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Patterns and drivers of alien plant species distribution in African forest habitats

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Richard Ndaki Banda

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Univ.-Prof. Mag. Dr. Franz Essl

Mitbetreut von | Co-Supervisor:

Dr. Ali Haroon Ali Omer MSc

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List of abbreviations

CHELSEA	: Climatology at High Resolution for the Earth's Land Surface Areas
DR Congo	: Democratic Republic of Congo
FAO	: Food and Agriculture Organisation
GLM	: Generalized Linear Model
IPBES	: Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
POWO	: Plants of the World
TDWG	: Taxonomic Databases Working Group
WCVF	: World Checklist of Vascular Plants
WEP	: World Economic Plants

Abstract

Globally, forests play vital roles in ecosystem processes and deliver ample services to people. Human activities have intentionally or accidentally moved species from their native regions across a geographical barrier into new habitats including forest ecosystems. The introduction of alien plant species in African forest habitats has the potential to transform these habitats and affect the services they provide for humans. Therefore, there is a need to assess the extent of alien plant species occurrence across African forest habitats. This study provides an assessment of the occurrence, spatial patterns, taxonomy, native origins, growth forms, economic uses, and drivers of alien (including planted) plant species richness across Africa's forests. Using the largest global vegetation plots database (i.e., sPlotOpen), the study identified 1,584 forest plots across 18 African countries. The forest plots extracted included plot data representing natural and semi-natural plant communities, while strongly human-altered systems like croplands and plantations were generally excluded. I used these plots information to assess spatial patterns and drivers of occurrence of alien plant species in Africa's forest habitats. I standardized the species names according to the World Checklist of Vascular Plants. Thus, only accepted plant species names according to WCVP were kept. The study recorded 1,433 alien plant species that occurred in at least one plot of African forest habitats. The results also show that these alien plant species were unevenly distributed across Africa, with the hotspots being the central and the eastern regions. The taxonomic analysis indicated that Fabaceae was the most represented family, and *Bauhinia* and *Senna* were the most frequent genera. On the regions of origin of the alien plant species, the results revealed that species predominantly originated from Southern America. Not surprisingly, 988 of the alien plant species in African forest habitat were free standing woody species (i.e., trees and shrubs). Alien plant species were used most commonly for medicinal purposes followed by material and environmental uses. I found that alien plant species richness in African forest habitat significantly increased with mean annual precipitation and significantly decreased with distance to cities, distance to seaports and mean temperature. This study provides baseline information on diversity and distribution of alien plant species within Africa's forest habitats that could help in forest management and conservation. The study results also highlight the combined roles of accessibility and environment in shaping patterns of alien plant species distributions in Africa.

Zusammenfassung

Wälder spielen global eine signifikante Rolle in den Ökosystemprozessen und stellen für die Menschheit eine Vielzahl von Dienstleistungen dar. Dieser Vorgang kann auf natürliche Weise oder durch menschliche Aktivitäten, absichtlich oder zufällig, erfolgen und zur Verbreitung von Arten in neue Lebensräume, einschließlich der Waldökosysteme, führen. Das Eindringen gebietsfremder Pflanzenarten in die afrikanischen Waldlebensräume birgt das Potenzial, signifikante Veränderungen der betroffenen Ökosysteme und ihrer Funktionen zu bewirken. Daher ist es notwendig, das Ausmaß des Vorkommens gebietsfremder Pflanzenarten in den Waldlebensräumen zu bewerten. Ziel der vorliegenden Arbeit ist die Bewertung des Vorkommens und der Ursachen gebietsfremder Pflanzenarten in Wäldern auf dem afrikanischen Kontinent. Die Zusammenführung umfassender Datensätze aus den globalen Vegetationsdatenbanken sPlot, World Checklist of Vascular Plants (WCVP) und den Datenbanken zu wirtschaftlichen Verwendungszwecken der World Economic Plants (WEP) wurde unter Verwendung der Programmiersprache R, Version 4.5.1, durchgeführt. Im Rahmen der Analyse wurden die räumliche Verteilung, die taxonomische Diversität, die Umweltfaktoren sowie die Verwendungsmerkmale der Arten untersucht. Die Ergebnisse zeigen, dass gebietsfremde Pflanzenarten ungleichmäßig verteilt sind. Hotspots sind in den zentralen und östlichen Regionen zu verzeichnen. Die taxonomische Analyse ergab, dass Fabaceae die am stärksten vertretene Familie sind, während die Gattungen *Bauhinia* und *Senna* am stärksten repräsentiert sind. Darüber hinaus zeigte die Reisezeit zu den Häfen keinen signifikanten Einfluss auf das Vorkommen der Arten, während die Intaktheit der biologischen Vielfalt und die Entfernung zu den Städten positive Zusammenhänge aufwies. Die höchsten Werte wiesen die medizinisch genutzten Arten auf, gefolgt von Arten, die als Material und für Umweltsanwendungen genutzt werden, was ihre Relevanz für den täglichen Lebensunterhalt und die ökologische Wiederherstellung widerspiegelt. Es besteht Bedarf an weiteren Studien, die sich mit den ökologischen Auswirkungen gebietsfremder Arten in Waldlebensräumen auseinandersetzen. Eine Überprüfung der ökologischen Auswirkungen und des ökologischen Nutzens der Arten ist erforderlich, um ein Gleichgewicht zwischen Naturschutz und wirtschaftlichen Gewinnen zu erreichen.

Introduction

Globally, forests play vital roles in ecosystem processes and deliver ample ecosystem services to people (World Bank Group, 2020). They provide shelter, food and breeding grounds for a wide range of plants, animals, fungi and microorganisms. Forests are increasingly affected by different anthropogenic activities. Biological invasion, for example, is an anthropogenic disturbance with profound and often cascading impacts on forest habitats (Liebhold et al., 2017). Historically, humans have accidentally and intentionally introduced several plants species into forest habitats across the globe (Hulme et al., 2008). Major efforts are essential to investigate the drivers and mechanisms of biological invasion within forest habitats. While some regions (e.g. Europe and America) are intensively researched, others, such as Africa, are understudied (Pyšek et al., 2008; van Kleunen et al., 2019). This imbalance might bias our knowledge of specific invasion patterns and mechanisms. Therefore, investigating biological invasion within Africa's forest habitats could offer a more comprehensive picture of biological invasions mechanism.

Africa's forests cover approximately 650 million hectares, representing about 16% of the global forest area, with most areas found in the central and southern parts of the continent (FAO, 2001; FAO 2025). The region hosts diverse forest ecosystems such as tropical rainforests, dryland forests, savanna woodlands, afro-alpine habitats, coastal montane and mangrove forests (Osewe et al., 2024). These ecosystems are crucial because they support various plants and animals and provide food and other essential services to people. However, occurrence of invasive plant species has caused degradation of resources across Africa. Invasive plants have affected native communities by altering ecosystem functions and disrupting natural regeneration (Barahukwa et al., 2023).

