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ALIEN FLORAS AND FAUNAS 22

Alien flora of Nigeria: taxonomy, biogeography, habitats, and ecological impacts

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Abstract Biological invasions remain one of the greatest threats to biodiversity and livelihoods, and are predicted to increase due to climate change and globalization. In this study, we produced a comprehensive checklist of alien plants in Nigeria from online flora databases, herbarium records, published field surveys, and questionnaires administered to botanical gardens. The resulting alien flora was classified into naturalized, invasive, and cultivated plants. We then fitted a random forest model to identify the attributes which facilitate the naturalization of alien plants in Nigeria. We also used separate chi-squared tests to investigate if the frequency of these attributes is significantly different between the naturalized and invasive plants. The results include 1,381 alien plant taxa, comprising 238 naturalized, 190 invasive, and 953 cultivated species. The naturalized and invasive plants (428 species) are from 91 families, with Fabaceae and Poaceae having the highest representations. The random forest model showed that life forms and local economic uses were the most important drivers of alien plant naturalization in Nigeria. Chi-squared tests revealed a non-random distribution of life forms, higher frequencies of naturalized plants from the Indomalaya and the Neotropics, greater introductions during the British colonial rule, and that naturalized species are mostly used for medicinal, ornamental, food, or animal fodder purposes. Naturalized and invasive plants were recorded in all regions of Nigeria and are mostly found in urban and agricultural landscapes. This baseline information can support further ecological studies and conservation actions in Nigeria.

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Introduction

For centuries, plants and animals have been moved across oceans and other natural barriers for food, trade, and other economic purposes (Essl et al. 2018; van Kleunen et al. 2018). Major exchange of plants and animals started in the medieval period and peaked in what was called the Columbian Exchange in the fifteenth and sixteenth centuries (Boivin et al. 2012; Martin et al. 2019). Currently, plant and animal introductions are largely driven by ornamental plant and pet trades (Beaury et al. 2021; Gippet and Bertelsmeier 2021). Studies show that anthropogenic activities such as cultivation, domestication, and germplasm transfers have had profound effects on terrestrial systems for 12,000 years (Ellis et al. 2021). Many introduced plants are widely used to the extent that some have now been fully integrated into cultural, traditional, and medicinal practices (Helzer and Machado 2011) and given local names in their novel regions (Borokini et al. 2013; Ajao et al. 2022). Moreover, some of these introduced floras have also contributed significantly to the economic development of the receiving countries. For example, four West African countries produce 70% of the global cocoa production, even though *Theobroma cacao* is native to Brazil (Wessel and Quist-Wessel 2015). The same goes for the global production of vanilla, 80% of which is produced in Madagascar, even though *Vanilla planifolia* is native to Mexico. Moreover, 75% of the global staple foods originate from 12 crops and five animals; for example, rice, maize, and wheat contribute nearly 60% of calories and proteins obtained by humans from plants (FAO 1996). These examples highlight the global scale of alien plant use in agricultural production and other socioeconomic activities (Khoury et al. 2014, 2016; Martin et al. 2019).

Some alien plants establish self-sustaining populations in the wild, becoming naturalized, and a subset of those become invasive (Richardson et al. 2000; Blackburn et al. 2011), and have severe ecological and economic impacts in their novel environments (Pyšek et al. 2017, 2020). Plant invasions cause a reduction in native species richness and abundance (Mollot et al. 2017; Hejda et al. 2021; Tallamy et al. 2021), local extirpation of native populations (Gallardo et al. 2019), disruption of mutualistic networks (Schweiger et al. 2010), and alteration of ecosystem services and functions (Vilà et al. 2011; Kumschick et al. 2015a, b). Invasive plants are considered ecosystem engineers because they alter wildfire frequency (Gaertner et al. 2014), nutrient cycling (Ehrenfeld 2010), and facilitate biogeomorphic changes (Fei et al. 2014). Invasive species have been linked with shifts in functional and behavioral traits of native species (Ruland and Jeschke 2020; Thouvenot et al. 2021), while hybridization and introgression between native and alien flora have also been reported (Harms et al. 2021; Hirashiki et al. 2021). Globally, invasive species are one of the main biodiversity threats (Brondizio et al. 2019; Essl et al. 2020; Nic Lughadha et al. 2020). Invasive species are associated with extinction threats of many plants listed in the IUCN Red List of Threatened Species (Downey and Richardson 2016; Dueñas et al. 2021). Moreover, 25% of plant extinctions and 33% of animal extinctions have been attributed to invasive species (Blackburn et al. 2019), especially in island ecosystems (Bellard et al. 2016; Russell et al. 2017). Managing invasive species is costly, ranging in billions of US dollars for national efforts (Pejchar and Mooney 2009; Haubrock et al. 2021).

There has been an increased effort to document alien floras worldwide and which species are potentially invasive. The first global inventory was the Global Naturalized Alien Flora (GLONAF; van Kleunen et al. 2015, 2019; Pyšek et al. 2017). The GLONAF database provides occurrence data of naturalized alien vascular plants across 1029 geographical regions, including 381 islands (van Kleunen et al 2019). It was followed by the Global Register of Introduced and Invasive Species (GRIIS), developed by the Invasive Species Specialist Group (http://griis.org/), which also provides country-level checklists of alien and invasive species (Pagad et al. 2022). Most African countries lack published checklists or databases of invasive alien plants, except for South Africa (Henderson and Wilson 2017), Namibia (Bethune et al. 2004a, b), Madagascar (Kull et al. 2012), Swaziland (SNTC, 2016), Zimbabwe (Maroyi 2006, 2012), East Africa (Witt et al. 2018), Ghana (Ansong et al. 2019), Egypt (El-Beheiry et al. 2020), Algeria (Meddour et al. 2020), Sudan and South Sudan (Omer et al. 2021), and the Democratic Republic of Congo (Bordbar and Meerts 2022). Efforts to bridge the gap in alien plant species inventory data in Africa have resulted in some studies (see Pyšek et al.

2017 for their overview) and global databases such as the Invasive Species Compendium (CABI, 2017) and the Global Invasive Species Database (GISD, 2017), which cover countries in the region. These databases, however, indicate that the African continent (except for South Africa) is seriously under-represented in terms of knowledge of its alien floras (Richardson et al. 2022). Documenting alien flora in specific geopolitical areas can help increase botanical knowledge to distinguish between native and naturalized flora, provide baseline information for mapping the presence and abundance of alien flora, and assess the vulnerability of ecosystems to biological invasion. In addition, given that invasive flora can easily spread across geopolitical boundaries, such information can facilitate regional coordination of invasive species prevention and control among neighboring countries.

