Alien flora of D.R. Congo: improving the checklist with digitised herbarium collections

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Abstract The Democratic Republic of the Congo (D.R. Congo) represents a striking gap of knowledge on alien plant species. In this paper, we use digitised herbarium collections to assemble a new checklist of alien plant species in D.R. Congo and to examine patterns in the alien flora. The new checklist comprises 436 alien species i.e., 189 (43%) casuals, 247 (57%) naturalised of which 80 (18% of aliens) are invasive. Discrepancies with previous databases are discussed. For many species in previous databases, all herbarium specimens come from cultivated specimens (e.g. botanic gardens) and we failed to find evidence for occurrence outside of cultivation. A total of 166 taxa were not included in previous lists, 41 of which are new records to the flora of D.R. Congo. Considering the size of the country and its rich native flora, the alien flora of D.R. Congo does not appear to be species-rich. The alien flora is particularly rich in Fabaceae (15%) and in annual species 163 (37%). The Americas are by far the most important source continent (65%) and the proportion of annuals of American origin is particularly large among the most widespread species. 90% of invasive species are from the Americas. Invasive success is discussed in terms of residence time. The very low number of

new species records after 1960 is similar to other African countries and could be due to decreasing sampling effort. The results illustrate how herbarium collections can be used to critically revise existing checklists of alien species in tropical Africa. Field work is urgently needed to improve coverage of recent introductions and to monitor the status of alien species, especially in protected areas and around botanic gardens.

Keywords Tropical forest • Botanic gardens • Global Naturalized Alien Flora database (GloNAF) • Global Register of Introduced and Invasive Species (GRIIS) • Central Africa

Declarations

Funding

No funding was received for conducting this study

Conflicts of interest/Competing interests

The authors have no conflicts of interest to declare that are relevant to the content of this article

Availability of data and material

All data are available in Supplementary Information

Code availability

Not applicable

Authors' contributions

FB assembled the checklist and analysed the data; PM designed the research, contributed to checklist validation, and wrote the manuscript.

Ethics approval

Not applicable

Consent to participate

Not applicable

Consent for publication

69 Not applicable

Introduction

Alien organisms represent an ever-increasing proportion of the biota worldwide and alien plant invasions have become a "hot topic" in biodiversity research (van Kleunen et al. 2015; Pyšek et al. 2017; Seebens et al. 2018). Tropical Africa is a major area for plant diversity (Küper et al. 2005; Sosef et al. 2017) and alien plant species could represent a serious threat (Stadler et al. 2000; Obiri 2011; Boy and Witt 2013; Foxcroft et al. 2013). However, with the notable exception of South Africa (Richardson et al. 2020), sub-Saharan Africa lags far behind for research on alien species (Pyšek et al. 2008; Turbelin et al. 2017; Essl et al. 2019).

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; Hamer et al. 2012; Groom et al. 2015; Latombe et al. 2017). Many tropical African countries suffer from a lack of alien species inventories despite recent efforts to fill this gap of knowledge (e.g., Maroyi 2012; Rejmánek et al. 2016; Witt et al. 2018; Ansong et al. 2019; Omer et al. 2021). Some recent national flora checklists incorporate information on introduced species (Mapaura and Timberlake 2004; Phiri 2005; Figueiredo and Smith 2008), as does the African Plants database (https://www.ville-ge.ch/musinfo/bd/cjb/africa/index.php?langue=an). In the last decade, considerable effort to synthesize information and to assemble regional and global checklists of alien plant species has been made under the impulsion of different actors (Groom et al. 2015). Two large, open-source databases have been produced, i.e., the Global Register of Introduced and Invasive Species (GRIIS) assembled by IUCN Invasive Species Specialist Group and hosted by GBIF (https://www.gbif.org) (Pagad et al. 2018), and the Global Naturalized Alien Flora database (GloNAF) (van Kleunen et al. 2019). These inventories are rapidly gaining popularity to analyse patterns in alien plant invasion at regional or global scale (Randall 2017; Turbelin et al 2017; Essl et al. 2019). However, for sub-Saharan Africa, they are often incomplete and suffer from taxonomic and biogeographic uncertainties (Meyer et al. 2016; Ansong et al. 2019; McGeoch and Jetz 2019).

The Democratic Republic of the Congo (further D.R. Congo) represents a striking gap of knowledge on alien plant species. D.R. Congo hosts ca. 11,000 native species with 18.3% endemism (Pyšek et al. 2017; Sosef et al. 2017). However, information on alien plant species in D.R. Congo is extremely scarce, with very few case studies (Zachariades et al. 2013; Useni Sikuzani et al. 2018; Mbale et al. 2019). Based on GLoNAF database, Pyšek et al. (2017) reported 522 naturalised species of seed plants in D.R. Congo, i.e., 4.5% of the total flora. Recently, we explored patterns in the alien flora D.R. Congo for the first time (Bordbar and

Meerts 2020). During the preparation of that work, it appeared that databases of alien species in D.R. Congo suffered from several shortcomings.

