (Fig. 4b, c). It is likely several naturalized plants entered the island this way, both native North American species, and those European weeds with naturalized populations in eastern North America.

Bermuda had primarily a trade economy from the 17th to nineteenth century, during which Bermudian seafarers travelled widely and brought home many plants they encountered abroad, which were planted in a 'trial and error' fashion (Reade 1883; Lefroy 1884); a practice which continued into the twentieth century (Britton 1918; Jones 1986). Governor Lefroy laments at length that ornamental horticulture, particularly flower gardening, was not widely undertaken by Bermudians in the 1870's, a situation he began to remedy with the import of seeds and plants from all over the world and professional gardeners from Britain (Lefroy 1884).

Attitudes to ornamental plants did change in this period, with most of Bermuda's total plant species, and ornamentals in particular, introduced between 1830 and 1930 (Fig. 4c). Landscaping of public spaces began in this period (Reade 1883; Britton 1918), including the establishment of the Public Gardens in 1898, which would become the Bermuda Botanical Gardens in 1958 (Department of Agriculture 1961). As Bermuda transitioned to a service economy based on tourism in the twentieth century, the interest in ornamental plants grew (Department of Agriculture 1961; Sterrer et al. 2004).

Legacy of the cedar blight

In the years immediately following the Cedar Blight of the 1940s, Bermuda's landscape changed from one covered with relatively few native species to one dominated by a diversity of introduced plants (Beard 1940; Groves 1955; Challinor and Wingate 1971; Sterrer et al. 2004; Wolsak et al. 2018).

The reforestation programme that began in 1949 has been acknowledged as responsible for the spread of now-invasive plants (Sterrer et al. 2004), however, we found relatively few introduction dates or first mentions of escaped species around 1949 (Fig. 4a). This suggests that although the numbers of plants being imported, propagated and planted at that time may have been high, few new species were being added to the flora. It is likely increased propagule pressure from species already present, combined with the arrival of new seed-dispersing birds and a newly barren landscape, triggered a population expansion for many planted species.

The reforestation programme involved planting imported trees, palms and shrubs along roadsides, on golf courses, on the islands of Hamilton Harbour and on all Government-owned land (Groves 1955; Challinor and Wingate 1971; Sterrer et al. 2004). Early in the programme, plantings suffered considerable losses due to wind and drought, demonstrating the need for hardier plants and the establishment of good windbreaks (Groves 1955). Plantings had to withstand what Beard (1940) refers to as the "constant desiccating sea winds", as well as summer temperatures over 27 °C (Currie 2018), and thin, free-draining, calcareous soils (Britton 1918). It is likely this focus on selecting woody species suited to the environmental conditions of a mid-oceanic island that precipitated their current dominance of the invasive flora. Trees and shrubs represent only 35% of the introduced flora, and only 19% of escaped species, but make up 48% of the invasive flora (Fig. 2). The reforestation programme facilitated the release of these salt-tolerant and wind-adapted species directly into the environment on a country-wide scale, which hastened their advancement along the invasion stage continuum. Considerable government funds were spent on these planting schemes (Groves 1955). Ironically, a substantial amount is now spent each year on invasive plant and habitat management and roadside weed control as a legacy of the Cedar Blight.

Comparing Bermuda's flora to other islands

Our inventory revealed a high proportion of introduced species (89.8%) in the Bermudian flora compared to just 9.5% native plants. This proportion is higher than reported for other oceanic islands such as the Azores, which host 1002 taxa that are 69% introduced and 31% indigenous (Silva and Smith 2004). Bermuda also has a high proportion of naturalized species compared to native ones. In a comparison of island floras across the globe, Essl et al. (2019) reported that 26% of the islands examined had more naturalized than native species. With 165 naturalized species to 151 natives, Bermuda fits within this minority.