This study is the first to comprehensively document alien flora in Nigeria. Beyond compiling a list of taxa, we investigated significant associations between the invasion status of the alien plants in Nigeria and their traits and other attributes. Specifically, we asked the following questions: (i) Which plant families have the greatest representation among the naturalized and cultivated alien plants in Nigeria? (ii) Do life form, residence time, and biogeographical region of origin influence the naturalization and invasion success of alien plants in Nigeria? (iii) Which habitats and geopolitical regions in Nigeria are the most invaded? (iv) Do the economic uses of alien plants in Nigeria contribute to their naturalization and invasion?

Methods

Study area

The Federal Republic of Nigeria (hereafter, Nigeria) covers a land area of 923,768 km^2, making it the 14th largest country by size in Africa. Nigeria is the most populous country in Africa, with an estimated 210 million people. The country's economy is the largest in Africa and is mainly driven by fossil fuel production distantly followed by agriculture. The Köppen-Geiger climate classification map (Beck et al. 2018) identified five main climatic zones in the country, including tropical rainforest, tropical monsoon, tropical wet and dry, arid hot desert, arid hot steppe, and temperate with dry and warm summer in the higher elevations (Fig. S1). Nigeria's ecological zones, based on the classification of Keay (1949), include the mangrove swamp forest along the coast, freshwater swamp forest, lowland rainforest, derived savanna, Guinea savanna, the largest savanna in Nigeria, Sudan savanna, and Sahel savanna, as well as montane vegetation in high plateaus and mountains in the north, the northeastern corner, and the southeastern parts of the country. The encroachment of the Saharan Desert in the northernmost fringes of the country is altering parts of the Sahelian vegetation (Fig. S2). The forest biomes in Nigeria are part of the Guinean-Congolian tropical rainforest and the Guinean forest of West Africa, which is one of the 36 biological hotspots of the world (Myers et al. 2000).

A great diversity of plants is harbored within these varied ecological zones. Roughly 8,000 native plants in more than 300 plant families and over 2,000 genera have been reported in Nigeria, of which about 100 are strictly endemic (Borokini et al. 2010; Borokini 2014). Furthermore, Nigeria is the center of origin or diversity for many crop plants such as *Vigna unguiculata* (cowpea), *V. subterranea* (Bambara groundnut), *Abelmoschus caillei* (West African okra), *Oryza glaberrima* (African rice), *Dioscorea* spp. (yams), *Macrotyloma geocarpum* (Kersting's groundnut), *Sphenostylis stenocarpa* (African yam bean), and *Psophocarpus tetragonolobus* (winged bean) (Blench 2006; NACGRAB 2008).

Data collection

A list of alien plants reported in Nigeria was compiled between 2012 and 2022. The data sources include open-access flora databases, online digitized herbaria collections and metadata, relevant floral compendia and checklists, and anthropology papers discussing historical plant introductions and their documented uses in Nigeria (Table S1). Data extraction was augmented with primary literature searches on Google Scholar using various Boolean arguments and keywords that include "floristic survey* OR checklist OR ethnobotanical OR ethnomedicinal w/1 survey OR weed* OR introduced OR exotic OR alien w/1 plant OR flora AND Nigeria." This produced over 600 floristic and ethnomedicinal articles that were screened to extract information on the alien plants in Nigeria. Additionally, plant inventory surveys were conducted in 32 botanical gardens in Nigeria between September 2012 and

December 2013 as part of building the Botanical Garden Conservation International (BGCI) Garden Search database. These data extraction processes resulted in 44,586 entries which were reduced to 10,007 taxa after removing duplicates and synonyms. Plants that are native to Nigeria (86% of the 10,007 taxa) were then removed from the list. The final list was further screened for taxonomic name standardization using the Plants of the World (POWO) database (https://powo.science.kew.org). Further taxonomic name resolution was conducted in R statistical software using: (a) *TPL* function in taxonstand package version 2.4 (Cayuela et al. 2021) for The Plant List backbone (TPL 2013), and (b) *gnr_resolve* function in taxize package version 0.9.100, which represented the World Checklist of Vascular Plants backbone (Govaerts et al. 2021; Chamberlain et al. 2022). This resulted in a final list of 1,381 alien plant taxa in Nigeria (for simplicity, they are termed 'species' hereafter) (Tables S2a and b).

The following information was compiled for each alien species: (a) plant family, (b) invasion status (naturalized, invasive, or cultivated, that is, not occurring in the wild), (c) biogeographical region of origin, (d) life form, (e) IUCN Red List category, (f) economic uses in Nigeria, (g) geographical distribution in Nigeria, (h) residence time in Nigeria, and (i) habitats where the species occur in Nigeria (Table S2). The invasion status of alien flora was assigned based on the consensus rating of three of the co-authors (ITB, QAA, and EIA) who have botanical experience in Nigeria. Naturalized alien plants are those that have become established in plant communities in new regions and maintain self-sustaining populations without human assistance but have not become invasive yet, and as such, are not having a discernable negative impact (Richardson et al. 2000; Blackburn et al. 2011). Invasive species are a subset of naturalized species that have severe ecological and economic impacts (IUCN 2000; Zhang et al. 2021), including alien weeds in agricultural fields. Information on casual species (sensu Richardson et al. 2000; Blackburn et al. 2011) is not available for Nigeria and, therefore, they were excluded from this study. Other alien species that are categorized as "cultivated" include plants that grow under propagation in home, botanical, and commercial horticultural gardens and in agricultural production but do not occur in the wild. The biogeographical classification of the regions of origin follows Udvardy (1975) and is based on the shared biogeography and evolutionary history of plants and animals: Neotropical, Indomalayan, Nearctic, Palearctic, Australasian, Afrotropical, and Oceania. Introduced plants that originated from West Africa were excluded from the list. Life forms were grouped into vines, trees, cycads (gymnosperms), shrubs, herbs, graminoids (including grasses and sedges), bryophytes, palms, and ferns (pteridophytes).

