

Patterns in the alien flora of the Democratic Republic of the Congo: a comparison of Asteraceae and Fabaceae

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Background and aims – This work provides the first pattern analysis of the alien flora of the Democratic Republic of the Congo (D.R. Congo), using Asteraceae and Fabaceae as a case study.

Methods – Based on herbarium collections, existing databases, and literature data, a database of 38 alien species of Asteraceae and 79 alien species of Fabaceae has been assembled. Patterns in the introduction pathway, phylogeny, life form, morpho-functional traits, geographic origin, and occurrence in D.R. Congo are explored.

Key results – America is the main source continent in both families, but Asia is also an important donor of Fabaceae. Taxonomic spectrum discrepancies between the alien and the native flora reflect the continent of origin. Sixty-six percent of alien Asteraceae have been accidentally introduced, most of which being annual weeds of disturbed soil. In contrast, 90% of alien Fabaceae have been deliberately introduced for forestry, agriculture, or environmental purposes, most of which being phanerophytes. Traits were compared between pairs of congeneric alien and native species. For Asteraceae, a sharp discrepancy was found in the life form spectrum (aliens: mostly therophytes; natives: phanerophytes). For Fabaceae, alien species had larger leaves and larger pods compared to their native congeners. The number of specimens in collections was positively correlated with the time since the date of first collection for both families. The Guineo-Congolian region has the highest number of alien Fabaceae, while alien Asteraceae are overrepresented in the Zambebian region.

Conclusions – Contrasting patterns between alien Asteraceae and Fabaceae in the flora of D.R. Congo in terms of life forms, trait divergence compared to the native flora, and occurrence, reflect the divergent biological attributes and relations to humans of the two families. The striking discrepancies between the two families call for analyses of patterns of alien flora at family level and warn against global generalisations.

Keywords – Alien; Asteraceae; checklist; congeneric pairs; Fabaceae; invasion; life form; naturalization; traits; tropical Africa.

INTRODUCTION

Non-native organisms represent an ever-increasing proportion of the biota worldwide (van Kleunen et al. 2015; Pyšek et al. 2017; Turbelin et al. 2017; Seebens et al. 2018; Essl et al. 2019) and the problem of alien species has become a global conservation issue (Mack et al. 2000; Pyšek & Richardson 2010; Lambertini et al. 2011; McGeoch et al. 2016).

Tropical Africa is one of the most species-rich regions in the world (Küper et al. 2005; Sosef et al. 2017) and alien species could represent a serious threat (Stadler et al. 2000; Chenje & Mohammed-Katerere 2006; Howard & Chege 2007; Binggeli 2011; Obiri 2011; Borokini 2011; Foxcroft et al. 2013). However, alien plant introductions have only recently been recognised as a priority concern in tropical Africa (Howard & Matindi 2003; Holou et al. 2013; Boy & Witt

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2013, IUCN/PACO 2013; Gichua et al. 2013; Seburanga et al. 2016; Turbelin et al. 2017). With the notable exception of South Africa (Richardson et al. 2020), sub-Saharan Africa lags far behind in terms of research on alien species (Binggeli et al. 1998; Pyšek et al. 2008), although there have been increasing efforts to fill this gap of knowledge during the last decade (e.g., Foxcroft et al. 2010; Borokini 2011; Obiri 2011; Boy & Witt 2013; Holou et al. 2013; Seburanga et al. 2016; Noba et al. 2017; Witt et al. 2018).

Compiling alien flora inventories is an essential step to initiate monitoring and assess the impact of alien species (Pyšek et al. 2004; Randall et al. 2008; McGeoch et al. 2016; Latombe et al. 2017). Exploring patterns in the alien flora of a territory can provide insights into the origin and pathways of introduction of aliens (Ansong et al. 2019). The alien and the native flora often have a distinct phylogenetic assemblage, which has implications for interactions with the resident biota (Divíšek et al. 2018). Pattern analysis in such inventories also helps prioritise management actions (Randall et al. 2008; McGeoch et al. 2016). Pattern analysis should include species traits and introduction characteristics (Dawson et al. 2011). Comparison of functional traits between the alien and the native flora has provided key insight into the biological attributes underlying establishment, naturalisation, and invasion success (Pyšek & Richardson 2007; Ordóñez et al. 2010; van Kleunen et al. 2010, 2014; Gallagher et al. 2015; Moravcová et al. 2015; Divíšek et al. 2018). However, the factors explaining the success of alien plant species, including propagule pressure and residence time, are different at different stages of the invasion (Dawson et al. 2009, 2011).

Many tropical African countries suffer from a lack of alien species inventories (but see Maroyi 2012; Rejmánek et al. 2016; Noba et al. 2017; Witt et al. 2018; Ansong et al. 2019). They seem to host relatively low numbers of alien species (Pyšek et al. 2017; Turbelin et al. 2017) possibly due to lower levels of anthropogenic pressure but also due to data deficiency (Pyšek et al. 2008; Essl et al. 2019).

The Democratic Republic of the Congo (further D.R. Congo) represents a major hotspot of biodiversity in Africa (Sosef et al. 2017). The native flora of D.R. Congo is estimated to comprise ca. 11,000 species with 18.3% endemism (Pyšek et al. 2017; Sosef et al. 2017). The forests of the Congo Basin (rainforest and dry tropical woodland) provide services of key importance to the sustainable development of Central Africa and the planet, including biodiversity conservation, carbon storage, climate stabilization, soil protection, and provisioning of natural resources (Kamdem-Toham et al. 2003; Harrison et al. 2016). However, the Congo Basin is subjected to steadily increasing human influence due to deforestation and urbanisation (Anonymous 2012; Potapov et al. 2013). Increasing human pressure could favour the expansion of non-native species (Mack et al. 2000; Kowarik 2003; Essl et al. 2019). In spite of its crucial importance for D.R. Congo to plant diversity conservation in tropical Africa, the information on alien plant species is extremely scarce (Boy & Witt 2013; Latombe et al. 2017), with very few case studies in the last decade (Zachariades et al. 2013; Useni Sikuzani et al. 2018; Mbale et al. 2019). Pyšek et al. (2017) reported 522 naturalized species in D.R. Congo, i.e., 4.5% of the total flora.

In this paper, we explore patterns in the alien flora of D.R. Congo for the first time. We focus on Asteraceae and Fabaceae, i.e., the two largest families in terms of native and naturalized species in sub-Saharan Africa (Klopper et al. 2007) and worldwide (Pyšek et al. 2017). Along with Poaceae, they are the three families most represented among successful invaders (Randall 2017). The comparison of those two families is particularly interesting because they have contrasting biological traits (nitrogen fixator vs. non-fixator), dispersal strategies (Asteraceae are often wind-dispersed), and relations to humans, with Fabaceae being widely used in agroforestry and agriculture (Richardson et al. 2004; Binggeli 2011).

We first assemble a checklist of alien species for the two families. Secondly, we examine the life form spectrum, geographic origin, introduction pathway, and taxonomic assemblage of the alien species. Thirdly, we compare alien and native species for life forms and traits, correcting for phylogenetic bias by using pairs of congeners. Lastly, we examine occurrence (expressed as the number of specimens) and alien species richness distribution among the different phytogeographic districts of D.R. Congo. We anticipate contrasting patterns between the two families, due to contrasting biological attributes and relations to humans.

MATERIAL AND METHODS

Study area

D.R. Congo covers 2,345,409 km² in Central Africa, spanning from 13°S to 5°N, and harbours at least five types of climate (according to the Köppen classification; Peel et al. 2007), i.e., tropical rain forest (Af), tropical monsoon (Am), tropical wet and dry (Aw), temperate with dry winter and hot summer (Cwa), temperate with dry winter and warm summer (Cwb). The vegetation of D.R. Congo is highly diversified depending on climate and phytogeographic context. White's (1983) phytogeographic system recognizes six phytochoria in D.R. Congo, i.e., four regional centres of endemism (RCE) (the Guineo-Congolian RCE, the Zambezan RCE, the Sudanian RCE, and the Afromontane archipelago-like RCE) and two transition zones, i.e., the Guineo Congolian/Zambezan regional transition zone and the Guinea-Congolia/Sudania regional transition zone. Robyns (1948) divided D.R. Congo into 10 phytogeographic districts, based on vegetation cover and flora. This phytogeographic system is no longer fully satisfying, but it is still in use in floristic publications because herbarium collections are managed accordingly.

Data assemblage

Species considered in this work are alien species that have been observed out of cultivation in D.R. Congo. This definition includes casual, naturalized (= established), and invasive species (Blackburn et al. 2011).

D.R. Congo entries in the Global Register of Introduced and Invasive Species (GRIIS, <http://www.griis.org>) (Pagad et al. 2018) and the GloNAF initiative (Global Naturalized Alien Flora) (<https://glonaf.org>) (van Kleunen et al. 2019) have been combined. The resulting species records have been checked for effective presence and status (native/alien)

in D.R. Congo based on herbarium collections available at BR (www.botanicalcollections.be), the digital Flora of Central Africa (www.floredafriquecentrale.be), the African Plant Database (APD) (www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php), and the Plants of the World Online (Kew) (www.plantsoftheworldonline.org).

The accepted names follow the APD, or Plants of the World Online for taxa not covered in the former reference. For species accepted in our checklist, the full scientific names with author names are given in table 1.