Alien species are organisms that have been moved by humans beyond the limits of their native geographic range (Blackburn et al., 2014; IPBES, 2023). Currently, a total of 16,429 alien taxa across geographic regions worldwide have naturalized, successfully established a self-sustaining population in at least one region outside of their native range (Davis et al., 2025). A subset of these naturalized plants has become invasive, threatening biological diversity, food security, and human health and well-being (IPBES, 2023). The spread of invasive alien species is one of the most important drivers of the global loss of biodiversity (IPBES, 2023). Although there are numerous drivers of alien species invasion, it remains unclear which

factors predominantly facilitate their establishment in the African forest habitats. In some cases, forests in urban and suburban landscapes have been found to contain a greater diversity of alien plant species than in those in landscapes dominated by less disturbed forests (Essl et al., 2011; Potter, 2024). This may lead to a conclusion that proximity to urban locations is one of the drivers of forest invasions. The likelihood of invasion is highest in fragmented forests within landscapes containing more than 10 % agricultural or developed land cover (Riitters et al., 2018). This suggests that agriculture and landscape structure are determinants of the spread of alien species. Viera et al. (2014) further suggested that proximity to residential areas is one of the causes of the spread of alien species as it has been found that the presence and diversity of alien plants in relatively undisturbed forests was associated to residential areas. However, Pysek et al. (2009) and Faulkner et al. (2020) recommended that the predominant driver of alien species invasion in forests is intentional introduction, reflecting deliberate human use of non-native species for forestry, agroforestry or other purposes.

The occurrence of alien plant species in African forest habitats has not been comprehensively evaluated, yet they have the potential to transform ecosystems and negatively affect human livelihoods. Alien plant species generate extensive financial costs relating to their removal, resource damages and losses (Diagne et al., 2021). Thus, there is an urgent need for an assessment of the extent of alien plant species occurrence across Africa's forests. Knowing the level of alien plant species incidences is crucial for formation of policy and effective management of biological invasions (Crooks, 2005). Having not comprehensively quantified the drivers and degree of spread by alien plant species in Africa's forests, this study provides a critical step to explain distribution patterns of alien plant species in forests.

This master thesis aimed to assess the distribution and diversity of alien plant species in African forest habitats. Specifically, it addresses the following research questions: (1) What is the extent and the spatial distribution pattern of alien plant species across African forest habitats? (2) How taxonomically diverse are the alien plant species? (3) What are the predominant native origins, growth forms and economic uses of the alien plant species? (4) What are the roles of anthropogenic pressures and environmental conditions in explaining the observed alien plant species richness?

Methods

Study area

This study focused on Africa which is the second largest continent with a total area of 30,365,000 km² (Britannica, 2025). Many regions of the continent are arid or semi-arid hence prone to extreme differences in the weather patterns, average annual rainfall ranges from less than 100 mm in desert regions to 10,000 mm in the wettest tropical parts of the continent (Niang et al., 2014). Substantial variations in rainfall and temperature exist as the continent ranges from hot deserts to equatorial rainforests. The central region of the continent experiences more rainfall and tropical climates. The topography is characterized by plateaus, mountains and coastlines along its edges. The African continent is habited with a large number of species and diverse habitats with a unique flora and fauna. The landscape ranges from tropical rain forests in the equatorial region to grasslands and savanna woodlands. It consists of the Sahara in the north and Kalahari deserts in the south. Climate change models show that Africa is the continent that is severely impacted by climate change (Niang et al., 2014).

African forest plots data

Data on distribution of alien plant species in Africa's forest habitats were obtained from the publicly available sPlotOpen database (Sabatini et al., 2021). sPlotOpen is a public global vegetation database, with data on plant species co-occurrence for 95,104 vegetation plots. To select plots within African forest habitats, I filtered sPlotOpen data to include only plots that are located in Africa and further refined to retain only those classified as forest plots. Therefore, the final dataset includes 1,584 unique forest plots located in 18 African countries (Table 1). The forest plots extracted from sPlotOpen included vegetation-plot data representing natural and semi-natural plant communities, while strongly human-altered systems like croplands and plantations were generally excluded (Bruehlheide et al., 2019). Then, I used the unique identification numbers to extract species list corresponding to the filtered African forest plots. I removed taxa to the genus level only (i.e., when the species names are missing) to increase the taxonomic resolution in the species list and enable the alignment with our databases (see below). Furthermore, I standardized the species names according to the World Checklist of Vascular Plants (WCVP) (POWO, 2025). Thus, only accepted plant species names according to WCVP were kept.

Table 1. Forest plots distribution, average plot size and median recording year across African countries. Median year information is unavailable for some countries because no plot recording dates were provided in the dataset.

Country	Number of plots	Average size of the plots	Median Year
Ivory Coast	518	400	4/17/2013
DR Congo	140	625	1/1/2012
Guinea	139	400	2/14/2013
Angola	135	100	5/27/2012
Burkina	123	25	10/7/2002
Senegal	119	400	12/10/2012
Liberia	80	400	5/24/2012
Ethiopia	67	400	1/1/2007
Madagascar	47	100	NA
Botswana	44	1000	11/28/2014
Namibia	44	1000	9/8/2008
Cameroon	33	100	NA
Zimbabwe	24	8950	NA
Gabon	22	100	NA
Tanzania	16	100	NA
Central African Republic	14	100	8/10/1973
Mauritius	10	100	NA
Morocco	9	100	6/19/2002
Total	1584		

Native and alien species status

Plants of the World Online database (POWO, 2025) was used to identify native and alien status of plants species that occur in African forest plots. For each of the 18 African countries in which the selected Africa forest plots occur, I extracted the list of native plant species from POWO. Each plant species in each plot was assigned a “native” status when it was within the list of native species of that country, or “alien” when

it was not found in that list. Note that alien species identified in the plots contain species independent if they were invading the plot on their own means (i.e., reproducing and spreading autonomously, being casual or established (Pysek et al. 2004) or if they had been planted by humans (i.e., plantations), as available data do not allow to differentiate them. The final list of alien plant species in African forests therefore included 21,507 records of alien plant species incidences across all the 1,584 plots.

Alien plant species taxonomy

I conducted a taxonomic analysis to assess the diversity of the alien plant species across African forest habitats. All plants recorded within the plots were identified to the genus and family levels, and accepted family and genus names were standardized using the WCVB backbone. To characterize floristic composition, I analyzed taxonomic incidences across all plots, then calculated family and genus level richness of alien species and their plot occupancy (i.e., the total number of unique families and genera present across all plots).

Alien plant species native origins, growth forms and economic uses

To assess if alien plant species in African forest plots come from specific native origin, I assigned each species to its continent(s) of origin, using the continental scheme of the Taxonomic Databases Working Group (i.e. the nine TDWG-I regions) (Brummitt, 2001). To do that, I combined the list of alien plant species in African forest plots with the global list of native distribution POWO. Then, I calculated the frequency of native origins among the list of alien plant species. Moreover, to assess if alien plant species in African forest plots are biased with regard to plant growth form, I assigned each species to its growth form. I collected growth-forms data from Omer et al. (2021). The growth forms were harmonized into seven standard categories: short-lived (i.e. annual or biennial), free-standing herb, long-lived free-standing herb, free-standing woody, aquatic, climber, epiphyte and parasite. As no species was aquatic, I did not consider this category in the analyses. Finally, to assess if alien plant species within Africa forest habitats have specific economic uses, I extracted the known economic uses of each alien plant species from the World Economic Plants (WEP) database (National Plant Germplasm System GRIN-GLOBAL; <https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearchWEP>). Then, I calculated the frequency of different economic uses among the list of alien plant species.