The distribution of alien species in Nigeria was based on herbarium occurrence records in the open-access flora databases (Table S1), primary literature, and consensus classification based on previous field sightings and reports by the three Nigerian coauthors. The distribution is expressed as presence in the six Nigerian geopolitical (regional) zones: north-west (NW), north-central (NC), north-east (NE), south-west (SW), south-south (SS), and south-east (SE). Alien plants were classified into one or more of the 21 broad categories of use in Nigeria based on available data and literature, while those with no known local use or information were categorized as "unknown" (Table S3). The IUCN conservation category for each plant was obtained from the IUCN Red List of Threatened Species database (IUCN 2022). For plants that have not yet been assessed, "not evaluated" (NE) was stated. Residence time represents the date of introduction of alien plants in Nigeria and was broadly classified into three categories: (a) pre-colonial era, dating from the historic periods to the nineteenth century, when plants were introduced by Portuguese explorers, trans-Saharan Arab and Berber traders, Austronesian Mariners, Christian missionaries, and stochastic sweepstakes trans-Indian and Atlantic Ocean crossings; (b) colonial era between mid-nineteenth century and 1960, when introductions were driven mainly by the British Colonial Government and Christian missionaries; and (c) postcolonial era, characterized by introductions by plant enthusiasts, botanical gardens, Government research institutions, and commercial horticultural gardens. Habitats of invasive and non-invasive naturalized plants in Nigeria were classified using the system based on Hejda et al. (2015) and introduced in detail by Pyšek et al. (2022). Each species can be found in one or more of the following habitat types: 1. Forests, 2. Open forests, 3. Scrub, 4. Grasslands (subdivided into 4a. Natural grasslands, and 4b. Human-maintained grasslands), 5. Sandy, 6. Rocky, 7. Dryland, 8. Saline, 9. Riparian, 10. Wetland, 11. Aquatic, 12. Man-made, further subdivided into 12a. urban habitats and 12b. Agricultural habitats. Finally, we compiled information on which of the invasive and naturalized plants are under cultivation.

Data analysis

We conducted statistical analyses to explore the frequencies of alien plant representations in plant families, life forms, biogeographic regions of origin, economic uses, geographical distribution, and invaded habitats in Nigeria. We fitted a random forest model to determine what attributes of the alien plants promote naturalization. Here, the invasion status of the alien plants in the dataset was formatted to binary response (introduced plants were scored 1 if they were classified as naturalized or invasive, while all cultivated alien flora were scored 0), and using bioregions, top four economic uses of all alien plant species in the dataset, life form, and local distribution in Nigeria as predictors. The random forest was fitted with 500 trees and four variables at each node. We used out-of-the-bag error to evaluate model accuracy for both the independent training (70% partitioned data) and test data (remaining 30% of the data) and Mean Decreased Gini metric to determine the contribution of each variable to the model. The random forest model was fitted in randomForest R package version 4.7–1.1 (Liaw and Wiener 2022).

Additional analyses were conducted on the naturalized and invasive flora dataset to identify significant differences between the two status categories. We used the chi-squared goodness of fit test, a non-parametric test, to evaluate if the frequency distribution of life forms, biogeographic region of origin, local economic uses, local distribution, and occupied habitat types in Nigeria significantly deviate from an expected probability distribution. Because the numbers of species assigned as palms and bryophytes were small, we removed these categories from the associations between life form and species status. Similarly, because the values in some habitat categories were small, we removed grassland (which is already accounted for in both natural grassland and human-maintained grassland categories), forests, saline, and sandy habitats. For any attribute where the frequency is less than 100, we used Yates continuity correction to estimate the P values for the chi-squared goodness of fit test. All analyses were conducted in R statistical software version 4.2.1 (R Core Team 2022).

Results

Cultivated alien flora

Our checklist includes 1,381 alien plant species recorded in Nigeria, of which 953 (69%) in 117 families were only found in cultivation (Table S2a), while the remaining 31% were naturalized or invasive (Table S2b). Arecaceae is the most represented (305 species) in the cultivated alien flora, distantly followed by Fabaceae (63), Araceae and Euphorbiaceae (37). As a result of the unusually high representation of Arecaceae, there were also more palms than other plant life forms in the cultivated alien flora. The majority of the palms were recorded in the Murtala Mohammed Botanic Gardens, Lagos, Nigeria. The cultivated alien flora also included 231 trees, 181 herbs, 145 shrubs, 57 vines, and 18 cycads, among others (Table S2a). A large proportion of the cultivated alien flora was introduced for ornamental purposes (754 species) and for food (146). Furthermore, 355 cultivated alien plants are native to the Neotropics, 245 plants are from the Indomalaya region, and 172 plants are of Australasian origin (Table S2a). None of the cultivated alien plants originate from Oceania. The South-West (868) and North-Central (559) regions have the highest richness of cultivated alien plants. However, the southern geopolitical zones (SW, SE, and SS) of Nigeria have a relatively high richness of cultivated alien plants compared to the northern zones (Table S2a).

Taxonomic structure of naturalized and invasive flora

There were 238 naturalized and 190 invasive plant species in Nigeria. Collectively, the 428 naturalized species represent 91 families and 270 genera (Table S2b). Fabaceae, with 79 species, is the most speciose, followed by Poaceae and Asteraceae (Table 1). However, almost one-quarter (24.2%) of all invasive species are grasses and sedges (Poaceae; Table 1). Other families with many invasive alien species include Asteraceae,

Table 1 A list of plant families with the highest number of representatives and invasion of naturalized and invasive species in Nigeria

Plant family	Naturalized	Invasive	Total
Fabaceae	63	16	79
Poaceae	11	46	57
Asteraceae	13	26	39
Convolvulaceae	13	8	21
Amaranthaceae	9	9	18
Malvaceae	6	10	16
Solanaceae	9	5	14
Cyperaceae	1	10	11
Rubiaceae	0	10	10
Euphorbiaceae	5	5	10
Lamiaceae	7	1	8
Pteridaceae	8	0	8

Fabaceae, Cyperaceae, Rubiaceae, and Malvaceae (Table 1). The 190 invasive alien species in Nigeria belong to 130 genera, with the most speciose genera being *Paspalum, Spermacoce* (six each), *Mimosa* (five), *Alternanthera,* and *Sida* (four each). Additionally, nearly all of the alien species in *Ludwigia* (five of six), *Euphorbia* (three of five), and *Cyperus* (three of four) have become invasive (Table S2b). Ten invasive and one naturalized alien species in Nigeria are also listed among 100 worst invasive species in the Global Invasive Species Database (2023).

Indicators of naturalization of alien plants

Using reformatted binary data for the status of alien flora in Nigeria (0 for cultivated and 1 for naturalized and invasive), the random forest model fitted with 70.0% of the data had an overall 86.1% accuracy, with a prediction accuracy of 92.6% on the training and 87.0% on the independent test data. Using the Mean Decreased Gini index to assess the contribution of variables to the probability whether an alien species remains only cultivated or becomes naturalized or invasive, life form contributed the most to the random forest model, followed by several local economic-use categories and local distribution of alien plants in Nigeria (Table 2; Fig. 1).