Screening of the herbarium collections (BR) resulted in a few additional alien species for D.R. Congo (i.e., Asteraceae: *Acmella uliginosa*, *Ambrosia maritima*, *Erigeron sumatrensis*, *Struchium sparganophorum*; Fabaceae: *Abrus precatorius*, *Acacia mangium*, *Acacia saligna*, *Arachis hypogaea*, *Canavalia ensiformis*, *Canavalia gladiata*, *Crotalaria incana*, *Crotalaria retusa*, *Desmodium scorpiurus*, *Desmodium tortuosum*, *Leptolobium panamense*, *Senna bicapsularis*, *Senna hirsuta*, *Senna sophera*, *Senna tora*, *Stylosanthes guianensis*, *Tephrosia noctiflora*, *Vigna campestris*, *Vigna subterranea* var. *subterranea*).

The status (native/alien) of a significant number of species is not easy to ascertain, in particular for species with a pantropical distribution, for which the region of origin is often difficult to trace (Binggeli et al. 1998; Gallagher 2016; Essl et al. 2019). The GloNAF list was found to include a few species that have native populations in D.R. Congo, based on the digital Flora of Central Africa and their occurrence in the natural vegetation; these were not considered further (i.e., Asteraceae: *Crepis hypochaeridea*, *Cyanthillium cinereum*, *Ethulia conyzoides*, *Laphangium luteoalbum*, *Lipotriche pungens* subsp. *pungens*, *Lipotriche scandens*, *Lipotriche scandens* subsp. *madagascariensis*, *Sigesbeckia orientalis*; Fabaceae: *Bauhinia tomentosa*, *Crotalaria agatiflora*, *Crotalaria agatiflora* subsp. *imperialis*, *Clitoria ternatea*, *Erythrina abyssinica*, *Guilandina bonducella*, *Mucuna pruriens*, *Mucuna pruriens* var. *utilis*, *Tephrosia purpurea* subsp. *leptostachya*, *Tephrosia pumila* var. *pumila*, *Vicia hirsuta*, *Vicia sativa* subsp. *cordata*, *Vicia sativa* subsp. *nigra*, *Vigna comosa* subsp. *comosa*, *Vigna unguiculata*).

Only records based on herbarium vouchers have been considered. Therefore, due to the lack of herbarium material, the following species in the GRIIS and GloNAF lists have been excluded from the database, i.e., Asteraceae: *Artemisia annua*, *Flaveria trinervia*, *Gnaphalium pensylvanicum*, *Montanoa hibiscifolia*, *Tagetes erecta*, *Youngia japonica*; Fabaceae: *Acacia decurrens*, *Aeschynomene americana*, *Cassia eremophila*, *Cassia surattensis* subsp. *glauca*, *Gliricidia sepium*, *Leucaena diversifolia*, *Mimosa invisa*, *Sesbania punicea*, *Vigna juruana*.

One species has been excluded due to unresolved synonymy (*Tagetes lucida*).

For the following species in the GRIIS and GloNAF lists, we failed to find evidence for presence out of cultivation; therefore, these have been excluded from this study (i.e., Asteraceae: *Gerbera jamesonii*, *Scorzonera hispanica*, *Senecio macroglossus*, *Sphagneticola trilobata*, *Symphotrichum squamatum*, *Tanacetum cinerariifolium*; Fabaceae: *Brownea hybrida*, *Calliandra surinamensis*, *Ceratonia siliqua*, *Hae-*

matoxylum brasiletto, *Hymenaea courbaril*, *Myroxylon balsamum*, *Sesbania grandiflora*, *Vigna umbellata*).

Ultimately, the database comprises 38 and 79 alien species for Asteraceae and Fabaceae, respectively (supplementary files 1 and 2). In total, 663 and 1138 native species were retrieved from the digital Flora of Central Africa for Asteraceae and Fabaceae, respectively.

Taxonomic spectrum, traits, and life form

Each species was assigned to a subfamily and tribe based on LPWG (2017) for Fabaceae and Fu et al. (2016) for Asteraceae. The taxonomic assemblages (i.e., tribe frequency distribution) of native and alien species were compared using Chi-squared tests.

For trait values, our primary source of information is the digital Flora of Central Africa. For some missing data, other databases were used, i.e., Plants of the World Online, Plant Resources of Tropical Africa (PROTA) (www.prota.org), and World Agroforestry (www.worldagroforestry.org).

For life form, Raunkiaer's classification was followed but, in a few cases, we had to make somewhat arbitrary decisions including, i) large lianescent plants with herbaceous pluriannual shoots renewed from the rootstock, and ii) robust shrub-like forbs with shoots renewed from rhizome at the onset on the rain season but persisting for several years if not destroyed by fire and re-sprouting from lateral buds. Both were treated as geophytes.

The following morpho-functional traits were recorded for all alien species, based mostly on the digital Flora of Central Africa. These traits capture different functional dimensions. For both families: height (m), leaf length and width (cm) (correlated to light capture strategy and competitive ability); for Fabaceae with compound leaves, individual leaflets were considered; for Asteraceae: flower head (capitulum) diameter (mm) (a proxy of floral display), achene length (mm), pappus length (mm) (related to reproductive strategy, propagule pressure, and dispersal ability); for Fabaceae: vexillum size (mm) or, alternatively, flower head diameter (mm) for species with clustered flowers (e.g., *Mimosa* spp.) (proxy of floral display), rachis length (cm) in compound leaves and petiole length (cm) in simple leaves, pod length (cm), seed length (mm) (related to reproductive strategy, propagule pressure, and dispersal ability). The upper and lower values of the variation range have been recorded from the above-mentioned floras, and the mean value was used in statistical tests.

Introduction pathway

Any alien species that is currently planted or cultivated (crops, ornamentals, forestry, and landscape) anywhere in D.R. Congo or elsewhere in tropical Africa has been considered as intentionally introduced. Our primary sources of information are the digital Flora of Central Africa, Plants of the World Online, Plant Resources of Tropical Africa (PROTA), and World Agroforestry.

Intentional introductions have been categorized as follows: ornamental, agriculture (including agroforestry, fodder, environmental purposes (soil fertilizer, etc.)), edible, for-

Table 1 – Alien Asteraceae and Fabaceae in the flora of D.R. Congo.

The list includes only those species that have been found out of cultivation and for which herbarium vouchers are available. Date = date of the most ancient specimen; n = total number of specimens.

Asteraceae					
Taxon	Date	n	Taxon	Date	n
<i>Acanthospermum australe</i> (Loefl.) Kuntze	1946	27	<i>Eleutheranthera ruderalis</i> (Sw.) Sch.Bip.	1973	12
<i>Acanthospermum glabratum</i> (DC.) Wild	1957	3	<i>Emilia sonchifolia</i> (L.) DC.	1899	14
<i>Acanthospermum hispidum</i> DC.	1909	90	<i>Erigeron bonariensis</i> L.	1910	288
<i>Acmella oleracea</i> (L.) R.K.Jansen	1896	7	<i>Erigeron karvinskianus</i> DC.	1959	3
<i>Acmella uliginosa</i> (Sw.) Cass.	1922	12	<i>Erigeron sumatrensis</i> Retz.	1913	36
<i>Ageratum conyzoides</i> L.	1812	553	<i>Galinsoga parviflora</i> Cav.	1914	89
<i>Ageratum houstonianum</i> Mill.	1937	17	<i>Galinsoga quadriradiata</i> Cav.	1970	7
<i>Ambrosia maritima</i> L.	1950	23	<i>Guizotia abyssinica</i> (L.f.) Cass.	1911	6
<i>Bidens bipinnata</i> L.	1906	15	<i>Gynura aurantiaca</i> (Blume) DC.	1930	4
<i>Bidens pilosa</i> L.	1888	370	<i>Sonchus asper</i> (L.) Hill	1911	86
<i>Blumea balsamifera</i> (L.) DC.	1933	11	<i>Sonchus oleraceus</i> L.	1900	42
<i>Calea urticifolia</i> (Mill.) DC.	1937	9	<i>Struchium sparganophorum</i> (L.) Kuntze	1895	95
<i>Chromolaena odorata</i> (L.) R.M.King & H.Rob.	1975	16	<i>Synedrella nodiflora</i> (L.) Gaertn.	1903	132
<i>Chrysanthellum indicum</i> DC.	1895	132	<i>Tagetes minuta</i> L.	1926	33
<i>Cichorium intybus</i> L.	1903	10	<i>Tagetes patula</i> L.	1888	26
<i>Cosmos bipinnatus</i> Cav.	1934	4	<i>Taraxacum officinale</i> F.H.Wigg	1847	6
<i>Cosmos sulphureus</i> Cav.	1900	15	<i>Tithonia diversifolia</i> (Hemsl.) A.Gray	1933	35
<i>Eclipta prostrata</i> (L.) L.	1888	271	<i>Tithonia rotundifolia</i> (Mill.) S.F.Blake	1919	22
<i>Elephantopus mollis</i> Kunth	1900	70	<i>Tridax procumbens</i> L.	1931	64
Fabaceae					
Taxon	Date	n	Taxon	Date	n
<i>Abrus precatorius</i> L.	1886	144	<i>Desmodium incanum</i> (Sw.) DC.	1938	2
<i>Acacia auriculiformis</i> A.Cunn. ex Benth.	1975	9	<i>Desmodium scorpiurus</i> (Sw.) Desv.	1976	3
<i>Acacia dealbata</i> Link	1937	2	<i>Desmodium tortuosum</i> (Sw.) DC.	1907	62
<i>Acacia farnesiana</i> (L.) Willd.	1888	34	<i>Dichrostachys cinerea</i> (L.) Wight & Arn. subsp. <i>cinerea</i>	1904	78
<i>Acacia mangium</i> Willd.	2010	1	<i>Erythrina poeppigiana</i> (Walp.) O.F.Cook	1920	7
<i>Acacia mearnsii</i> De Wild.	1925	9	<i>Haematoxylum campechianum</i> L.	1930	6
<i>Acacia melanoxylon</i> R.Br.	1937	1	<i>Lablab purpureus</i> (L.) Sweet subsp. <i>purpureus</i>	1947	1
<i>Acacia podalyriifolia</i> A.Cunn. ex G.Don	1937	4	<i>Leptolobium panamense</i> (Benth.) Sch.Rodr. & A.M.G.Azevedo	1940	15
<i>Acacia saligna</i> (Labill.) H.L.Wendl.	1937	2	<i>Leucaena leucocephala</i> (Lam.) de Wit	1908	65
<i>Adenantha pavonina</i> L.	1923	27	<i>Indigofera suffruticosa</i> Mill.	1908	40
<i>Albizia chinensis</i> (Osbeck) Merr.	1925	32	<i>Inga edulis</i> Mart.	1931	9
<i>Albizia lebeck</i> Benth. (L.)	1903	87	<i>Mimosa diplotricha</i> C.Wright ex Sauvalle	1931	20
<i>Albizia saman</i> (Jacq.) F.Muell.	1932	9	<i>Mimosa pigra</i> L.	1888	318
<i>Arachis hypogaea</i> L.	1900	53	<i>Mimosa pudica</i> L.	1903	53
<i>Bauhinia acuminata</i> L.	1909	6	<i>Pithecellobium dulce</i> (Roxb.) Benth.	1932	13
<i>Bauhinia monandra</i> Kurz	1931	7	<i>Parkinsonia aculeata</i> L.	1903	17
<i>Bauhinia purpurea</i> L.	1906	15	<i>Peltophorum pterocarpum</i> (DC.) K.Heyne	1903	20
<i>Bauhinia variegata</i> L.	1937	7	<i>Phaseolus lunatus</i> L.	1896	59
<i>Brownea coccinea</i> Jacq.	1919	7	<i>Pterocarpus indicus</i> Willd.	1936	2