Drivers of alien plant species richness

I considered a range of variables as the potential drivers of alien plant species richness in Africa's forests. For each plot, I extracted mean annual temperature and total precipitation (average of the baseline period 1979–2013) from the CHELSA climate database (Karger et al., 2017), distance to nearest seaport and nearest city from Nelson (2019), mean native species richness from Cai et al. (2023), and biodiversity intactness (i.e., average abundance of native terrestrial species in a region compared with their abundances before pronounced human impacts) from Newbold et al. (2016). To test for the association between alien plant species richness and the above-mentioned drivers, I run a Generalized Linear Model (GLM) with a negative binomial distribution to deal with overdispersion in the data. A Correlation test for the driver variables was conducted and some were found to be highly correlated. However, the GLM for each explanatory variable was run separately to avoid affecting the results of individual variable.

Results

Distribution and characteristics of African forest plots

The final dataset of vegetation plots categorized as forest habitats included 1,584 plots located in 18 African countries. These were extracted from the sPlotOpen global vegetation plots database with the highest number of plots recorded in Ivory Coast (518 plots), followed by the Democratic Republic of Congo (DR Congo) (140 plots) and Guinea (139 plots). Fewer numbers of plots were observed in countries such as Mauritius (10 plots) and Morocco (9 plots). Plot size varied between 25 m² and 33,800 m², with median size being 400 m². Plots have been surveyed between 1973 and 2014 with a median year being 2007.

Spatial distribution of African forest plots showed uneven distribution across the continent (Fig. 1). Plots were mostly distributed in clusters. The clusters may be associated with availability of plots data and differences in environmental conditions. More plots were concentrated in west Africa, in the eastern part there were few forest plots in Ethiopia, Tanzania and in the islands of Madagascar and Mauritius. In the southern part, some plots were identified in Namibia, Democratic Republic of Congo, Angola, Zimbabwe and Botswana. In the north some plots were displayed in Morocco. As far as physical features are concerned, there is notable presence of plots along coastal regions and islands.

Native and alien plant species diversity in African forest plots

Overall, the number of native and alien plants species combined per plot range from 1 to 196, with a median of 8 plant species. The plots varied in size, ranging from 25 m² and 33,800 m². Across all the 1,584 plots, alien plant species were recorded in 582 plots (36%). In the plots containing alien plants species, the number of alien plant species per plot range did not change (from 1 to 196 species), but the median increased from 8 to 17 plant species. The proportion of alien plant species to the native species ranges from 0 with no alien species in the plot to 1 with all the plant species recorded in the plot being alien. Moreover, the richness of alien plant species in African forest plots range from a minimum of 1 to a maximum of 119 species per plot (Fig 1).

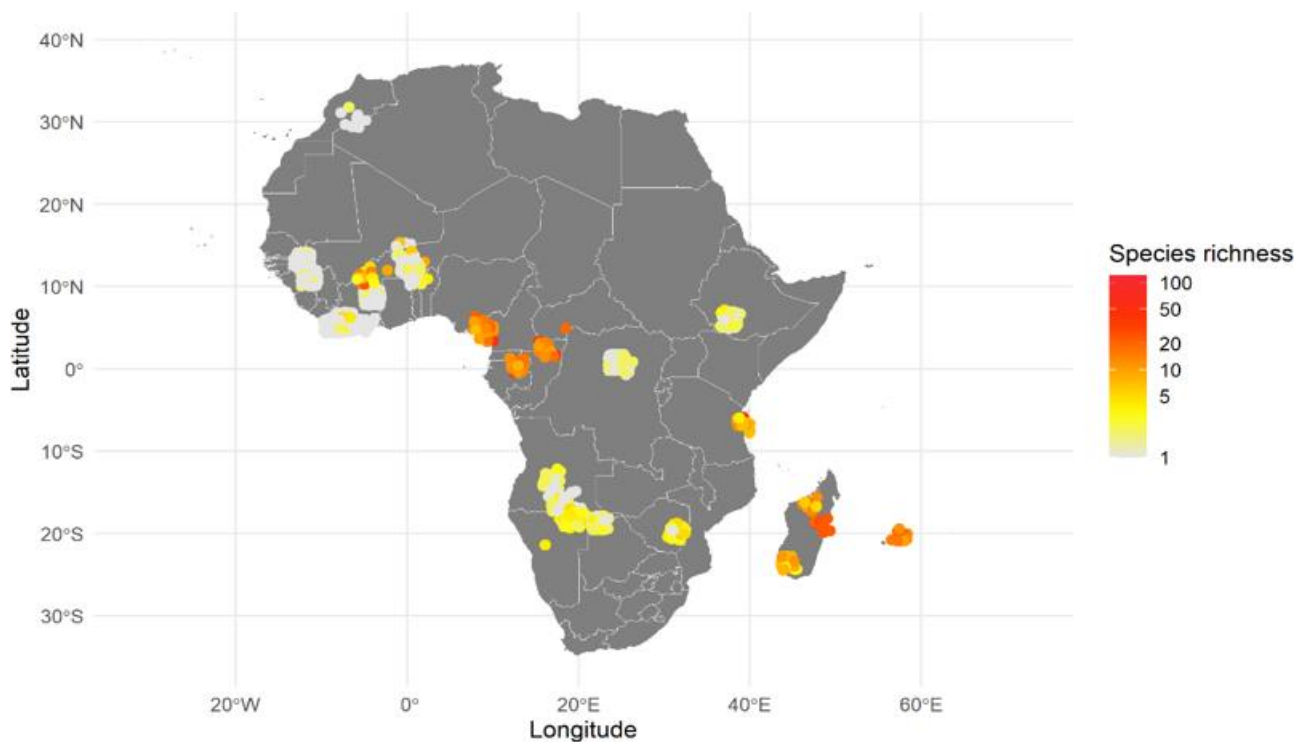


Fig 1. Map of Africa showing the locations of forest plots included in this study. Dots represent locations of the plots (jittered to enhance visualization). The color of the dots represents alien species richness (i.e., number of alien plants per plot).

Alien plant species taxonomic composition

The resulted list of alien plant species showed that there are at least 1,433 alien plant species found in African forest habitats. This number includes all species that are not native to the country where a plot is found. It is amalgamation of planted occurrences and of species that are invading on their own (i.e., being

casual or established). The distribution of the alien species varied considerably. A few species were recorded several times (e.g., *Achyranthes aspera* was recorded 28 times), however, most species were recorded only once (Supporting Information Table S1). The results also showed that the alien species belong to 151 families (Supporting Information Table S2) and 673 genera (Supporting Information Table S3). On the genus level, species of the genus *Bauhinia* were recorded most frequently (94 plots), followed by species of the genus *Senna* (50) (Fig. 2). On the family level, Fabaceae family dominated among the alien plant species, appearing in 403 plots (Fig. 3).