Attributes associated with the naturalization and invasion of alien flora in Nigeria

Life form

There was a non-random distribution of life forms ($\chi^2 = 103.8$, df = 7, $P < 0.001$) among the naturalized and invasive alien flora in Nigeria. There were 188 (44% of the total number of naturalized) herbaceous naturalized species, of which 100 have become invasive (52.6% of the total invasive species; Table 2). However, the graminoid naturalized species have higher likelihood of becoming invasive than other life forms (71%, representing 56 invasives out of 68 graminoid in total; Fig. 2). Also, herbs (53.2%), shrubs (46.4%), and vines (46%) have relatively high percentage representation of species that have become invasive (Table 2).

Biogeographic region of origin

Over 80% of the naturalized and invasive species in Nigeria originated from the Neotropics (228 species) and the Indomalaya (116 species), while the Nearctic region had the lowest floristic representations (21 species; Table 2; Fig. 3a). Naturalized species were over-represented compared to invasive species among plants originating from the Neotropics ($\chi^2 = 4.4$, df = 1, $P = 0.04$) and the Indomalaya ($\chi^2 = 7.48$, df = 1, $P = 0.006$). For other biogeographic regions, there were no statistical differences ($P > 0.05$) in the origin of naturalized and invasive species.

Local distribution in Nigeria

The southern zones of Nigeria (SW, SE, and SS), dominated by tropical rainforest, harbor more naturalized species than the savanna and semi-arid northern zones (NC, NW, and NE; Table 2, Fig. 3b). There were no statistical differences ($P > 0.05$) between the naturalized and invasive species for the six geopolitical zones in Nigeria. Furthermore, 33 naturalized and 33 invasive species were recorded in all geopolitical zones in Nigeria. The former group included plant species mainly grown as food crops, for example, *Moringa oleifera*, *Carica papaya*, *Zea mays,* two *Capsicum* spp., and seven *Amaranthus* species. The

Table 2 Frequency of the attributes of alien flora in Nigeria and their contribution to the random forest model explaining the status of species. The random forest model included life forms (one variable), biogeographical realm of origin (six variables), geopolitical regions in Nigeria (six variables), and selected ecological use classifications (nine variables). Higher Mean Decreased Gini values indicate higher contribution and relative importance to the random forest model

Attribute	Frequency of ecological status			Random Forest	
	Cultivated	Naturalized	Invasive	Total	Mean Decreased Gini
Life forms					68.33
Bryophyte	1	4	0	5	
Cycads	18	0	0	18	
Ferns	4	22	2	28	
Graminoids	10	12	56	78	
Herbs	181	88	100	369	
Shrubs	145	28	13	186	
Vines	57	37	17	111	
Palms	306	0	1	307	
Trees	231	47	1	279	
Biogeography of origin					
Indomalayan	245	77	39	361	5.04
Neotropical	355	116	112	583	9.15
Palearctic	92	29	22	143	6.69
Nearctic	22	11	10	43	1.69
Afrotropical	124	22	12	158	4.88
Australasian	172	16	14	202	3.60
Local spread in Nigeria					
South-West	868	213	166	1247	5.55
South-East	444	183	139	766	12.29
South-South	443	180	139	762	13.14
North-Central	559	135	124	818	9.19
North-East	101	80	79	260	12.40
North-West	100	93	94	287	20.95
Selected local economic uses					
Medicinal	91	89	48	228	24.89
Ornamental	754	94	30	878	39.41
Food	146	47	15	208	15.53
Unknown	6	16	57	79	13.09
Fodder	21	41	52	114	16.36
Cover crops	3	11	4	18	3.18
Wood	38	9	0	47	2.34
Agroforestry	13	13	0	26	2.10
Fuelwood	7	19	1	27	3.46
Residence time					
Pre-colonial	nc	64	18	82	
Colonial	nc	168	169	337	
Post-colonial	nc	6	3	9	

nc = not classified

most widely distributed invasive species included *Leptochloa panicea* (Fig. 4a), which also has a cosmopolitan biogeographic origin, *Paspalum distichum* (Fig. 4b), *Amaranthus spinosus* (Fig. 4c), *Ludwigia hyssopifolia* (Fig. 4d), *Mimosa pigra* (Fig. 4e), and *Spermacoce ocymoides* (Fig. 4f).

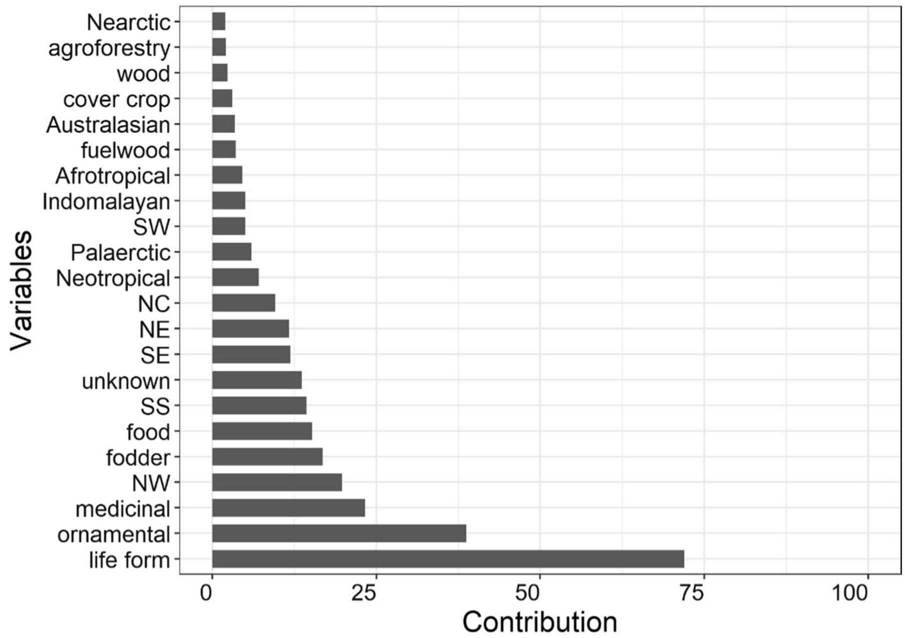


Fig. 1 A plot of the variables and their Mean Decreased Gini value, representing their relative contribution to the random forest model explaining the status of species in the alien flora in Nigeria