Table 1 (continued) – Alien Asteraceae and Fabaceae in the flora of D.R. Congo.

The list includes only those species that have been found out of cultivation and for which herbarium vouchers are available. Date = date of the most ancient specimen; n = total number of specimens.

Taxon	Date	n	Fabaceae		
			Taxon	Date	n
<i>Caesalpinia decapetala</i> (Roth) Alston	1911	46	<i>Neustanthus phaseoloides</i> var. <i>javanica</i> A.N.Egan & B.Pan	1941	7
<i>Caesalpinia pulcherrima</i> (L.) Sw.	1890	52	<i>Schizolobium parahybum</i> (Vell.) Blake	1931	13
<i>Caesalpinia sappan</i> L.	1930	15	<i>Senna alata</i> (L.) Roxb.	1895	67
<i>Cajanus cajan</i> (L.) Huth	1846	95	<i>Senna bicapsularis</i> (L.) Roxb.	1903	34
<i>Calopogonium mucunoides</i> Desv.	1931	48	<i>Senna hirsuta</i> (L.) H.S.Irwin & Barneby	1919	60
<i>Canavalia ensiformis</i> (L.) DC.	1903	24	<i>Senna occidentalis</i> (L.) Link	1888	244
<i>Canavalia gladiata</i> (Jacq.) DC.	1900	134	<i>Senna obtusifolia</i> (L.) H.S.Irwin & Barneby	1893	118
<i>Cassia bacillaris</i> L.f.	1918	20	<i>Senna septemtrionalis</i> (Viv.) H.S.Irwin & Barneby	1903	44
<i>Cassia fistula</i> L.	1931	9	<i>Senna siamea</i> (Lam.) H.S.Irwin & Barneby	1919	41
<i>Cassia grandis</i> L.f.	1930	6	<i>Senna sophera</i> (L.) Roxb.	1910	28
<i>Cassia javanica</i> L.	1954	5	<i>Senna spectabilis</i> (DC.) H.S.Irwin & Barneby	1905	73
<i>Cassia surattensis</i> Burm.f.	1932	10	<i>Senna tora</i> (L.) Roxb.	1911	29
<i>Centrosema plumieri</i> (Pers.) Benth.	1920	49	<i>Stylosanthes guianensis</i> (Aubl.) Sw.	1952	22
<i>Centrosema pubescens</i> Benth.	1948	30	<i>Tamarindus indica</i> L.	1895	27
<i>Clitoria laurifolia</i> Poir.	1930	22	<i>Tephrosia candida</i> DC.	1931	5
<i>Crotalaria incana</i> L.	1914	7	<i>Tephrosia noctiflora</i> Bojer ex Baker	1921	20
<i>Crotalaria juncea</i> L.	1932	14	<i>Macroptilium longepedunculatum</i> (Mart. ex Benth.) Urb.	1902	18
<i>Crotalaria micans</i> Link	1928	16	<i>Vigna radiata</i> (L.) R.Wilczek	1903	33
<i>Crotalaria retusa</i> L.	1904	114	<i>Vigna subterranea</i> (L.) Verdc. var. <i>subterranea</i>	1909	16
<i>Crotalaria spectabilis</i> Roth	1933	21	<i>Zornia latifolia</i> Sm.	1932	47
<i>Delonix regia</i> (Bojer ex Hook.) Raf.	1895	45			

estry, other uses (including medicinal). Many species have several uses, and, in such cases, somewhat arbitrary choices had to be made.

Comparison of congeneric alien and native species

Trait comparison between the native and the alien flora is subjected to phylogenetic bias because the two groups have different phylogenetic/taxonomic compositions. To overcome this bias, trait comparisons were performed between congeneric alien and native species. Congeneric species pairs have been successfully used in the comparative biology of alien species (Grotkopp & Rejmánek 2007; Pyšek & Richardson 2007; van Kleunen et al. 2010; Godoy et al. 2011; Gallagher et al. 2015).

Selection of congeneric pairs

The database was screened for genera comprising both native and alien species in D.R. Congo. Some genera comprised more than one alien and/or native species. In such cases, the selection of congeneric species pairs was based on the most recent infrageneric phylogeny or taxonomy. As a rule, the native species most closely related to the alien species were selected. When several species met the selection crite-

riion, a “pseudospecies” was created by calculating the average of trait values of all the species in the group (Asteraceae: *Bidens* (natives), *Erigeron* (aliens), *Gynura* (natives), *Mikania* (natives), and *Sonchus* (aliens and natives); Fabaceae: *Canavalia* (aliens), *Cassia* (aliens), *Clitoria* (natives), *Erythrina* (natives), *Vigna* (natives), and *Zornia* (natives)). For the comparison of life form, a nominal trait, “pseudospecies” could not be computed and all congeneric species fulfilling the selection criteria were included. For Asteraceae, as only seven genera comprised both native and alien species, one intergeneric comparison within the same tribe was also included (i.e., tribe Eupatorieae: *Ageratum conyzoides* (alien) and all native *Mikania* species). Eight and 18 phylogenetically independent comparisons fulfilled the selection criteria for Asteraceae and Fabaceae, respectively (supplementary files 3 and 4). The same traits were recorded for congeneric natives as for the aliens (see above), using the same sources of information.

Continuous traits were compared using Student’s *t*-tests on paired data or its non-parametric counterpart Wilcoxon signed rank test. The life form spectrum of native and alien species was compared using Fisher’s exact test.

Number of specimens and occurrence

The distribution within D.R. Congo was recorded as presence/absence in Robyns' (1948) phytogeographic districts based on exhaustive screening of the collections at BR.

The number of herbarium specimens in the collections at BR has been used as a proxy for the extent of occurrence of the species in D.R. Congo, assuming that more widespread species tend to be more often collected, everything else being equal (Stadler et al. 1998; Crawford & Hoagland 2009; Maroyi 2012). Alien species can differ in their extent of occurrence due to different times since introduction (Seebens et al. 2018). The date of the introduction of alien species in D.R. Congo is not known. Instead, the collection date of the most ancient specimen in the collections has been used as a proxy. Establishment success and range size can also be influenced by traits. Multiple regressions were used to examine if the number of specimens (dependent variable) is correlated to time since the first collection and to morpho-functional traits (independent variables).

The collected data were analysed using Microsoft Office Excel 2016, PAST v.3.25 (Hammer et al. 2001), and RStudio v.1.1.442. (RStudio Team 2015).

RESULTS

Asteraceae

Taxonomic spectrum, life form, continent of origin, and mode of introduction – Twenty and 11 tribes are represented among native and alien Asteraceae, respectively. The taxonomic spectrum of the two groups is remarkably different ($\chi^2_{obs} = 135.33$, d.f. = 9, $P < 0.001$). The following tribes are strongly overrepresented in alien species: Heliantheae (aliens: 21%; natives: 4.4%) and Millerieae (aliens: 18.4%; natives: 0.5%). The following three tribes are strongly underrepresented in alien species: Vernoniaceae (natives: 23.8%; aliens: 5.26%), Senecioneae (natives: 20.5%; aliens: 5.3%), and Gnaphalieae (natives 12.5%; aliens: 0%) (fig. 1).