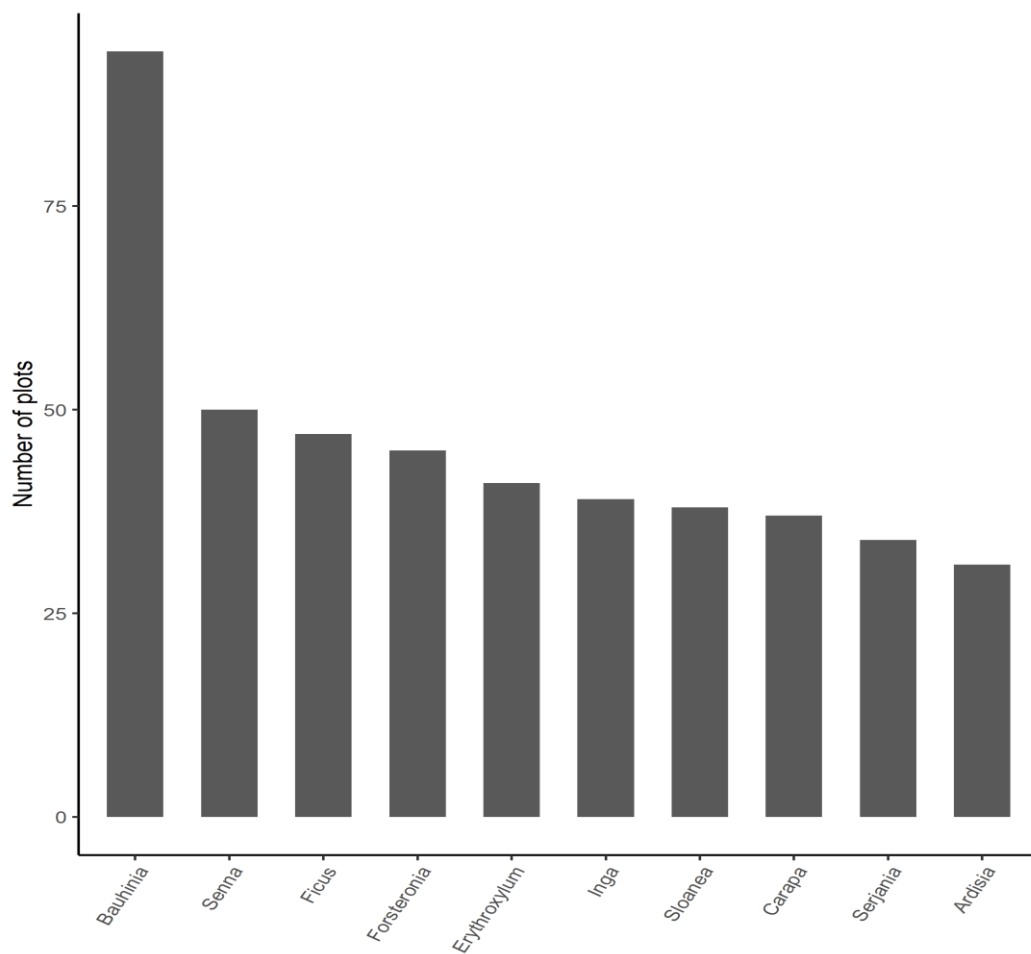


Fig 2. Ten most dominant genera of alien plant species identified in the African forest plots. Bars represent the total number of plots where each of the genres were recorded.

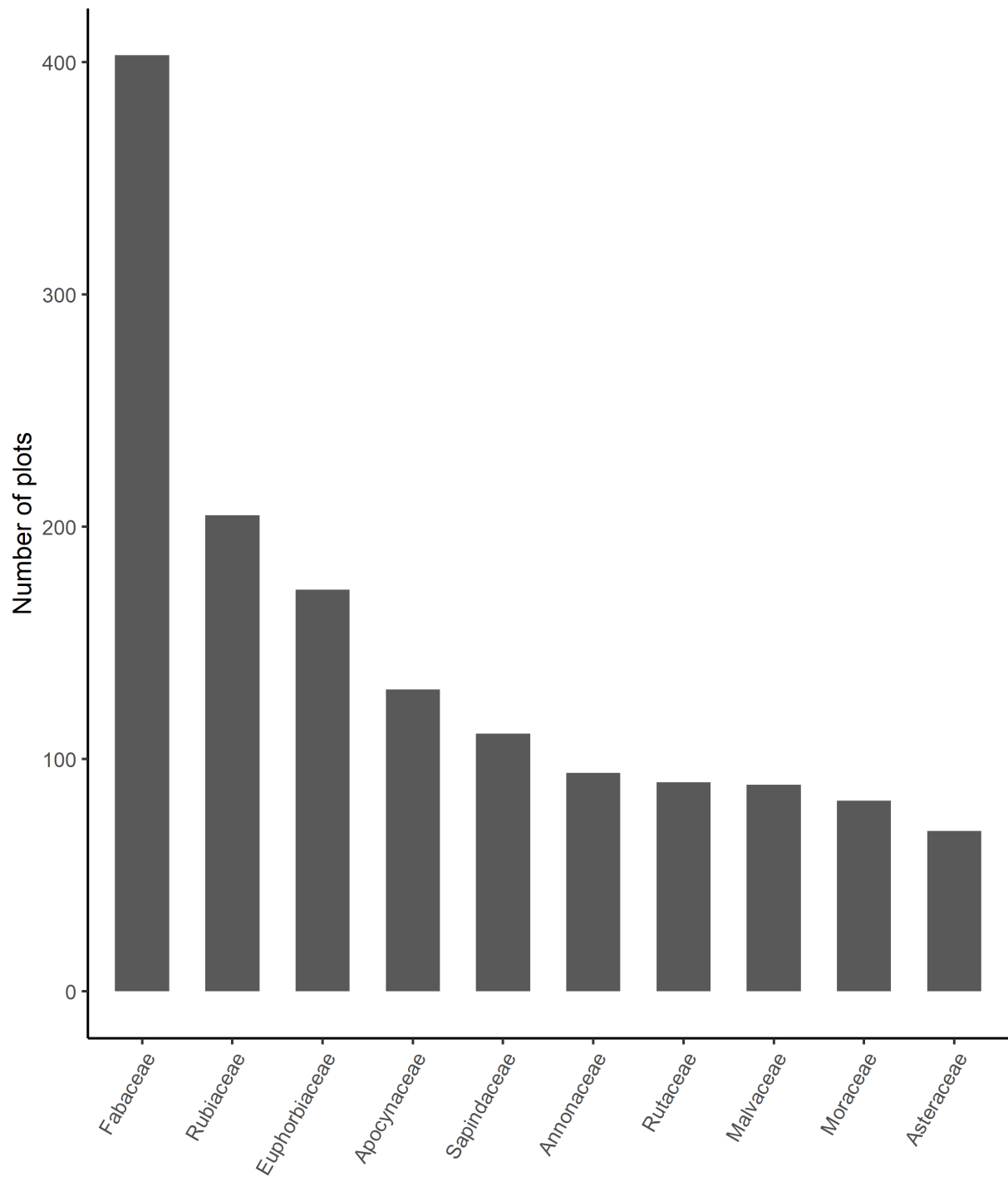


Fig 3. Ten most dominant families of alien plant species identified in African forest plots. Bars represent the total number of plots where each of the families were recorded.

Alien plant species native origins

The results on the origin of the alien plant species showed uneven contributions of the different continents of origins. South America registered the highest number of alien plant species, with Africa coming second, followed by Northern America and Tropical Asia, while the remaining continents contributed only few numbers of species (Fig 4).