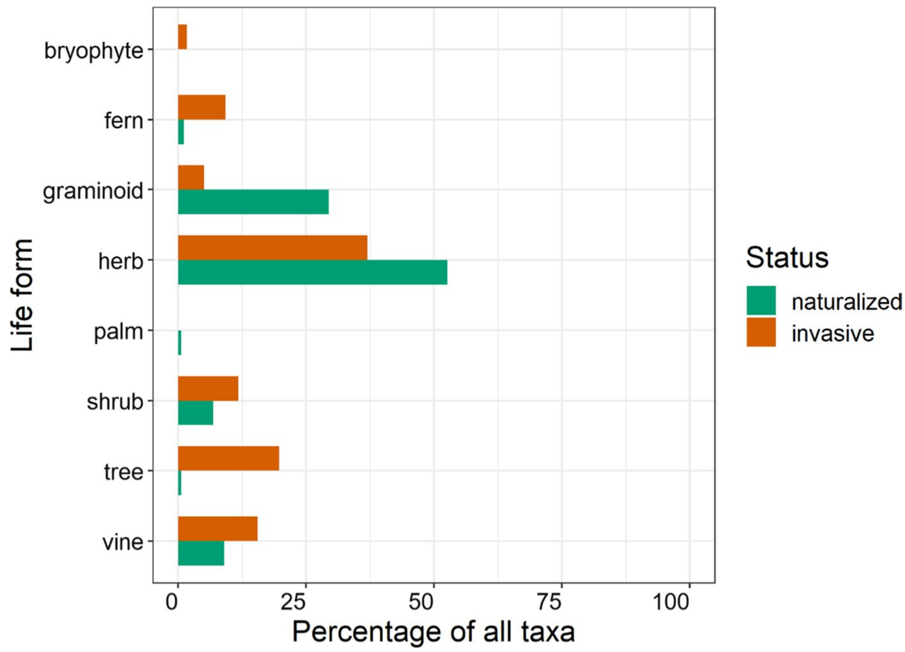
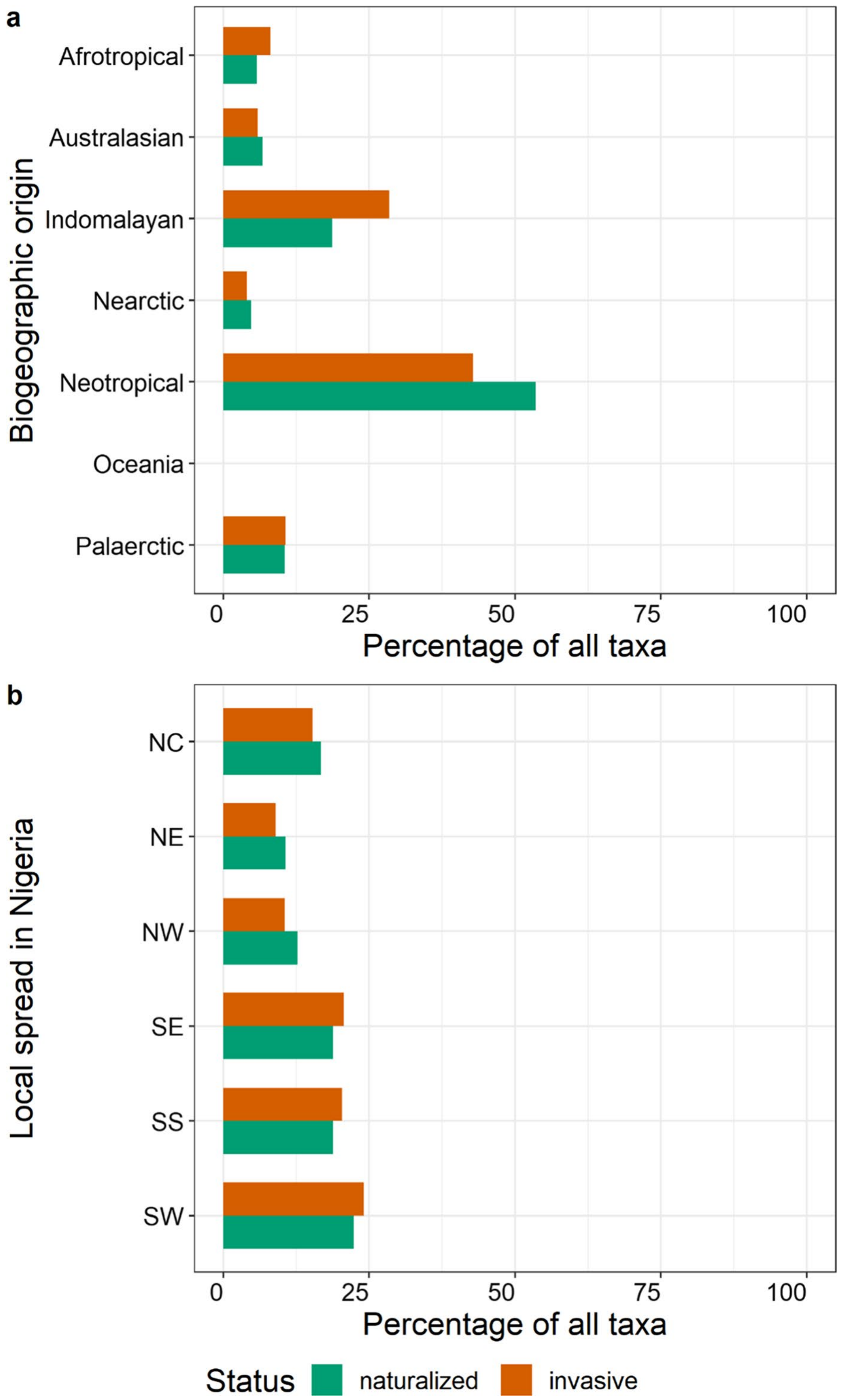


Fig. 2 Percentage of the total of naturalized (n = 238 species) and invasive (n = 190 species) alien flora in Nigeria according to their life form

Local economic uses of naturalized species in Nigeria

The top four most common uses of naturalized and invasive species in Nigeria are medicinal, ornamental, fodder, and food (Table 2). However, 73 naturalized species have no known local use in Nigeria based on literature review. Chi-squared test results showed statistically higher representation of naturalized species used for medicinal ($\chi^2 = 7.15$, df = 1, $P = 0.008$), ornamental ($\chi^2 = 28.85$, df = 1, $P < 0.001$), and food purposes ($\chi^2 = 11.98$, df = 1, $P < 0.001$), while invasive species representation was higher among species used as fodder ($\chi^2 = 6.39$, df = 1, $P = 0.01$) and those

Fig. 3 Percentage of the total of naturalized (n = 238) and invasive (n = 190) species in Nigeria according to their, **a** biogeographic realm of origin and **b** local spread in Nigeria expressed as the presence in geopolitical zones (see text for description). Note that each species can have more than one biogeographic origin and be locally spread in more than one region in the country



with unknown uses ($\chi^2 = 40.47$, df = 1, $P < 0.001$). In addition, we noted that 120 of the 428 naturalized and invasive species are under varying levels of cultivation including horticulture, home gardening, desert control, agroforestry, urban landscaping, production forestry, secondary forests, commercial production, as well as subsistence and commercial agriculture (Table S2b).