There are several patterns in Bermuda's naturalized and invasive flora that are consistent with reported global patterns. These include ornamental horticulture as the primary pathway of introduction of invasive species (Guézou et al. 2010; Rejmánek 2014; van Kleunen et al. 2018; Rojas-Sandoval and Ackerman 2021), and thus intentional introduction being responsible for the majority of invasive species (Silva and Smith 2004; van Kleunen et al. 2018; Rojas-Sandoval and Ackerman 2021). In addition, species from Asia are well represented in the naturalized flora of Bermuda reflecting strong representation among naturalized species globally (van Kleunen et al. 2015; Pyšek et al 2017). Worldwide, islands also have more naturalized woody species than annual herbs (Pyšek et al 2017), a pattern that Bermuda adheres to. Of the 1424 species introduced to Bermuda, only 52 or 3.7% have become invasive. This conversion rate falls around the middle of the 1–6% range reported for other oceanic island groups (Kueffer et al. 2010).

Comparing families

At the global scale the naturalized flora is dominated by the Fabaceae, Poaceae and Asteraceae families (Pyšek et al. 2017), at the regional scale in the West Indies (Rojas-Sandoval and Ackerman 2021) and Central America (Rojas-Sandoval et al. 2023), and among island groups such as the Galapagos (Guézou et al. 2010), and Puerto Rico and the Virgin Islands (Rojas-Sandoval and Acevedo-Rodríguez 2015). Bermuda's introduced and naturalized flora is also dominated by Asteraceae, Fabaceae and Poaceae, however these families are not well represented in the invasive flora (Fig. 1). For example, in Bermuda *Leucaena leucocephala* is the only invasive from the Fabaceae. Kueffer et al. (2010) examined plants invasive in 30 island groups across the Atlantic, Caribbean, Pacific and Indian Ocean, and found that Fabaceae are over-represented among consistently invasive species across these islands. Similarly, Bermuda has only two

Asteraceae and four Poaceae classified as invasive (Tables S2 & S3). This under representation should be subjected to future study. It is likely a result of our application of the term 'invasive' only to plants widely dispersed into wild habitats, while others consider agricultural and garden weeds as invasive (e.g. Rojas-Sandoval and Acevedo-Rodríguez 2015).

The palm family Arecaceae is an important source of potentially invasive plants in tropical regions, with a high risk of spread through bird dispersal of species with fleshy fruits (Meyer et al. 2008; Rejmánek 2014). Palms were the fourth most introduced family in the Bermudian flora (Fig. 1; Table S2), with their introduction driven by the low native palm diversity (one endemic species only) and the popularity of palms in ornamental horticulture, particularly for tourism developments. Thus far Bermuda has only a single invasive palm, the Chinese fan palm *Livistona chinensis*, however naturalized populations of *Phoenix reclinata* and *Ptychosperma elegans* have appeared in natural habitats in recent years which may continue to persist and spread. These three palms represent only 4.3% of Bermuda's 69 introduced palm species. Naturalization rates among introduced palms are similarly low in French Polynesia (12%) and La Reunion Island (10%) (Meyer et al. 2008). However, 27 of the 69 palms first appear in the Bermudian literature less than 21 years ago, suggesting they may be recent introductions that have not had time to naturalize and could in the future.

Comparing life forms

Although forbs form the largest proportion of Bermuda's introduced flora (40% of introduced species), they represent only 8% of the invasive flora (Fig. 2). This is in contrast to the regional pattern within the West Indies where herbaceous plants comprise the largest segment 29% (Rojas-Sandoval and Ackerman 2021) to 31% (Rojas-Sandoval et al. 2017) of the invasive flora. As with families, this discrepancy is likely due in part to the way we defined invasive species and life forms. Ruderal and agricultural habitats are important for invasive plants in the West Indies (Rojas-Sandoval et al. 2017). As neither ruderal nor agricultural land is extensive in Bermuda, weeds of these habitats, which are often herbaceous, did not meet the dispersal or dominance criteria in our framework (Methods S1). Also, we used the value 'ferns' as a separate life form, comprising an additional 10% of Bermuda's invasive flora (Fig. 2), while other studies did not separate ferns from other herbaceous life forms (Rojas-Sandoval et al. 2017; Rojas-Sandoval and Ackerman 2021). The poor representation of forbs in Bermuda's invasive flora is also likely a reflection of lower propagule pressure compared to woody life forms (Fig. 2).