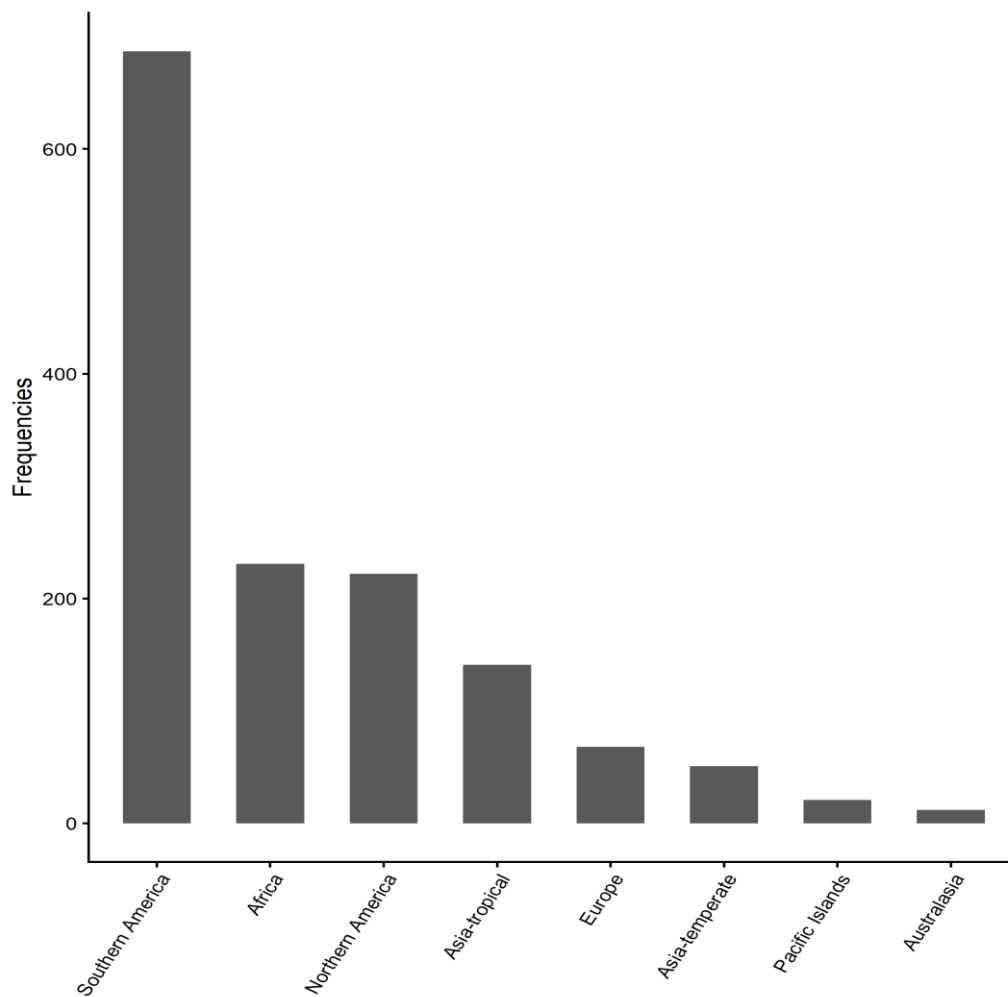


Fig 4. Continents of origin of alien plant species found in African forest plots. If a species is native to more than one continent, then it is assigned to each continent.

Alien plant species growth forms

Alien plant species were categorized into different growth forms of epiphyte, climbers, parasites, free-standing woody, short-lived herb and long-lived herb (Table 2). Free-standing woody species such as trees and shrubs were by far the most abundant growth form (988), followed by climbers such as woody or

herbaceous species that depends on surrounding vegetation (265) and short-lived herbs (154). Epiphytes (31) and parasites (7) were the least recorded (Fig. 5).

Table 2. Frequency distribution of alien plant species among the growth form categories across the African forest plots.

Growth Forms	Frequency
Free standing woody	988
Climber	265
Short lived herb	154
Epiphytes	31
Parasite	7

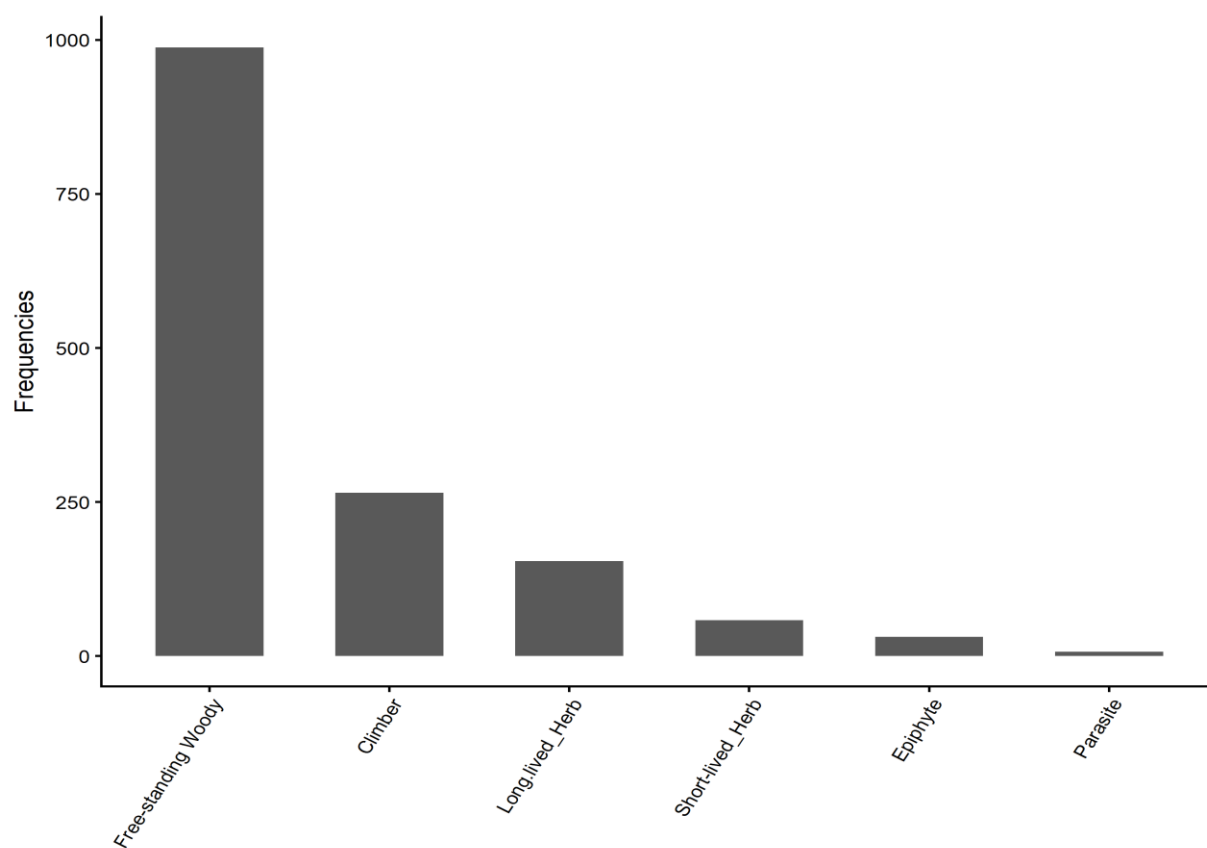


Fig 5. Frequency distribution of alien plant species across the plots among the growth form categories.