Habitat types

Naturalized and invasive species occur in 10 of the 14 habitat types considered in this study (in all but forest, sandy, rocky and saline habitats, Fig. 5). The habitat in which the largest number of naturalized and invasive alien species occur is urban (317 out of 428 species or 74.4%), followed by agricultural (64%), open forest (49.1%), natural grasslands (38.5%), and scrub (23.4%); all remaining habitats harbor less than 100 naturalized species (Fig. 5). The habitats with the least occupation by naturalized and invasive plants were riparian (six invasive and nine naturalized species) and aquatic (seven invasive and 12 naturalized species). We found a significant association between habitat type and species invasion status ($\chi^2 = 43.9$, df = 9, $P < 0.001$). There was a higher proportion than expected of naturalized species in open forests (122 species), scrub (68), human-maintained grasslands (37), and urban (183). For invasive species, there was a higher proportion of species in agricultural habitats (146 species), dryland (49), natural grasslands (82), and wetlands (29) than expected.

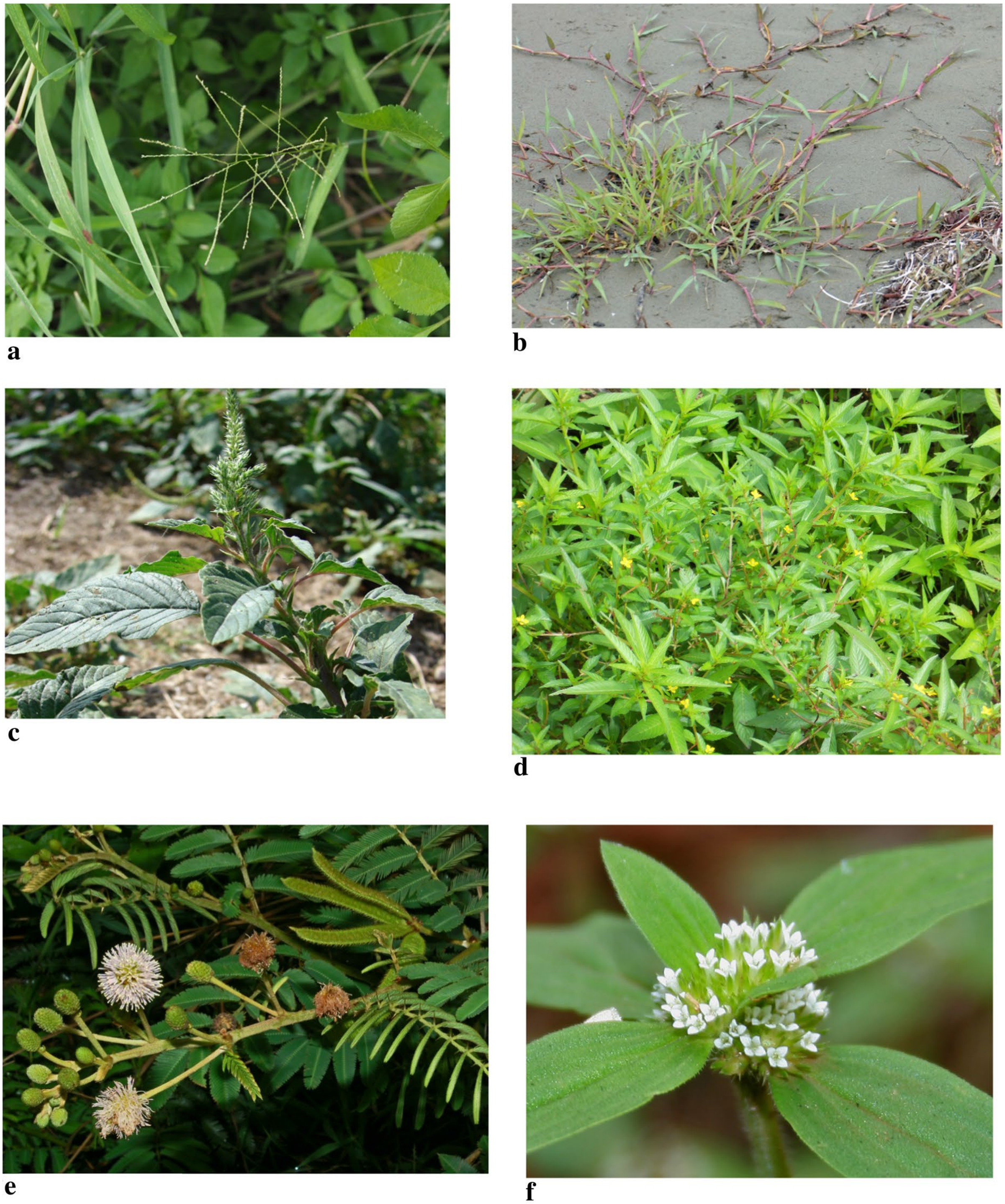
Residence time

The majority of the naturalized and invasive alien species in Nigeria were introduced during the colonial period (337 species), roughly half (169) of them have become invasive, while 82 and nine species were introduced in the pre- and post-colonial periods, respectively. The chi-squared test showed a statistically higher representation of invasive species among plants introduced in the colonial period ($\chi^2 = 21.7$, df = 1, $P < 0.001$), contrary to the significantly higher representation of naturalized species introduced in the pre-colonial era ($\chi^2 = 20.7$, df = 1, $P < 0.001$). However, we did not observe any statistical difference between naturalized and invasive species introduced post-colonially.

Discussion

The list of alien species in Nigeria that we present in this paper is not exhaustive and is bound to grow as international trade and tourism increase. Many plants are still being introduced into Nigeria, especially by private and commercial floriculturists, plant enthusiasts, and botanical gardens. The vast majority of the cultivated alien species are reported in botanical gardens and represent potential sources of new invasions. Similar findings have echoed through several publications showing that horticulture is the main pathway for plant introduction into many countries and regions (e.g., Hulme et al. 2017; van Kleunen et al. 2018; Guo et al. 2019; Arianoutsou et al. 2021; Sirbu et al. 2022; Kinlock et al. 2022). To obtain a complete picture of plant invasions in Nigeria, floristic surveys of urban green spaces, home gardens, and plant inventories held by botanical gardens and commercial floriculturists should be conducted. We identified 428 naturalized alien species in Nigeria, which is a major update of the 102 previously reported in the GRIIS database (Borokini et al. 2021). This naturalized flora can be compared, in terms of richness, with 436 naturalized species in the Democratic Republic of Congo (Bordbar and Meerts 2022), 113 in Sudan and South Sudan (Omer et al. 2021), 108 in Algeria (Meddour et al. 2020), 548 in Southern Africa (Henderson 2007), 129 in Egypt (El-Beheiry et al. 2020), 291 in Ghana (Ansong et al. 2019), and over 180 in Angola (Figueiredo and Smith 2022).