A total of 74% of alien Asteraceae originated from America, far ahead of all other continents (3–8% each) (fig. 2). Sixty-six percent of aliens have been introduced to D.R. Congo accidentally. Most deliberate introductions correspond to ornamental species (24% of aliens) (fig. 3). Therophytes accounted for 71% of alien Asteraceae, far more than all other life forms (fig. 4).

Number of specimens and distribution within D.R. Congo – The alien species with the oldest herbarium specimens from D.R. Congo are *Ageratum conyzoides* (first collection in 1812), *Taraxacum officinale* (1847), and *Bidens pi-*

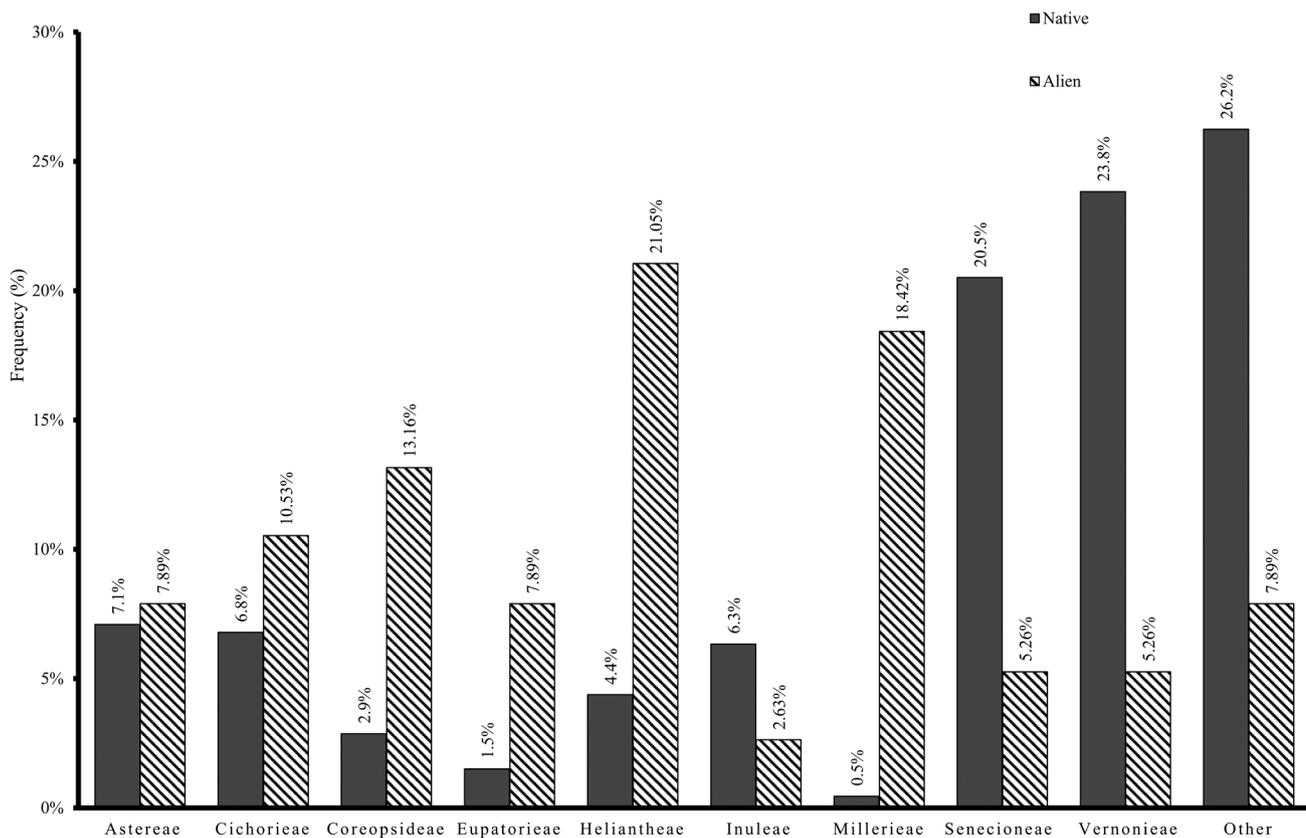


Figure 1 – Taxonomic spectrum of alien (n = 38) and native (n = 663) species of Asteraceae in the flora of D.R. Congo ($\chi^2_{obs} = 135.33$, d.f. = 9, $P < 0.001$).

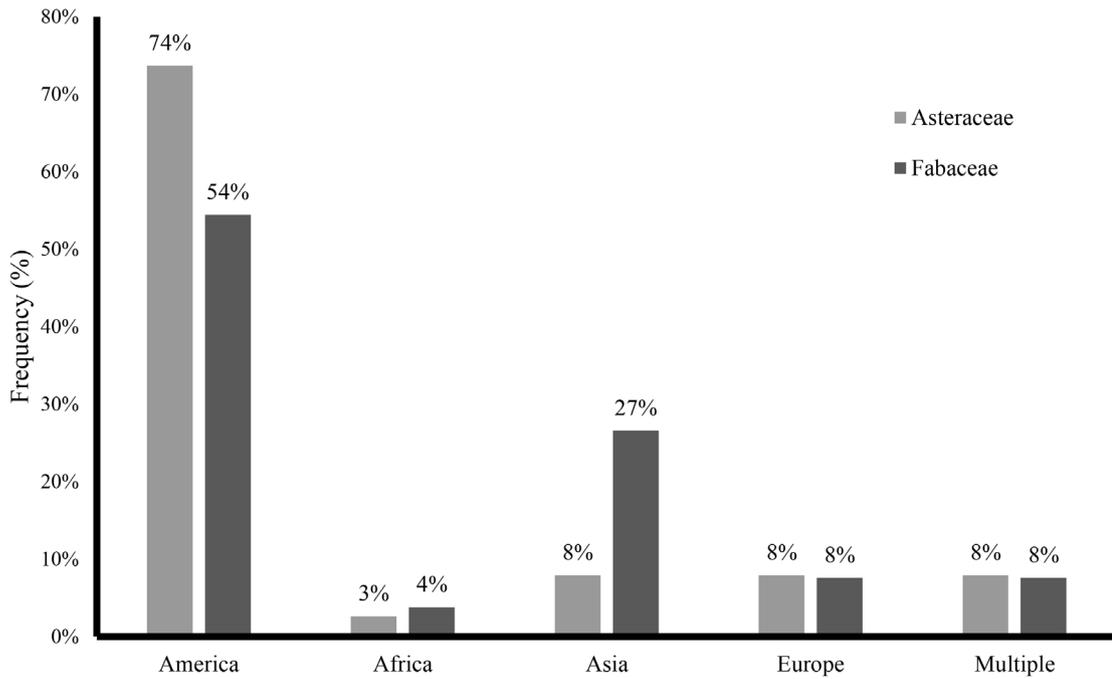


Figure 2 – Geographic origin of alien species of Asteraceae (n = 38) and Fabaceae (n = 79) in the flora of D.R. Congo. Fisher’s exact test: P = 0.14952.

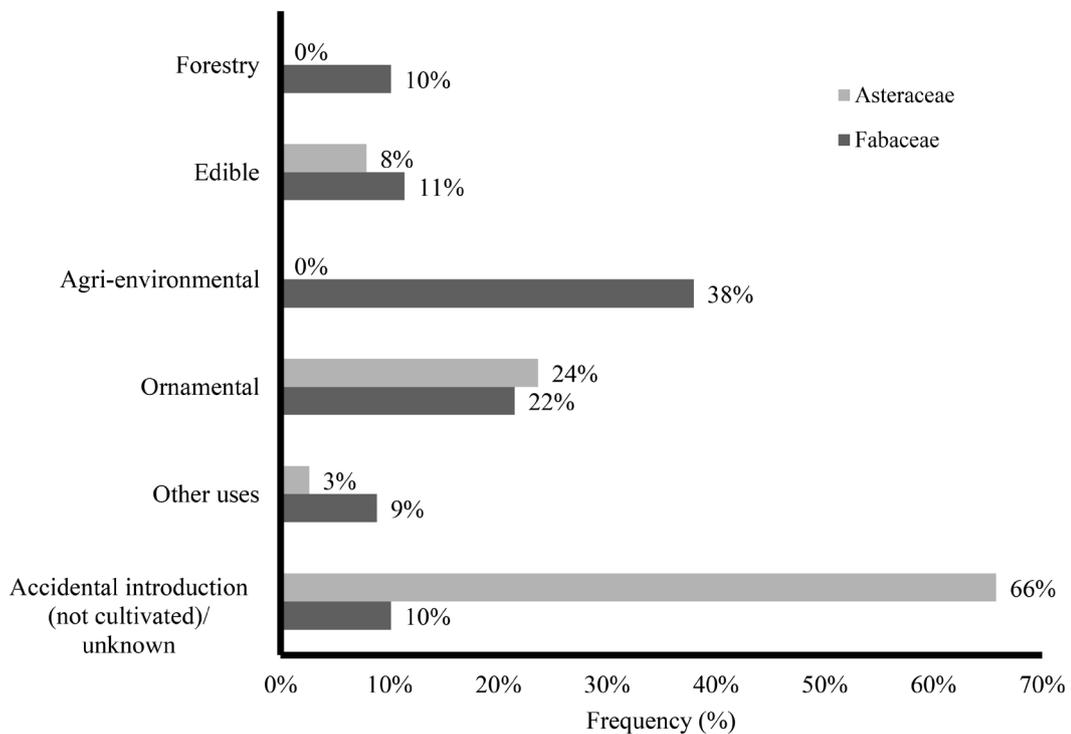


Figure 3 – Introduction pathway of alien species of Asteraceae (n = 38) and Fabaceae (n = 79) in D.R. Congo. Fisher’s exact test: P < 0.001.