Alien plant economic uses

The result on the alien plant species economic uses illustrated that the medicinal usage had the highest number of species recorded, followed by material and environmental uses. Other categories like social use, bee plants, invertebrate food and non-vertebrate poison (plant species that produce chemical compounds toxic to invertebrates) had fewer species incidences (Fig. 6).

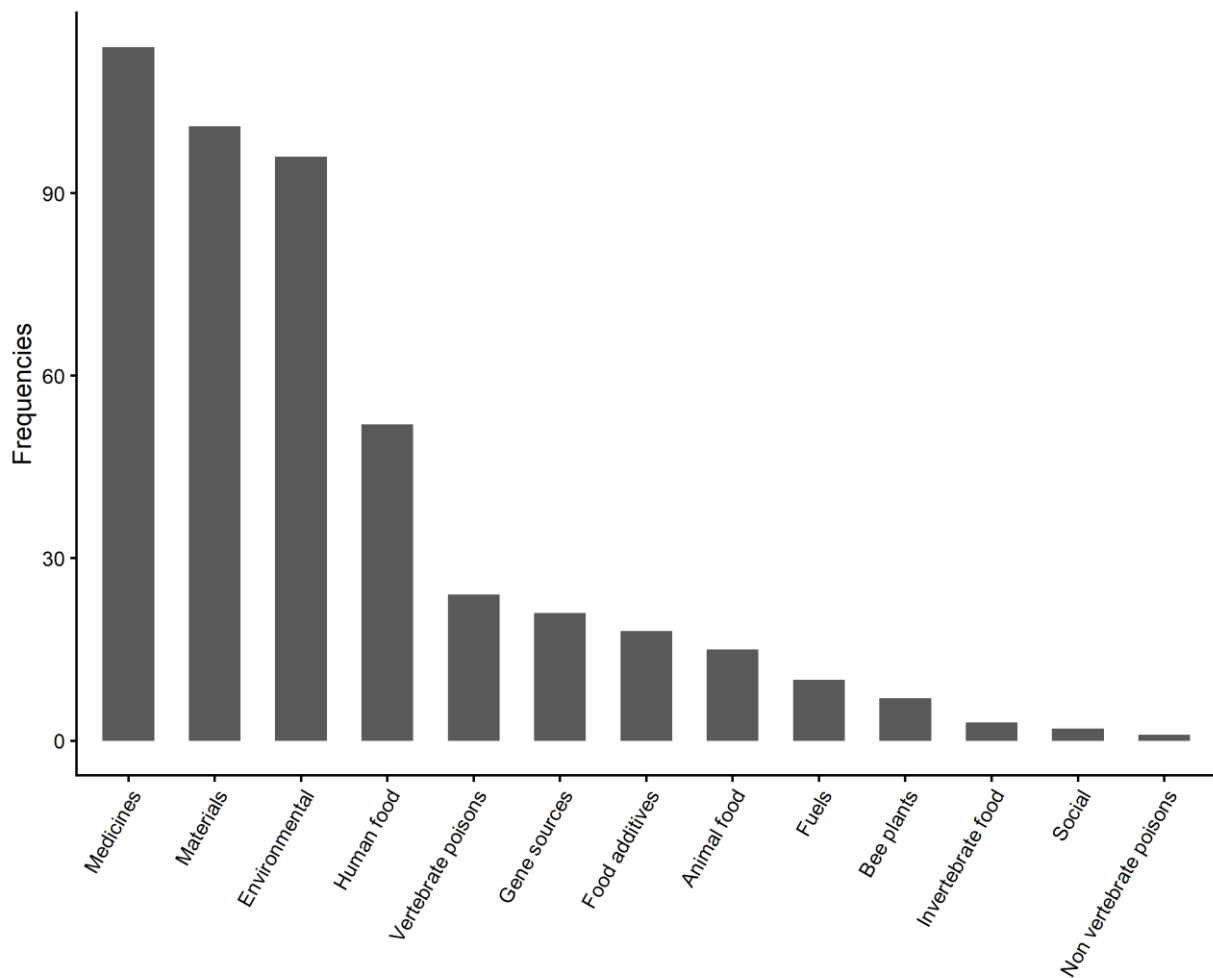


Fig 6. Frequency distribution across different economic use categories of alien plant species recorded in African forest plots.

Drivers of alien species richness

Environmental conditions and accessibility correlate with the richness (i.e. the number) of alien plant species across Africa's forest plots (Table 3 and Fig. 7). Significantly, higher number of alien plant species were recorded in plots with lower annual mean temperature with $p < 0.001$. Annual precipitation suggests a significant positive relationship with $p < 0.001$, this indicates that wetter areas tend to have more alien

species. Forest plots that were located close to cities and seaports were richer in alien plant species compared to plots far away from the cities and seaports with ($p < 0.001$ in both cases). This means that alien species richness declines as distance from seaports and cities increased. Furthermore, the association between biodiversity intactness and alien plant species richness across Africa's forests showed a positive non-significant relationship with $P < 0.139$. The study results also showed that native species richness had no significant effect on alien plant species with $p = 0.651$. This suggests that native species richness does not have a detectable effect on alien species richness in this model (Table 3).

Table 3. Generalized Linear Models (GLM) testing results for the relationship between alien plant species richness and distance to cities, distance to seaports, native richness, annual mean temperature, annual precipitation, and biodiversity intactness.

Predictor	Estimate	Std. error	Z value	P value
Distance to seaports	-0.30	0.061	-4.96	$0 < 0.001$
Distance to cities	-0.35	0.060	-5.82	$0 < 0.001$
Native richness	0.026	0.059	0.45	0.651
Annual mean temperature	-0.50	0.060	-8.22	< 0.001
Annual precipitation	0.33	0.063	5.16	< 0.001
Biodiversity intactness index	0.09	0.063	1.47	0.139