Fabaceae, one of the largest plant families of native flora and the second largest of endemic flora in Nigeria (Borokini 2014; Bello et al. 2021) has the greatest share of naturalized and invasive plants, which may indicate taxonomic affinities between native and naturalized alien flora in the country. Leguminous alien plants are evenly distributed across the various life forms and found in all regions in Nigeria, occurring mostly in urban and agricultural landscapes; more than half (58.9%) of these plants originate from the Neotropics. Of the 79 naturalized leguminous species, only four do not have known economic use, indicating a strong human relationship with the introduced plants



a b c d e f

Fig. 4 Plates of six selected invasive plants in Nigeria: **a** *Leptochloa panicea* (source: Plants of the World Online), **b** *Paspalum distichum* (source: Calflora), **c** *Amaranthus spinosus* (source: College of Agriculture, Forestry and Life Sciences, Clemson University), **d** *Ludwigia hyssopifolia* (source: Japan International Research Center for Agricultural Sciences), **e** *Mimosa pigra* (source: Wikipedia), and **f** *Spermacoce ocymoides* (source: Wikispecies). These selected plants represent the top six genera with all or most alien members in Nigeria being categorized as invasive and relatively widely distributed in Nigeria

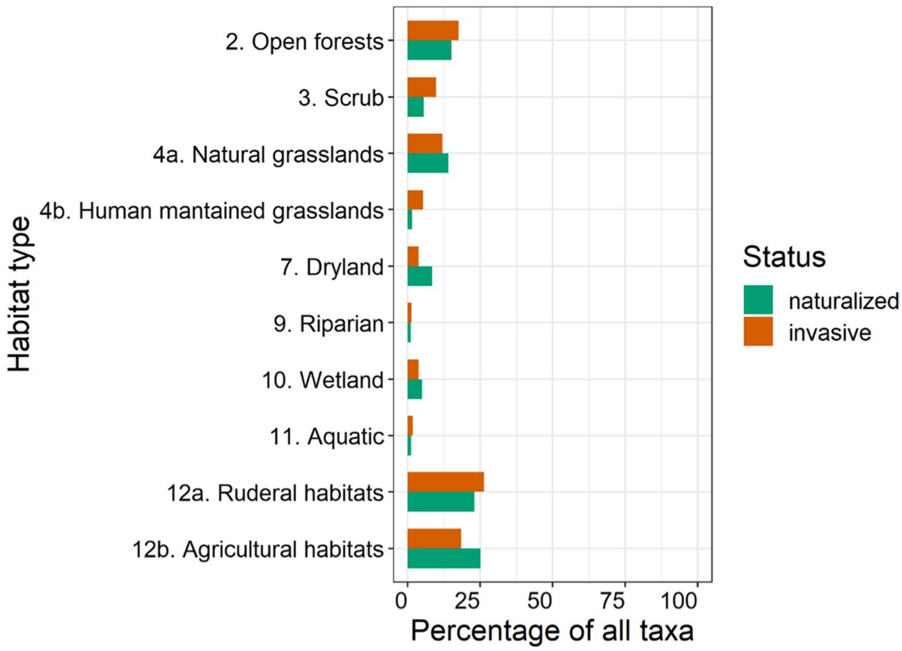


Fig. 5 Occurrence of naturalized and invasive species in habitat types in Nigeria expressed as the percentage of the total of naturalized (n = 238) and invasive (n = 190) species. Because the number of species was too small in forests, saline, and sandy habitats, these were removed from the analyses

in this family. Fabaceae was also cited as having the highest number of representatives among naturalized plants in Algeria, Sudan and South Sudan, the Democratic Republic of Congo, South Africa, Ghana, and Eastern Africa (Henderson 2007; Witt et al. 2018; Ansong et al. 2019; Bordbar and Meerts 2020; Meddour et al. 2020; Omer et al. 2021). However, compared to only 20% of alien plants in Fabaceae that have become invasive in Nigeria, over 80% of alien plants in Poaceae have become invasive, making it the family with the largest percentage of invasive species in Nigeria. Generally, grasses possess traits that facilitate long-distance dispersal, establishment, colonization, and transformation of novel environments, and resilience to disturbance and drought (Linder et al. 2017; Leal et al. 2022). These traits may account for Poaceae being one of the most globally distributed plant families (Linder et al. 2017), and representing some of the most noxious weeds in the world (Pyšek et al. 2012; Sutton et al. 2019). Moreover, humans have spread grasses globally for livestock production; therefore, intentional introductions may have supported propagule pressure and facilitated accidental plant movements (Scasta et al. 2015).

Our study identifies biological attributes associated with the likelihood of naturalization and invasion of alien species in Nigeria (e.g., Pyšek and Richardson 2007; van Kleunen et al. 2010; Pyšek et al. 2015). The random forest model and the chi-squared tests highlight a strong association between life form and the invasion success of alien plants in Nigeria, with herbs and graminoids most represented among the invasive species. This is congruent with previous studies that reported a significant association between life forms and the invasion of alien plants in other countries (Mehraj et al. 2018; Li and Shen 2020). However, the life form in itself cannot explain the invasion status of alien species; rather, several functional traits associated with a given life form may account for the ecological success in novel environments (Goodwin et al. 1999; Moravcová et al. 2015; Wavrek et al. 2017). One advantage of herbaceous plants is their relatively short generation time allowing them to respond faster to novel ecological conditions (Andreasen and Baldwin 2001; Compagnoni et al. 2021). Furthermore, many naturalized and invasive herbs in our data set are of tropical origin, that is, Neotropics and Indomalaya; therefore, it is not surprising that biogeography was a factor significantly associated with the naturalization of alien flora in Nigeria. This may suggest that ecological affinities between the native and invaded ranges facilitate naturalization, possibly due to the conservatism of their ecological niches (Mehraj et al. 2018; Pinna et al. 2021). Studies have shown that habitat filtering may support the naturalization and invasion of alien plants if the native and invaded ranges share similar ecological conditions (Hejda et al. 2015; Buckley and Catford 2016; Divíšek et al. 2018). Several countries, including Ghana, South Africa, and the Canary Islands (Spain), also reported that the largest percentage of naturalized alien flora in their respective study areas are of Neotropic origin (Henderson and Wilson 2017; Ansong et al. 2019; Morente-López et al. 2023).