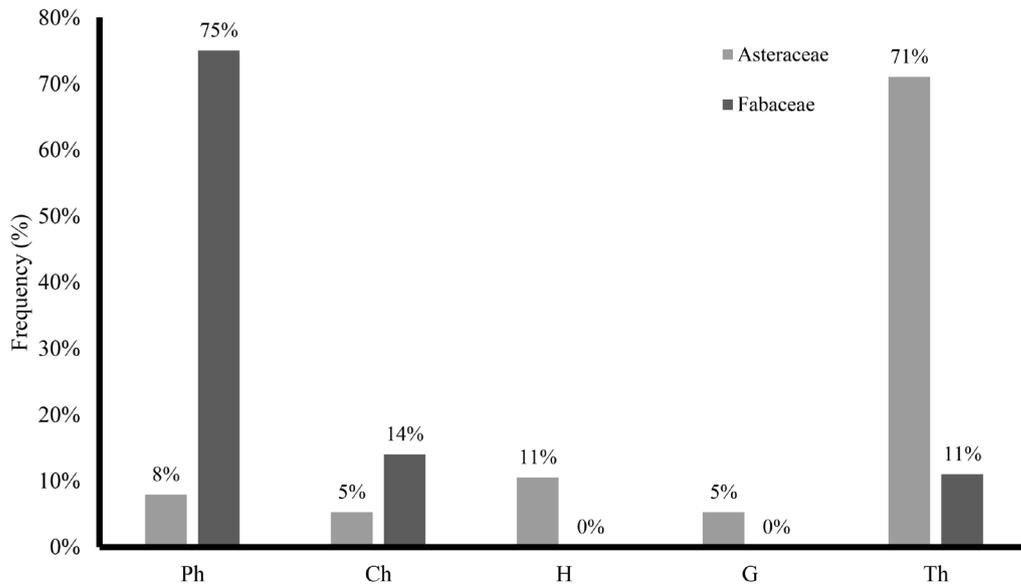


Figure 4 – Life form spectrum of alien species of Asteraceae (n = 38) and Fabaceae (n = 79) in the flora of D.R. Congo. Ph: Phanerophytes; Ch: Chamaephytes; H: Hemicryptophytes; G: Geophytes; Th: Therophytes. Fisher’s exact test: $P < 0.001$.

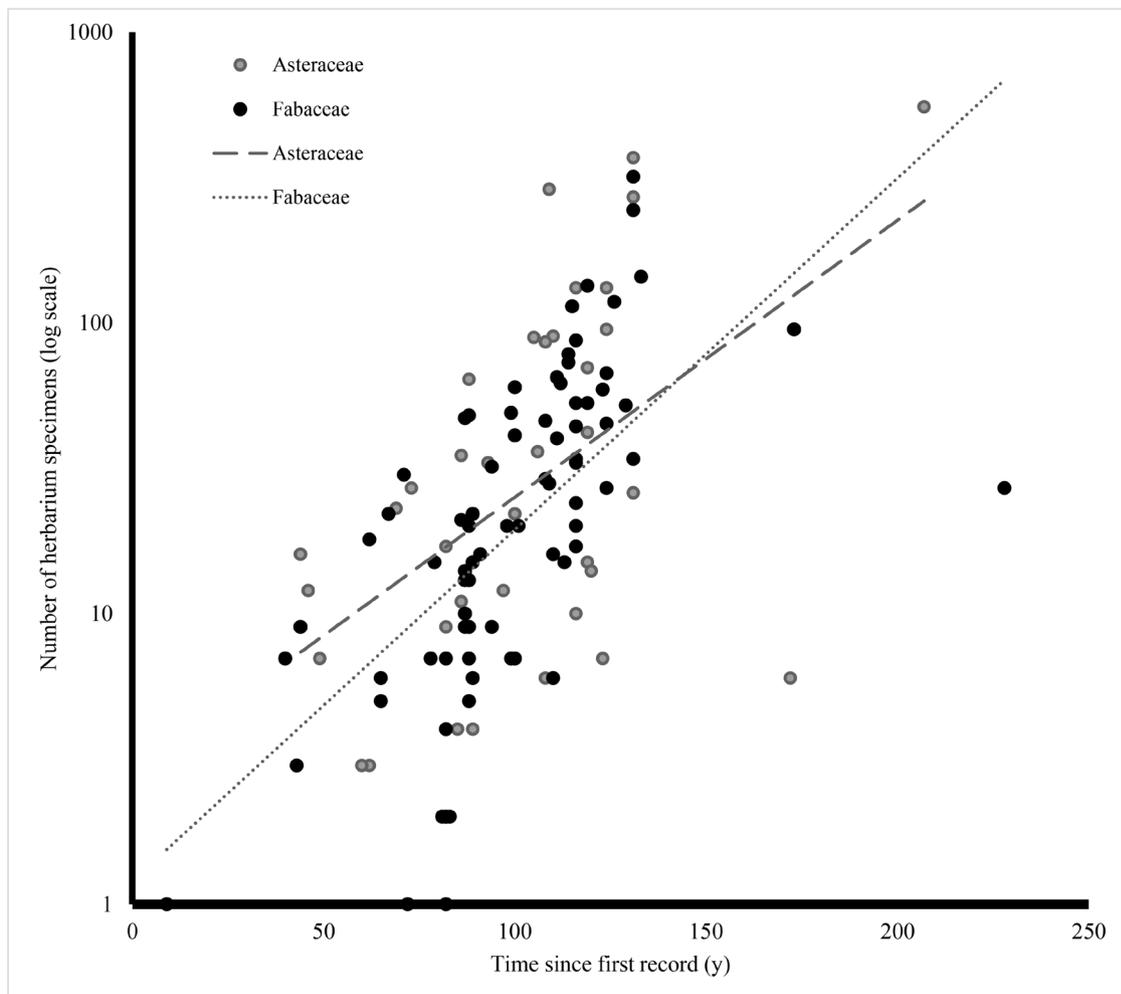


Figure 5 – Number of herbarium specimens of alien Asteraceae (n = 38) and Fabaceae (n = 79) as a function of time elapsed since the first record in D.R. Congo. (Asteraceae: adjusted $R^2 = 0.19$, $P < 0.05$; Fabaceae: adjusted $R^2 = 0.38$, $P < 0.001$).

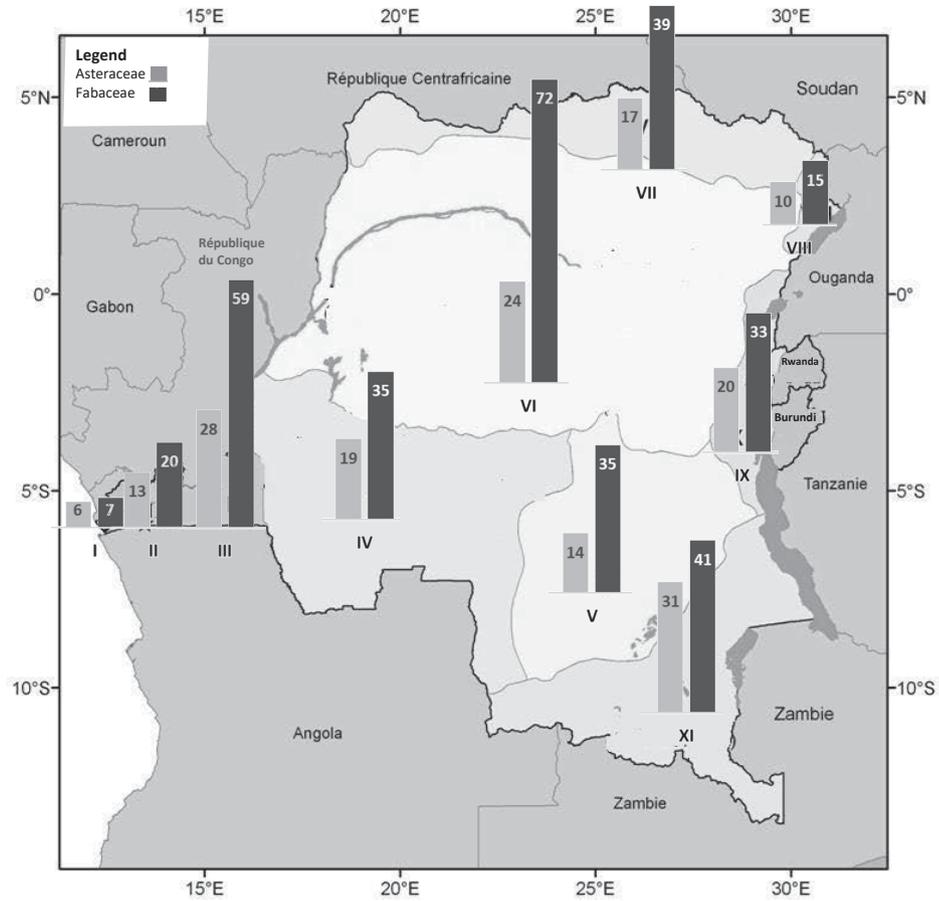


Figure 6 – Number of alien species of Asteraceae and Fabaceae in the 10 phytogeographic districts of D.R. Congo as defined by Robyns (1948). I. Côtier. II. Mayumbe. III. Bas-Congo. IV. Kasai. V. Bas-Katanga. VI. Forestier Central. VII. Ubangi-Uele. VIII. Lac Albert. IX. Lacs Édouard and Kivu. XI. Haut-Katanga.