Our results are more comparable to islands at a wider geographic scale. In a study of island groups across the Atlantic, Pacific and Indian Oceans, Kueffer et al. (2010) reported that 57% of invasive species were trees or shrubs, which is comparable to Bermuda's 48% trees and shrubs.

Comparing pathways

A review of invasive species across 18 Caribbean island groups showed that 18% were unintentional introductions, while 82% were intentionally introduced (Rojas-Sandoval and Ackerman 2021). Bermuda's invasive species broadly follow this regional introduction pattern, with 6% accidental and 94% intentional introductions, suggesting that biosecurity measures aimed at intentional imports of plant material and seeds should be prioritized over those to prevent stowaways and contaminants.

Ornamental horticulture is a significant pathway of introduction for naturalized and invasive plant species globally (Rejmánek 2014; van Kleunen et al. 2018), regionally within the wider Caribbean (Rojas-Sandoval et al. 2017; Rojas-Sandoval and Ackerman 2021) and on other oceanic archipelagos (Kueffer et al. 2010) such as the Galapagos (Guézou et al. 2010) and the Azores (Smith and Silva 2004). As 75% of Bermuda's invasive plants also arrived for ornamental purposes, the need for improved regulation of both commercial and private imports of ornamental plants is apparent.

Deliberately introduced, woody life forms, particularly those producing edible fruit, are overrepresented in the naturalized floras of islands globally (Pyšek et al. 2017), a pattern which Bermuda follows. The recent covid-19 pandemic has increased awareness of Bermuda's reliance on imports and resulting lack of food security. This has made curbing the commercial sale and private distribution of invasive plants that produce edible products particularly problematic. The availability of seeds from online retailers has widened

the pool of what is available to Bermudian home gardeners and the island's commercial horticulture sector. Therefore, the risk of a new invasive plants arriving is probably very high.

Donor regions

Bermuda's native flora contains Caribbean species at the northern limits of their range, overlapping species shared with southeastern North America (Hemsley 1884; Britton 1918; Groves 1955; Sterrer et al. 2004), so it is not surprising to find plants from both tropical and temperate continents naturalizing under these conditions. Asia, particularly temperate Asia, is the largest donor of naturalized plants to other regions of the world (van Kleunen et al. 2015; Pyšek et al 2017). Accordingly, temperate Asia is the most important donor to Bermuda's flora, supplying the most invasive species (22 spp.), the most escaped species (118 spp.) and the most introduced species (352 spp.). The Southern hemisphere continents are underrepresented as donors of naturalized plants at the global scale (van Kleunen et al. 2015) but this is not the case for Bermuda's invasive flora, where South America, Africa and Australasia are well represented (Fig. 3).

Limitations of this study and areas for future research

Synthesizing information from historic texts, particularly those not based on direct observation by the authors (eg. Hemsley 1884) introduces a risk of reporting error. Similarly, the use of data from non-scientific sources and unconfirmed reports from non-specialists introduces the risk of mis-identification of species. By removing doubtful names at the start of the analysis, we are confident that we minimized these sources of error as much as possible. Our inventory has identified several introduced and invasive plants that need further expert verification, as we suspect they are still mis-identified. Genera that require species identity to be confirmed include *Abutilon* (2 invasive species) (Table 2), *Cardiospermum* (3 invasive species), *Clematis* (3 invasive species), and *Ipomoea* (numerous naturalized and cryptogenic species, Table S3). Invasive species that need expert confirmation are *Ardisia elliptica*, *Asparagus densiflorus*, *Elaeagnus pungens*, *Jasminum simplicifolium subsp. australiense, Megathyrsus maximus, Pittosporum viridiflorum, Salvinia auriculata* and *Volkameria glabra*. We anticipate that following revision by family or genera experts the names and numbers of invasive and naturalized species in this dataset may change. Bermudian resources for identifying Poaceae in particular are lacking and given the importance of this family in both the native and naturalized floras (Fig. 1), this should be addressed as a priority.