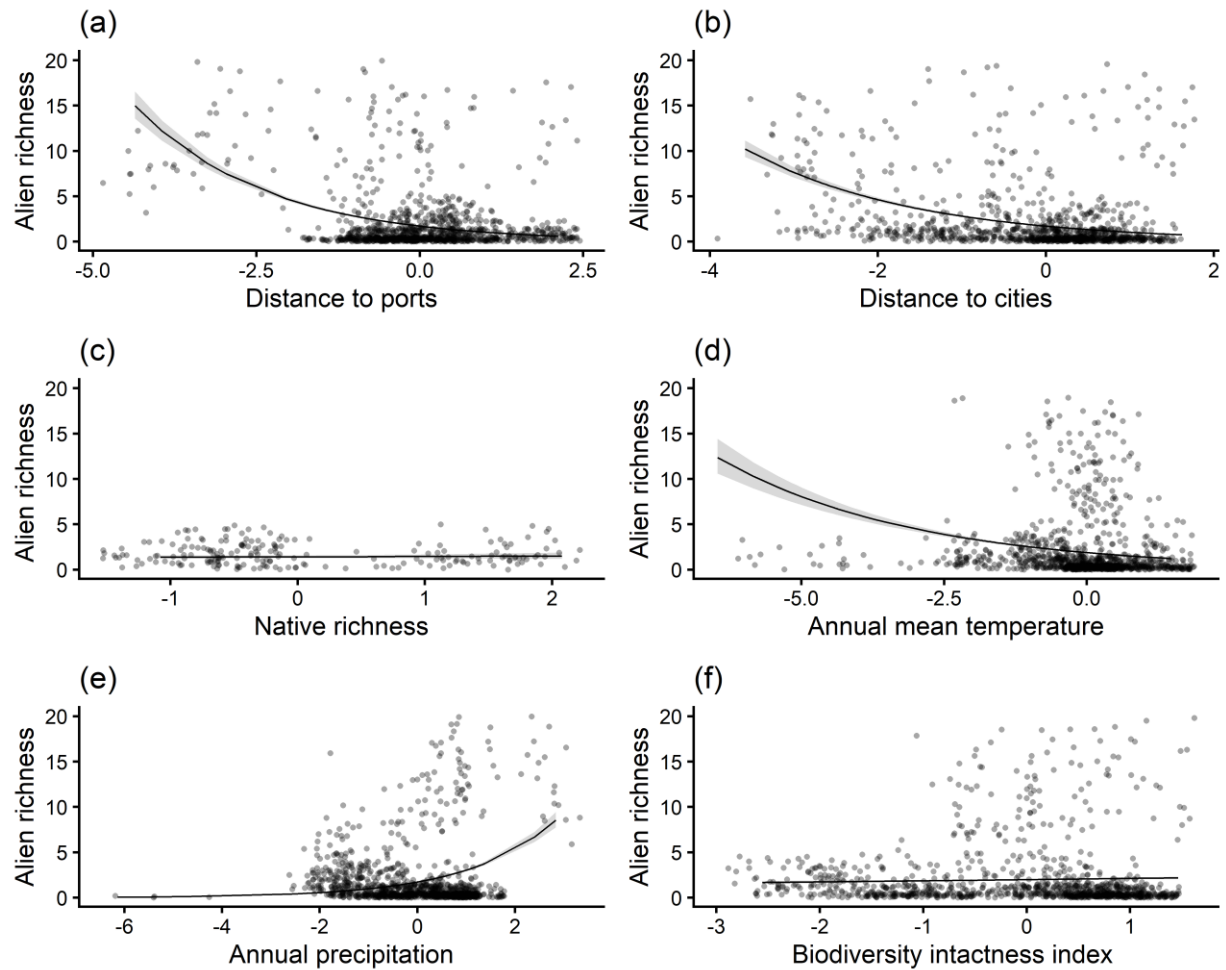


Fig 7. Richness of alien plant species in African forest plots in relation to (a) distance to seaports, (b) distance to cities, (c) native species richness (d) annual mean temperature (e) annual precipitation and biodiversity intactness index (f). The solid black lines are the predicted relationships from GLMs and the dashed grey lines indicate the 95% confidence intervals. The values of alien species richness are shown as dots.

Discussion

Distribution and characteristics of African forest plots

The uneven distribution of forest plots across the African continent with plots clustered within only 18 African countries reflects sampling biasness. Reddy and Davalos (2003) reported that biodiversity sampling in Africa is strongly influenced by accessibility factors such as proximity to roads, rivers and cities leading to uneven spatial representation. Regions that are more accessible have been studied more intensively than remote locations, politically unstable regions and areas with poor infrastructures. This has resulted in variations in data availability, research capacity and site accessibility. There has also been inequality in research interests, funding opportunities and technical expertise across Africa, regions with strong research institutions and conservation projects tend to support more ecological data than those with limited resources. Kapfer et al. (2017) reported that historical vegetation plots are frequently revisited because they provide long-term ecological data, but their repeated use has resulted into sampling biases. In addition, Küper et al. (2006) found that plants distribution records in sub-Saharan Africa were highly uneven, with some regions having extensive records while others remained poorly documented.

Native and alien plant species diversity in African forest plots

The results indicated that alien plant species were widespread occurring in 36% of the total plots with their presence appearing to be associated with plots containing high overall species richness. The wide range in alien species richness per plot, indicates that alien species spread intensity varies among plots. Some plots contained only a few alien species, while others were heavily invaded. This may also reflect on resources availability amongst the plots. The hotspots of alien plant species distribution in central and eastern Africa as well as the islands of Madagascar and Mauritius might be due to wide range of favorable environmental conditions that support greater diversity of alien plant species. Stein et al. (2014) reported that environmental variations is one of the strongest predictors of species diversity because variations in vegetation, climatic conditions, soils, and topography create a wider range of ecological niches and habitats. Dawson et al. (2017) also found that alien species richness is higher in warm and productive regions where climatic conditions favor their establishment. Therefore, the patterns observed especially in central Africa may be due to its favorable climatic conditions and huge forests cover, which provide suitable

habitats for a wide range of species (Hulme, 2009). The high concentration of alien plant species in coastal regions is likely linked to global trade. According to Hulme (2009) the exposure of the coast regions to trade in merchandise imports has accelerated biological invasions, especially for island ecosystems.

Distribution of alien plant species across taxonomic groups

The alien plant species were ranked based on family and genus hierarchy to assess the taxonomic diversity. Among genera, *Bauhinia* was the most dominant, followed by *Senna*, *Ficus* and *Forsteronia*, while genera such as *Serjania* and *Ardisia* occurred in fewer plots (Fig. 3). The high frequency of *Bauhinia* and *Senna* may be due to their economic uses and strong ecological adaptability in different habitat categories. Some studies have found that some *Bauhinia* species are extensively used in traditional medicine and food, making them culturally and economically significant (Chen et al., 2024). These uses can lead to deliberate cultivation or spread, increasing their frequency in forest habitats. Further, studies on *Senna* species reported that the species can grow in a wide range of habitats across geographic ranges and can tolerate a variety of climatic conditions, demonstrating its ecological plasticity (Weldemariam and Dejene, 2021). Among plant families, Fabaceae were identified as the most dominant family, followed by Rubiaceae and Euphorbiaceae, (Fig. 4). This dominance may be in connection to their broad ecological tolerance, high dispersal capacity and economic uses. Members of Fabaceae are highly diverse and thrive across diverse conditions with nitrogen-fixation abilities and functional adaptability (Sazada, 2025; Vitousek, 2013). Similarly, Rubiaceae include species that are well adapted to diverse climatic and edaphic conditions, which may explain their widespread occurrence across the identified plots (Yang et al., 2025). However, families such as Rutaceae, Malvaceae, Moraceae, Asteraceae and genera *Serjania* and *Ardisia* were less frequently recorded, this might be due to their less economic importance and ability to adapt in different environmental conditions. According to Pennington et al. (2009) their lower representation may be due to narrower ecological niches and limited distribution compared to the dominant families. Specialization can limit the geographical range of organisms, thus promoting endemism (Nery et al., 2023). It is also possible that these families are more sensitive to environmental constraints or human disturbance, which may influence their lower spatial occurrence. The taxonomic analysis overall patterns of dominance, suggest that

species with broad ecological tolerance and effective dispersal strategies are more likely to be widely represented across plots, while less adaptable remain restricted in terms of distribution.