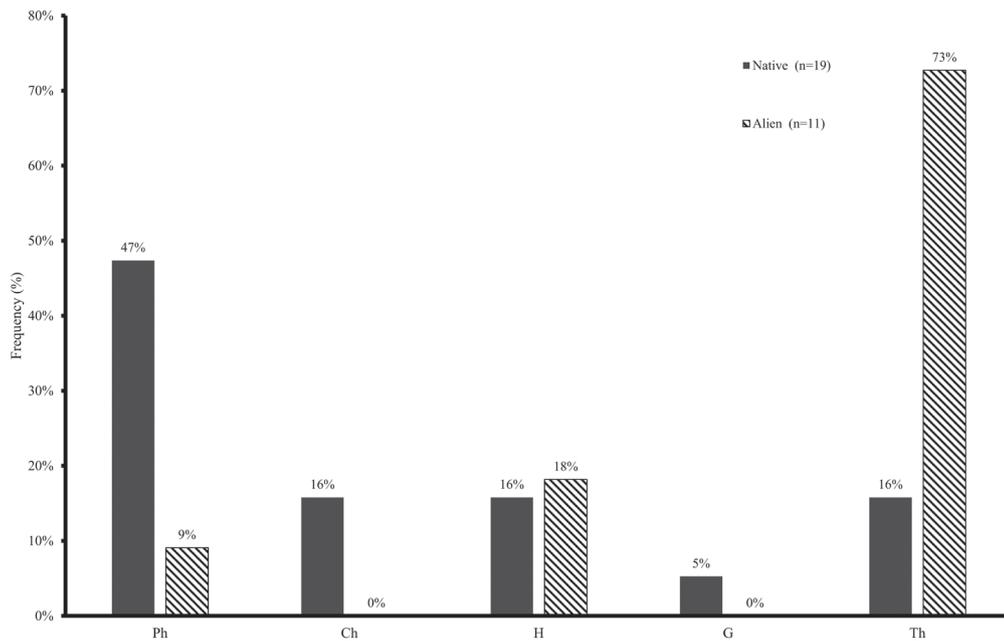


Figure 7 – Life form spectrum of congeneric alien and native Asteraceae in the flora of D.R. Congo. Ph: Phanerophytes; Ch: Chamaephytes; H: Hemicryptophytes; G: Geophytes; Th: Therophytes. Fisher’s exact test: P = 0.01171.

Table 2 – Trait comparison of congeneric alien and native species (Asteraceae and Fabaceae).

Values are means \pm standard deviations. See supplementary files 3 and 4 for species included in the comparison. n.s. (not significant); $P > 0.10$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Asteraceae			
Trait	Natives (n = 8)	Aliens (n = 8)	Paired test (W: Wilcoxon test; t: Student's <i>t</i> -test)
Height (m)	0.97 \pm 0.43	0.85 \pm 0.68	W = 27 n.s.
Leaf length (cm)	12.48 \pm 8.94	9.90 \pm 4.84	W = 22 n.s.
Leaf width (cm)	4.24 \pm 2.60	3.76 \pm 1.96	W = 20 n.s.
Capitulum diameter (mm)	10.99 \pm 6.85	10.07 \pm 5.85	W = 22 n.s.
Pappus length (mm)	5.47 \pm 2.38	5.29 \pm 2.70	t = 0.2 n.s.
Achene length (mm)	4.21 \pm 2.73	4.12 \pm 3.74	W = 20 n.s.
Fabaceae			
Trait	Natives (n = 18)	Aliens (n = 18)	Paired test (W: Wilcoxon test; t: Student's <i>t</i> -test)
Height (m)	6.95 \pm 11.73	7.43 \pm 8.95	W = 102 n.s.
Rachis length (cm)	7.98 \pm 9.52	13.05 \pm 14.13	W = 143**
Leaflet length (cm)	3.87 \pm 3.12	6.04 \pm 4.73	W = 157***
Leaflet width (cm)	2.37 \pm 2.46	3.61 \pm 3.70	W = 141**
Floral display (mm)	17.7 \pm 13.48	20.45 \pm 12.43	W = 97 n.s.
Pod length (cm)	6.34 \pm 4.89	10.72 \pm 9.73	W = 119**
Seed length (mm)	7.63 \pm 5.48	7.67 \pm 5.80	W = 92 n.s.

losa, *Eclipta prostrata*, and *Tagetes patula* (all 1888). The most recent first collection dates are for *Eleutheranthera ruderalis* (1973) and *Chromolaena odorata* (1975). Of the 38 alien Asteraceae in the database, the species with specimen numbers > 100 were, in descending order: *Ageratum conyzoides* (553 specimens), *Bidens pilosa* (377), *Erigeron bonariensis* (288), *Eclipta prostrata* (271), *Chrysanthellum indicum* (132), and *Synedrella nodiflora* (132) (table 1). Multiple regression analysis using time since the first collection and functional traits as explanatory variables was significant (adjusted $R^2 = 0.19$, $P = 0.053$) (fig. 5). Time since the most ancient collecting date was the only significant independent variable in the model ($t = 3.63$, $P < 0.001$). The number of alien Asteraceae species recorded in the 10 phytogeographic districts of D.R. Congo ranged from six (Côtier district) to 31 (Haut-Katanga district) (fig. 6).

Congeneric pairs – The following genera of Asteraceae have been included in the comparison of congeneric species: *Bidens*, *Blumea*, *Elephantopus*, *Emilia*, *Erigeron*, *Gynura*, *Sonchus*, and one intergeneric comparison within the tribe Eupatorieae (*Mikania* vs. *Ageratum*). The life form spectra of native and alien Asteraceae are significantly different (Fisher's exact test: $P = 0.007$) (fig. 7). Phanerophytes are much less represented in aliens (8%) compared to natives (41%), while therophytes are the most frequent life form in alien Asteraceae (75% vs. 18% in natives). No significant difference was found for any quantitative trait between native and alien Asteraceae (table 2).

Fabaceae

Taxonomic spectrum, life form, continent of origin, and mode of introduction – Thirty-one and 16 tribes are represented among native and alien Fabaceae, respectively. The taxonomic spectrum of the two groups is strikingly different ($\chi^2_{\text{obs}} = 135.9$, d.f. = 13, $P < 0.001$). The following tribes are strongly overrepresented in alien species: Acacieae (aliens: 10.1%; natives: 2%), Caesalpinieae (aliens: 10.1%; natives: 1.3%), and Cassieae (aliens: 19%; natives: 4%). In contrast, the following three tribes are underrepresented in alien species: Phaseoleae (natives: 23.4%, aliens 15.2%), Dalbergieae (natives: 12.1%, aliens: 5.1%), and Detarieae (natives: 11.4%, aliens: 2.5%) (fig. 8).

Fifty-four percent of alien Fabaceae originated from America followed by Asia (27%), the other continents representing only 4–8% each (fig. 2). As much as 90% of alien Fabaceae appear to have been intentionally introduced, most of which for agri-environmental purposes (soil amendment, erosion mitigation, agroforestry, forage) (38%), ornament or amenity (22%), and forestry (10%) (fig. 3). Phanerophytes (75%) are the most frequent life form, far more than chamaephytes (14%) and therophytes (11%) (fig. 4).

Number of specimens and distribution within D.R. Congo – Of the 79 alien Fabaceae in the database, the species with specimen numbers > 100 were, in descending order: *Mimosa pigra* (318 specimens), *Senna occidentalis* (244), *Abrus precatorius* (144), *Canavalia gladiata* (134), *Senna obtusifolia* (118), and *Crotalaria retusa* (114). The species with the oldest collecting dates in D.R. Congo are *Cajanus cajan* (first record in 1846), *Abrus precatorius* (1886), *Mi-*

mosa pigra (1888), *Senna occidentalis* (1888), and *Acacia farnesiana* (1888). The most recent first collection dates are for *Acacia mangium* (2010) and *Desmodium scorpiurus* (1976) (table 1). Multiple regression using time since the first collection and functional traits as explanatory variables was highly significant (adjusted $R^2 = 0.38$, $P < 0.001$) (fig. 5), with two significant predictors, i.e., time since first collection ($t = 5.38$, $P < 0.001$) and height ($t = -1.99$, $P = 0.049$). Small-sized species tended to have larger specimen numbers, all else being equal. The number of alien Fabaceae species ranges from seven (Côtier district) to 72 (Forestier Central district) (fig. 6). The latter region concentrates 91% of all aliens Fabaceae recorded in D.R. Congo (72 of 79), far ahead of all the other regions. Five species, i.e., *Bauhinia monandra*, *Brownea coccinea*, *Cassia grandis*, *Desmodium incanum*, and *Pterocarpus indicus*, were recorded only in the Forestier Central district.