Research focused on the species we identified as cryptogenic may allow their native or non-native status to be confirmed in the future. If we applied the classification framework (Methods S1) assuming that all 12 cryptogenic species were non-native, 8 species would be considered naturalized. We were not able to make a determination for two species. A synonym of *Oplismenus compositus* appears in the Bermuda herbarium, but this name does not appear in the literature so this may be a mis-identification of *Oplismenus hirtellus* which is considered native (Britton 1918; Wardman 1971) and has two subspecies that are synonyms of *O. compositus* (POWO 2023). For *Paspalum conjugatum* the local distribution is not known well enough to determine if it is self-sustaining in the wild or widely dispersed. The two cryptogenic species of *Ipomoea* would be considered invasive if their non-native status was confirmed. *Ipomoea indica* is widespread in the country, occurs in multiple habitats, persists at sites for many years and produces abundant seedlings in the wild. *Ipomoea purpurea* is also reportedly widespread, however confusion with *I. indica* obscures its known distribution.

Preparation of this inventory did not involve any study-specific field surveys of naturalized or invasive vegetation, so we also anticipate new field data will improve our plant list and future assessment of species invasion stages. Equally importantly, any casual or introduced species that are no longer present can be noted as such, although this is hard to verify, particularly as known casual populations are not monitored. Future work should investigate impacts of invasive plants following field surveys. We made no attempt to incorporate impact into our classification, other than observing that some plants appear to dominate a habitat, where few other species grow (question 10, Methods S1). We classified 43 species as invasive based on answers to questions 1–9 in our framework (Methods S1), and 9 more were added by including question 10. The assumptions made to answer this question need to be assessed in the field. Regardless of these limitations our inventory is an important baseline and

provides a Bermudian data point and additional oceanic island data point for global studies.

Improving representation of the introduced flora in national herbarium collections should also be a priority for future work. Of the 273 sheets we examined at the Bermuda Natural History Museum, the native, naturalized and invasive flora were well represented, while only 53 introduced species that remain in cultivation were present. Expanding the collection will facilitate other botanical studies, allow confirmation of species identity by experts and aid future identification of new naturalized populations of represented plants.

Implications for risk assessments

The results of the public consultation on Bermuda's Invasive Alien Species Act 2021 indicate that public opinion is divided on the need to regulate the importation, propagation and sale of non-native plants. Support for restrictions on plant sales and cooperation with the current risk assessment process for imports is low.

By quantifying how dominated Bermuda's flora is by introduced species and highlighting that intentional introduction of ornamental plants has resulted in most of Bermuda's invasive species, we hope to demonstrate the extent of the problem to the horticulture sector, policy makers and the public. Our inventory will be a resource for those undertaking risk assessments as well as horticulturalists seeking native species or non-naturalized introductions for their planting projects.

Conclusion

Severe habitat degradation during the twentieth century, followed by active reforestation with introduced species has left Bermuda with a substantial invasive plant problem (Sterrer 2004; Marshall et al. 2005; Wolsak et al. 2018; Copeland et al. 2020). By creating this inventory of the Bermudian flora, and developing a standardized invasion stage classification (Methods S1), we have captured the current state of this problem and its origins. Future reapplication of this invasion stage classification will allow new introductions to be tracked and emerging naturalized and invasive species to be identified, which should allow timely mobilization of resources to address them. Additionally, by demonstrating that ornamental horticulture was responsible for the introduction of most invasive plants, we hope to encourage greater cooperation with risk assessments and biosecurity policies.

Acknowledgements The authors would like to thank the reviewers and editors for their time and helpful comments. We also acknowledge the assistance of the Bermuda Government, Department of Environment and Natural Resources.

Author contributions AC compiled the species list, undertook data analysis and wrote the manuscript. WD advised on data collation, preparation, analysis and presentation, and edited the manuscript.

Funding AC is supported by a Durham Doctoral Scholarship from the Faculty of Science, Durham University, and wishes to thank the Garden Club of Bermuda for additional support.

Declarations

Conflict of interest The authors have no conflicts or competing interests.

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