Alien plant species native origins, growth forms and economic uses

The results revealed that alien plant species predominantly originated from Southern America followed by Africa and Northern America. The difference in native origins suggests that the spread is strongly influenced by human activities and environmental suitability. Historically, both Southern and Northern America have long histories of agricultural and horticultural exports and imports with Africa (Pinilla and Aparicio, 2015). This may increase the likelihood of species being transported unintentionally or deliberately across these continents. These suggestions are in agreement with Hulme (2009) who found that trade routes and shipping connections between continents can act as major pathways for the spread of alien species. Another important driver suggested is environmental conditions similarities. Southern America and Africa share similar climatic conditions, which may enhance the survival and establishment of introduced species. This is in agreement with the findings of Fan et al., (2025) that species are more likely to naturalize in recipient regions where climates are similar to those of their donor regions. However, species from other regions such as Europe, Asia and Australia may face greater environmental variations, reducing their success as invaders in Africa. Knowing the dominant native regions of alien species is crucial for developing prevention strategies towards high-risk pathways and regions.

Growth forms demonstrated that free-standing woody species such as trees and shrubs were the most dominant species, followed by climbers and short-lived herbs. Epiphytes and parasites were the least recorded. The free-standing woody species may be the most common growth forms in forest plots because they form the main structure of the forest. Trees and shrubs have larger sizes, longer lifespan, and ability to occupy both canopy and understory layers (Díaz et al., (2016). The results also suggests that epiphytes and parasitic plants are generally the least recorded because they occupy more specialized ecological niches and are often under-recorded in vegetation surveys because many occur in the higher canopy, making it hard for them to be detected than trees, shrubs, climbers, or herbs which are found closer to the ground (Palacios and Franco, 2001).

The frequency distribution of use categories reveals a strong dominance of medicinal, followed by material, and environmental uses compared to other categories. Studies across Africa and tropical regions consistently reported that alien plant species are frequently used for medicinal purposes more than for other categories like food or ornamentals. For example, Githae et al. (2015) found that a large proportion of alien species in Kenyan agroforestry were valued for their medicinal properties. This suggests that most alien species were intentionally introduced for medicinal, material or conservation purposes, highlighting the role of humans in driving the alien plant species patterns and richness. The high representation of medicinal uses may also reflect the reliance on traditional remedies and local means. Material and environmental categories also showed high frequencies, indicating the importance of these resources in construction, tools, and environmental management practices. These findings provide evidence on the crucial roles of natural resources in sustaining livelihoods, particularly in Africa where access to industrial alternatives is limited. However, other categories such as fuels, bee plants, invertebrate food and poison-related uses had lower frequency. This low dominance may be explained by limited demand or ecological constraints affecting the availability of suitable species for these purposes. The pattern may also explain biases as knowledge about medicinal and material uses is often more widely shared and documented than knowledge related to specialized categories such as bee plants, poisons or ritual uses (Rafiu and Omotayo, 2025). Therefore, the lower representation of some categories may be partly as a result of underreporting rather than true scarcity. Understanding these patterns provides important insight into human and environment interactions and can guide conservation and policy efforts.

I found that while travel time to cities and seaports, mean temperature and total precipitation significantly influence the alien plant species richness, the influence of biodiversity intactness and native species richness was not significant. The negative relationship revealed between travel time to cities and seaports suggests that proximity to seaports and urban centers play an important role in shaping alien species distribution. Urban areas and ports undergo human activities and land use practices which might lead into the introduction or spread of alien species. Marques et al. (2020) suggest that alien species often flourish and become invasive in urban ecosystems, urbanization provides resources, which allows alien species to

flourish. Trade and transport infrastructure (seaports) facilitates the introduction and spread of alien species by acting as entry points and dispersal corridors (Bagnara et al., 2022). Annual mean temperature also showed strong negative relationships, suggesting that cooler conditions are more favorable for the alien plant species than warmer conditions. Plants naturalization significantly depends on ecological similarities between donor and recipient regions (Fan et al., 2025). The finding that the species preferred cooler weather conditions, raise suggestions that the alien plant species might have been introduced from cooler climatic regions. This is also in agreement to a study on invasive alien plant species in Korea which found that hotspots of alien plants were associated with lower climatic stress, characterized by low variability in temperature and precipitation, (Oh, et al., 2021).

Mean annual precipitation showed strong positive relationship with alien plant species number per plot ($ES = 0.565$, $p = <0.001$). Areas with high precipitation have abundant resources and tend to support more species. These are also regions with more agricultural activities which may lead to the introduction of alien species. The biodiversity intactness and native species richness revealed non-significant positive relations which seem to contradict with the idea that diverse communities resist invasion (Yuan and van Kleunen, 2022). It might be that there are several other ecological reasons like abundant resources and more heterogeneous habitats, instead of resisting invaders, these systems may actually support more species overall. These suitable conditions might favour both native and alien species, leading to a positive correlation between alien plants richness and biodiversity intactness and native species richness. The results concur with the findings of Tarasi and Peter, (2017) suggesting that exotic richness increases with biodiversity richness. Sometimes disturbances like construction works, agriculture and fire incidences can create empty niche for alien species establishment (Davis et al., 2001). Overall, the results highlight the combined importance of accessibility and environmental factors in explaining variation in alien plant species richness.

Conclusion

The study aimed at examining the distribution of alien plant species diversity and the factors driving their spread and richness across the African forest habitat. The results showed that African forests plots are clustered and unevenly spread in different regions around the continent. Alien plant species are equally

unevenly distributed across the forest plots with higher concentrations occurring in central and eastern Africa and Madagascar. Taxonomic analysis revealed that alien species belonged to a larger number of genera than families with the free-standing woody species being the most common growth form. The alien plant species in African forest plots were predominantly originated from South America. The results further highlight that most alien plant species might have been introduced mainly for medicinal purposes. The combination of accessibility and environmental factors are suggested to be the main drivers of the species richness. Proximity to cities and seaports, were among the strongest predictors of alien species richness with high species richness recorded in areas close to the cities and seaports. Climatic conditions also contributed, with colder and wetter areas supporting greater alien species richness.

My findings provide insights for predicting spatial patterns and for informing management and planning strategies aimed at mitigating or monitoring biological invasions. However, the study also faced limited geographic coverage, missing variables and incomplete species records. Further, future studies should include additional environmental factors and socioeconomic activities to understand the processes driving alien species spread and support conservation and management strategies.

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Supporting Information

Table S1: list of alien plant species and the number of their records in African forest plots

<https://raw.githubusercontent.com/rndakibanda2804-ui/Richard-Ndaki-Banda-thesis-project/refs/heads/main/species%20table.csv>

Table S2: list of families and the number of their records in African forest plots

<https://raw.githubusercontent.com/rndakibanda2804-ui/Richard-Ndaki-Banda-thesis-project/refs/heads/main/families%20table.csv>

Table S3: list of genera and the number of their records in African forest plots

<https://raw.githubusercontent.com/rndakibanda2804-ui/Richard-Ndaki-Banda-thesis-project/refs/heads/main/genra%20table.csv>