Comparison of congeneric native and alien species – The following genera have been included in the analysis: *Abrus*, *Acacia*, *Albizzia*, *Bauhinia*, *Caesalpinia*, *Canavalia*, *Cassia*, *Clitoria*, *Crotalaria*, *Desmodium*, *Erythrina*, *Indigofera*, *Peltophorum*, *Pterocarpus*, *Senna*, *Tephrosia*, *Vigna*, and *Zornia* (supplementary file 4).

Therophytes are slightly less frequent in alien Fabaceae (14%) compared to congeneric natives (17%). However, the life form spectra of the two groups are not significantly different (Fisher's exact test: $P = 0.71$) (fig. 9). Congeneric natives and aliens were significantly different for three quantitative traits, i.e., rachis length, leaflet length, leaflet width, and pod length. Alien species had ca. 61% longer rachis,

64% longer and 66% wider leaflets compared to their native congeners, and ca. 59% longer pods (table 2).

DISCUSSION

To the best of our knowledge, our work represents the first assessment of the alien flora of D.R. Congo in terms of taxonomic assemblage, morpho-functional traits, pathway of introduction, region of origin, and occurrence. The approach is focused on Asteraceae and Fabaceae, the two largest families in the flora of D.R. Congo, representing together 22.4% of the total alien flora.

D.R. Congo does not appear to host large numbers of alien plant species in comparison to other tropical African countries (table 3). This is surprising considering that D.R. Congo is the largest tropical African country. Tropical Africa, in general, does not appear to be a hotspot of alien species (van Kleunen et al. 2015; Turbelin et al. 2017). Following Foxcroft et al. (2010), the lower extent of alien plant invasions in African savannas is attributable to lower rates of intentional plant introductions, the role of large mammalian herbivores, and the adaptation of African systems to fire. Tropical savannas may also be relatively resistant to invasion due to resource limitation (Taylor et al. 2018). The relatively low economic development is another factor explaining low levels of biological invasions (Essl et al. 2019).

It is also quite possible that our database is incomplete. Although the flora of D.R. Congo is well represented in collections (5629 specimens for the 117 alien Asteraceae and Fabaceae species), alien species records are scarce for the last decades. Of the 117 alien species in this study, as few

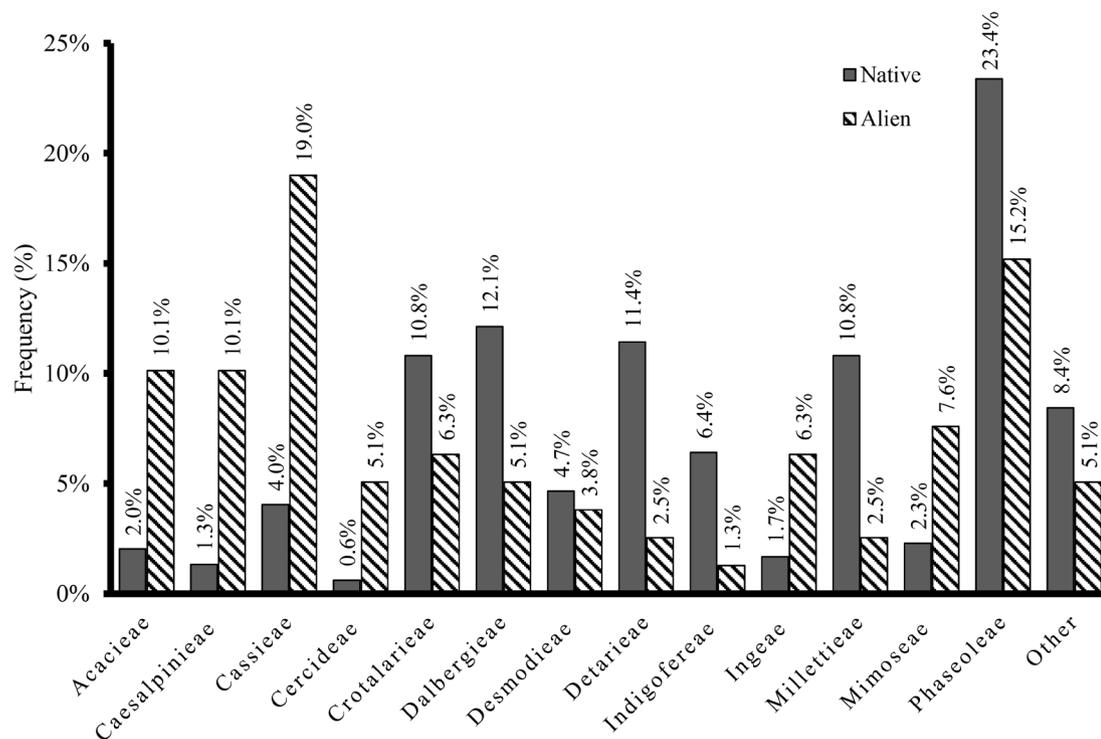


Figure 8 – Taxonomic spectrum of alien ($n = 79$) and native ($n = 1138$) Fabaceae in the flora of D.R. Congo ($\chi^2_{\text{obs}} = 135.93$, d.f. = 13, $P < 0.001$).

Table 3 – Alien Asteraceae and Fabaceae in D.R. Congo, other African countries, and the world.

The total number of species for both families in the listed regions and, between brackets, the percentage of alien flora.

	Asteraceae	Fabaceae
D.R. Congo (this work)	38 (7.3%)	79 (15.1%)
Ghana (Ansong et al. 2019)	22 (7.5%)	66 (22.6%)
Zimbabwe (Maroyi 2012)	53 (13.6%)	49 (12.5%)
East Africa (Witt et al. 2018)	17 (10%)	27 (16%)
Madagascar (Kull et al. 2011)	50 (4.3%)	224 (19%)
The world (Pyšek et al. 2017)	1343 (10.2%)	1189 (9%)

as 35 (13 Asteraceae and 22 Fabaceae) have been collected after 2000 (supplementary files 1 and 2). Therefore, the collections do certainly not provide an up to date picture of the alien flora in D.R. Congo, recent introductions certainly being underrepresented. This limitation must be kept in mind when interpreting our results.

Contrasting patterns between Fabaceae and Asteraceae

A striking result is the discrepancy between alien Asteraceae and Fabaceae for most of the investigated features. The differences in the introduction pathway, life forms, traits, and distribution are mutually consistent, in line with divergent biological attributes and relations to humans between the two families.

Geographic origin of aliens – Asteraceae and Fabaceae in D.R. Congo primarily originate from the Americas (74% and 54%, respectively). This result confirms previous work pointing to the prominent contribution of the Americas to the alien flora of Africa, due to a legacy of a long history of trade and exchange between tropical America and Africa, starting long before colonisation (Chevalier 1931; Wild 1968; Rousset & Juhe-Beaulaton 1992; Katz 1998; Maroyi 2012; Witt et al. 2018; Ansong et al. 2019). Such exchanges may explain both accidental introductions (mostly Asteraceae, e.g., *Ageratum conyzoides* and *Bidens pilosa*) and deliberate introductions of crops and other edible species (mostly Fabaceae; e.g., *Canavalia ensiformis* and *Phaseolus lunatus*). Interestingly, the contribution of Asia as a region of origin is much larger for Fabaceae compared to Asteraceae, probably due to relatively recent deliberate introductions for agriculture and

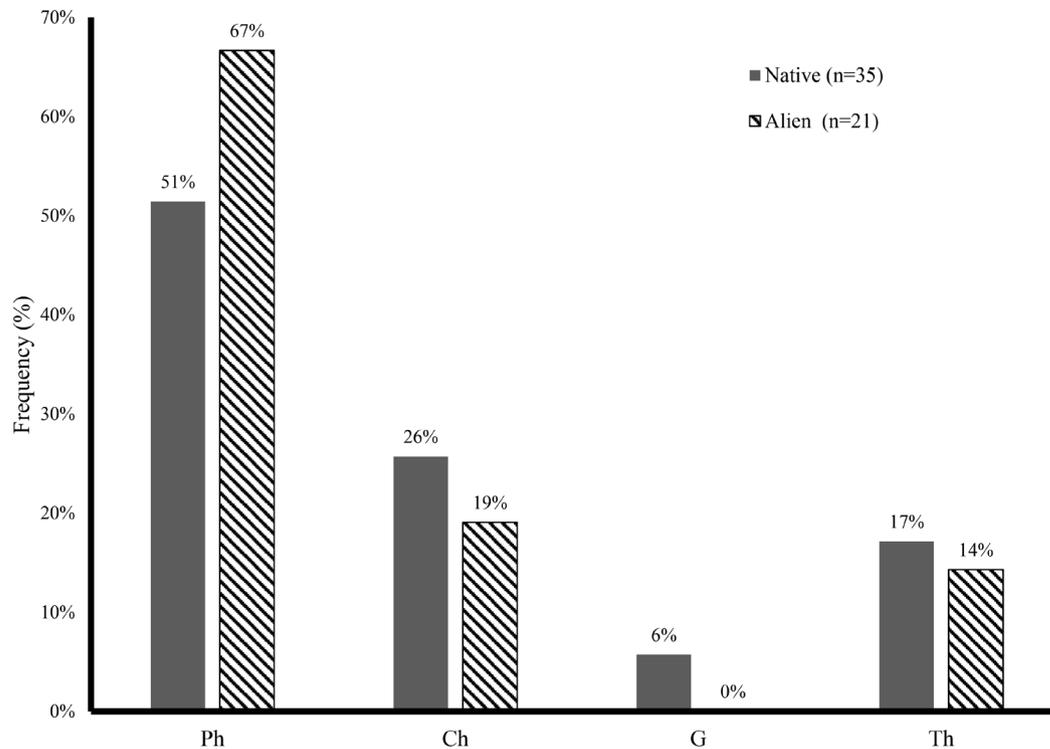


Figure 9 – Life form spectrum of congeneric alien and native Fabaceae in the flora of D.R. Congo. Ph: Phanerophytes; Ch: Chamaephytes; G: Geophytes; Th: Therophytes. Fisher’s exact test: P = 0.717.

agroforestry (e.g., *Pterocarpus indicus* (first record: 1936) and *Crotalaria spectabilis* (1933)).