This study demonstrates the significant impacts of anthropogenic activities on the invasion process. Humans accidentally or deliberately transport species from their native regions to novel areas, create disturbance in ecosystems that facilitate colonization by alien plants, and directly or indirectly assist these alien species with acclimatization and spread. The random forest model shows a high association between the naturalization of alien plants and their local uses for medicinal, ornamental, fodder, and food purposes in Nigeria. Ornamental alien plants may have been deliberately introduced for such purposes based on the desired traits they possess (e.g., brightly colored flowers); however, the medicinal uses of many alien plants were discovered post-introduction. Additionally, returning enslaved people from Central and South America may have popularized the local uses of the introduced plants from the Neotropics. The finding from this study is congruent with literature showing that the economic uses of introduced plants were a major driver of their naturalization (Theoharides and Dukes 2007; van Kleunen et al. 2020). Many published ethnobotanical papers demonstrated the use of alien plants for medicinal purposes in Nigeria (e.g., Lawal et al. 2010; Borokini et al. 2013). However, the economic uses of these alien plants may reduce the public's willingness to acknowledge their ecological implications and cooperation in their management and control. For example, despite the global recognition of *Chromolaena odorata* as an invasive plant, many studies have reported its potential use in the agricultural land fallow system, phytoremediation, and traditional medicine in Sub-Saharan Africa (Uyi et al. 2014). Human activities facilitating the naturalization of alien plants were also observed in our study – most naturalized and invasive plants are located in areas of the major human footprint, such as urban centers and agricultural landscapes. This agrees with previous studies that have reported that urban areas are hotspots for biological invasions (Chytrý et al. 2008; Aronson et al. 2014; Gaertner et al. 2017). Residence time played an important role in the naturalization and invasion status of introduced plants: the majority of naturalized and invasive plants in Nigeria arrived when the country was under British rule, which was characterized by the heightened global movement of food and timber crops by the colonial government, returning enslaved people, and Christian missionaries.

However, it is important to note that many cultivated alien plants have contributed immensely to agricultural production and economic development in Africa. Nigeria, for example, is the largest global producer of several alien crops, including *Manihot esculenta* (cassava), *Colocasia esculenta* (taro cocoyam), and *Xanthosoma sagittifolium* (tania cocoyam), while West Africa combined has the highest *Theobroma cacao* (cocoa) production in the world (Onyeka 2014; Otekunrin et al. 2021). A significant portion of timber production in Nigeria also comes from industrial plantations of alien *Hevea brasiliensis* (Pará rubber tree), *Gmelina arborea* (gmelina), *Pinus caribaea* (Caribbean pine), *Tectona grandis* (teak), and *Eucalyptus* species (Akpan-Ebe 2017). *Zea mays* (maize), *M. esculenta*, *Oryza sativa* (rice), *Solanum lycopersicum* (tomato), and *Capsicum* spp. (chili peppers) have completely revolutionized local food systems and become the most consumed food in Nigeria. Introduced plants with significant economic uses are widely accepted in Nigeria because these food crops have desirable traits such as greater yield than the native crop relatives, faster vegetative growth, and relative ease of propagation. For example, *Zea mays* replaced sorghum and millet, Asian rice replaced African rice, while drought-tolerant cowpea varieties developed and introduced from India replaced local landraces (Havinden 1970). Consequently, several research institutes were established by the government for genetic improvements and conservation of these introduced plants. For instance, about 45% of plants being conserved in one of the major ex situ conservation sites in Nigeria (Borokini et al. 2010) are naturalized aliens. However, embracing alien food crops comes with a cost, such as genetic erosion of native food crops in West Africa and globally (FAO 1996).

Checklists of naturalized and invasive plants provide baseline data upon which further investigations should be conducted to elucidate the ecological and evolutionary processes aiding naturalization and invasion by alien species at various spatial scales. Therefore, beyond creating checklists of naturalized and invasive species that are crucial to improve our understanding of biological invasions (e.g., van Kleunen et al. 2015; Pyšek et al. 2017, 2020), it is advisable to study their direct and indirect impacts on communities and ecosystems (Jeschke et al. 2014; Kumschick et al. 2015b). Additionally, plant introductions do not only impact the receiving communities but also affect the wild stocks from where they were harvested. For example, our checklist of alien flora in Nigeria includes 22 near-threatened species, 47 vulnerable, 36 endangered, 25 critically endangered, and one extinct in the wild on the IUCN Red List of Threatened Species (Table S2; IUCN 2022). This highlights the importance of global trade regulations, such as CITES, to discourage overexploitation of these plants in their native distribution ranges for introduction to other regions. However, populations of introduced taxa could be used for demographic and genetic rescue programs of vulnerable taxa in their home ranges. Moreover, regional and global cooperation and exchanging information on alien flora are important to effectively manage biological invasions (Hierro et al. 2005; Latombe et al. 2017). Previous studies showed the rapid spread of *Chromolaena odorata* across West and Central African neighbors after its accidental introduction in Nigeria in 1937 (Uyi et al. 2014). A similar pattern of regional spread of invasive plants was also reported from South Africa, the entry point, to Zimbabwe, Malawi, and East Africa (Faulkner et al. 2017).

At the global scale, plant introductions continue to increase, resulting in greater chances for alien plants to naturalize and invade new regions (Seebens et al. 2017). Since not all introduced plants become invasive (Williamson and Fitter 1996; Jeschke and Pyšek 2018), it is increasingly important to identify traits associated with plant invasions at various spatial scales. We have shown that herbaceous, graminoid, and vine alien flora, and introduced plants originating from other tropical ecosystems, such as the Neotropics and Indomalaya, have greater chances of becoming naturalized and invasive in Nigeria. Such knowledge has significant conservation and policy implications, particularly in raising public awareness of deliberate and accidental plant introductions and strengthening public–private partnerships on ornamental plant introduction, trade, and propagation in Nigeria. Given limited funding and technological capacity to enforce quarantine laws and research activities, we recommend that priorities be given to preventing the introduction of alien plants with these attributes and public awareness of the ecological impacts of invasive species in Nigeria. We also recommend the establishment of state and federal registers of all botanical gardens and private floriculturists and their floristic inventories, similar to those managed by the Royal Horticultural Society in the UK (see Dehnen-Schmutz et al. 2007) and the United States Plants Invasive Species Database (Sutherland 2004).

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