The prominent contribution of America to alien Asteraceae and Fabaceae is reflected in the distinct phylogenetic assemblage of the alien flora, with Heliantheae (8 species) and Cassieae (16 species), two mostly American tribes, over-represented among aliens.

Introduction pathway – Most of the alien Fabaceae (71 of 79, i.e., 90%) have been intentionally introduced to D.R. Congo primarily for forage, fertilizer, and agroforestry (38%). The high proportion of phanerophytes amongst alien Fabaceae (59 of 79, i.e., 75%) can be explained by the deliberate introduction for agri-environmental purposes as the main source of successful aliens in the flora of D.R. Congo. Intentional introduction facilitates the spread of alien species (Pyšek et al. 2011). Silviculture and agroforestry are major pathways of alien species introduction, and both have contributed noxious invasive woody species in the tropics (Richardson 1998; Richardson et al. 2004; Binggeli 2011). Our results show that the Forestier Central district, mostly in Guineo-Congolian rainforest, hosts a particularly large number of alien Fabaceae. This possibly points to a role of botanical gardens and forestry experimental stations in the introduction of those legumes, as two important agronomic and botanical research centres of the Belgian colony (Yangambi and Eala, both with botanical gardens and nurseries) were situated in the Forestier Central district (Binggeli et al. 1998). Tropical botanical gardens are known to be an important source of alien plant naturalisation in Africa (Dawson et al. 2008).

The pattern is quite different for Asteraceae, with 66% of alien species introduced accidentally. This is consistent with the large proportion of therophytes among alien Asteraceae. Alien Asteraceae are mostly annual weeds on disturbed ground. The two most collected species are *Ageratum conyzoides* and *Bidens pilosa*, which both have spread quickly in D.R. Congo due to their efficient dispersal mechanisms (anemochory and epizoochory, respectively) while remaining restricted to waste ground and fallow fields. The large number of alien Asteraceae in Haut-Katanga can be interpreted in this context because short cycling Asteraceae are well-adapted to the strongly seasonal climate of the Zambesian region. Masocha et al. (2011) showed that alien Asteraceae are favoured by frequent burning in Zambesian savannas. Most of the deliberately introduced Asteraceae species were imported for ornamental purposes, and some of them have successfully naturalised (e.g., *Tithonia diversifolia* in SE D.R. Congo). In other parts of tropical Africa, ornamentals in amenity gardens are also a major source of alien plant introductions (Foxcroft et al. 2008; Bigirimana et al. 2012). However, such garden escapes often appear to be restricted to road verges and other human transformed habitats probably because of their high requirements for nutrients (Witt et al. 2019).

Traits – We compared congeneric alien and native species in order to avoid bias due to different taxonomic assemblages in alien and native flora. For Asteraceae, aliens comprised a much larger proportion of therophytes compared to native species. This suggests that alien Asteraceae do not occupy

the same habitats as their native congeners. As previously discussed, most alien Asteraceae in D.R. Congo are weeds on disturbed ground. Such species probably do not represent a major threat to native biota of high conservation value in D.R. Congo. In contrast, there were no differences for continuous traits between alien and native Asteraceae. Dawson et al. (2011) insists that traits do not play a prominent role in explaining the success of alien tropical plants compared to propagule pressure, for instance. It is also possible that traits not considered in the present work account for the success of alien species, including specific leaf area (SLA) and other traits related to resource capture and use (Grotkopp & Rejmánek 2007; Pyšek & Richardson 2007; van Kleunen et al. 2010; Moravcová et al. 2015).

The pattern was quite different for Fabaceae with phanerophytes being the most frequent life form in both aliens and natives. Fabaceae are one of the largest families in a broad range of forest and woodland types in D.R. Congo (Lebrun & Gilbert 1954). Most of the alien Fabaceae are trees and shrubs that have been introduced for agroforestry and landscape purposes, a well-known introduction pathway for noxious aliens elsewhere in Africa (Richardson 1998; Richardson et al. 2004; Binggeli 2011). The Forestier Central district, which concentrates the largest number of alien legumes, corresponds to the rainforest region of D.R. Congo. Thus, in contrast to Asteraceae, congeneric alien and native legumes could co-occur in the same vegetation types. Implications for conservation management need to be investigated.

Interestingly, alien legumes tend to be bigger than congeneric natives, significantly so for rachis, leaflet size, and pod length. This could be explained by a strong filter acting during the establishment, most likely due to the intentional selection of alien species with a syndrome of increased vigour for agroforestry (most species) and subsistence agriculture (e.g., *Canavalia ensiformis* and *Vigna radiata*). It would be interesting to test if larger leaf size implies higher competitive ability in alien species. While having larger fruits, alien Fabaceae do not have larger seeds, suggesting that larger pods could translate into larger seed output, itself a strong determinant of the rate of spread of alien species (Dawson et al. 2011; Moravcová et al. 2015).

Introduction and large-scale cultivation of alien woody species without weed risk assessment is in conflict with sustainable development (Richardson 1998). In this regard, it is particularly worrying that an assessment of forest genetic resources in D.R. Congo by the FAO (Malele Mbala 2003) failed to discriminate between native species of high conservation value and alien species, recommending conservation of *Acacia auriculiformis*, *Albizia lebbek*, *Cassia siamea*, and *Leucena leucocephala*, four notoriously noxious alien species.

Establishment and success of alien species – There is extensive variation among alien species in the number of specimens held in herbarium collections (from 1 to 553). Much of that variation is explained by the time elapsed since the most ancient collecting date. Records increased at a similar rate with time in the two families, suggesting that time since introduction is the driver of that relationship. However, while

an early specimen obviously implies early introduction, species with more recent first records are not necessarily more recent introductions. Variation in record numbers can also be due to species-specific time-lags (Binggeli et al. 1998) and could indicate that different species have reached different stages in the invasion process (Blackburn et al. 2011). Species with the largest numbers of records can be safely considered as naturalized, and some of them possibly as invasive (e.g., Asteraceae: *Ageratum conyzoides*, *Bidens pilosa*, *Chrysanthellum indicum*, *Erigeron bonariensis*, *Eclipta prostrata*, *Synedrella nodiflora*; Fabaceae: *Abrus precatorius*, *Canavalia gladiata*, *Crotalaria retusa*, *Mimosa pigra*, *Senna occidentalis*, *Senna obtusifolia*). Many of them were most likely introduced in the precolonial period (Binggeli et al. 1998). However, species with low numbers of specimens could still be naturalized only locally. Field observations are urgently needed to ascertain the status (casual/naturalized/invasive) of most species in our database.

Interestingly, height had a significant negative effect on the number of records in Fabaceae. Small shrubs and forbs reach reproductive maturity earlier than tall trees and could therefore have shorter generation time and potentially higher rates of population increase.

CONCLUSION

The comparison of alien Asteraceae and Fabaceae in the flora of D.R. Congo has highlighted contrasting patterns in terms of geographic origin, life form, introduction pathways, occurrence, and trait divergence with the native flora. The striking discrepancies between the two families call for analyses of alien introductions at the family level and warn against generalisations based on the global flora.

Information on alien plant species in D.R. Congo is scanty. Future research should be directed in at least two directions. First, producing a reliable checklist validated by critical examination of herbarium material is a key priority. Secondly, fieldwork is urgently needed to assess the status of alien species, and possible impacts on native biota across the different natural regions of D.R. Congo. This is indeed a huge task, considering the size of the country and logistic difficulties. Protected areas should be priority targets in this process (Foxcroft et al. 2013), especially in parts of the country subjected to increasing anthropogenic pressure.

SUPPLEMENTARY FILES

Four supplementary files are associated with this paper:

Supplementary file 1: Database of alien Asteraceae in the flora of D.R. Congo.

<https://doi.org/10.5091/plecevo.2020.1754.2219>

Supplementary file 2: Database of alien Fabaceae in the flora of D.R. Congo.

<https://doi.org/10.5091/plecevo.2020.1754.2221>

Supplementary file 3: Congeneric comparisons of traits and life forms of native and alien Asteraceae. All genera in the flora of D.R. Congo comprising both native and alien species have been considered. See Material and methods for species selection methods.

<https://doi.org/10.5091/plecevo.2020.1754.2223>

Supplementary file 4: Congeneric comparisons of traits and life forms of native and alien Fabaceae. All genera in the flora of D.R. Congo comprising both native and alien species have been considered. See Material and methods for species selection methods.

<https://doi.org/10.5091/plecevo.2020.1754.2225>

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