During the last decade, research on the flora of D.R. Congo has received strong impetus under leadership of Meise Botanic Garden (Belgium), with important progress in the production of the Flore d'Afrique centrale (Sosef 2016). At the same time, digitisation of the rich plant collections from D.R. Congo in BR has made a huge number of materials easily available and searchable through a user-friendly portal (Vissers et al. 2017). Digitisation of Congolese collections in BR is now almost complete, with 490.000 images available online. (http://www.botanicalcollections.be/). Other digitised specimens are available through the GBIF portal (https://www.gbif.org). Digitisation of herbarium collections greatly facilitates access to information and opens exciting new research possibilities (Stropp et al. 2016; Soltis 2017; James et al. 2018). Herbarium collections have been successfully used to assemble alien species checklists (Stadler et al. 1998; Crawford and Hoaglan 2009; Maroyi 2012; Fuentes et al. 2013).

In this paper, we use digitised herbarium collections to assemble a new checklist of alien plant species in D.R. Congo. First, based on herbarium specimens, all records in GloNAF and GRIIS lists are checked for effective presence outside of cultivation in D.R. Congo, geographic distribution, and date of first record. Secondly, based on extensive data mining from digitised collections, we systematically tracked species not recorded in either list. Based on the new list, we provide the first comprehensive overview of the alien flora of D.R. Congo, in terms of phytogeographic origin, taxonomic assemblage, life forms, date of first record and occurrence.

Materials and methods

Study area

The Democratic Republic of the Congo covers 2,345,409 km^2 in Central Africa, spanning from 13°S to 5°N (altitude range: 0--5110 m). Its population is ca. 86 million. D.R. Congo was governed by the king of Belgium since 1885 and was a Belgian colony from 1909 to 1960. D.R. Congo has proportionally fewer paved highways than any country in Africa and its nominal GDP per capita is one of the lowest in the world (Herderschee et al. 2012). Agriculture is the largest sector in economy with 10 million ha cultivated (FAO 2013). D.R. Congo comprises 18% of the world's tropical forests, but the Congo Basin is subjected to steadily increasing

human influence due to deforestation and urbanisation (Anonymous 2012; Potapov et al. 2013), which could favour the expansion of non-native species (Essl et al. 2019).

D.R. Congo harbours at least five types of climates (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, including Guineo-Congolian rainforest, Zambezian dry tropical woodlands and grasslands, afromontane and afroalpine communities (White 1983). Robyns (1948) divided D.R. Congo into 10 phytogeographic districts, based on vegetation and flora. Although this phytogeographic system is no longer fully satisfying, it is still in use in floristic publications because herbarium collections are managed according to it.

The most important source of floristic information for D.R. Congo is the Flore d'Afrique centrale (1948-) (hereafter FAC), in production since 1948, still incomplete (Sosef 2016). FAC now covers ca. 70% of the estimated 11,000 vascular plants in D.R. Congo. FAC includes both native and introduced species. Other important floras and catalogues, with narrower geographic coverage, include Robyns (1947), Robyns and Tournay (1955), Troupin (1956), Pauwels (1993), and Lejoly et al. (2010).

Data assemblage; effective presence in D.R. Congo

Species considered in this work are alien species that have been observed outside of cultivation in D.R. Congo. This definition includes casual, naturalised (= established), and invasive species following the definition of Richardson et al. (2000, 2011), Pyšek et al. (2004) and Blackburn et al. (2011). The Global Register of Introduced and Invasive Species (GRIIS, http://www.griis.org) (Pagad et al. 2018) comprises 397 alien seed plants for D.R. Congo (Groom et al. 2020). The GloNAF database, in principle limited to naturalised species, comprises 522 entries for D.R. Congo. Other online database and information facilities were explored for additional species, in particular the World Checklist of Selected Plant families (WCSP 2014) (https://wcsp.science.kew.org), Plants of the World Online (Kew) (www.plantsoftheworldonline.org) (POWO), the African Plant Database (APD) (www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php) and the Invasive Species Compendium (ISC) (https://www.cabi.org/isc/).

The floristic and phytosociological literature was extensively searched for additional alien species. Published volumes of FAC since 1948 (partly available online:

www.floredafriquecentrale.be) were searched extensively. Other important sources were Pauwels (2014), and Lejoly et al. (2010). Checklists of alien species in neighbouring countries were mined to orient herbarium collection search for more species (Mapaura and Timberlake 2004; Phiri 2005; Bigirimana 2011; Maroyi 2012; Rejmánek et al. 2016; Anonymous 2016; Noba et al. 2017; ; Witt et al. 2018; Ansong et al. 2019).

All entries, both from GRIIS and GloNAF lists, and additional species from all other sources, were checked for effective presence in D.R. Congo. Effective presence is testified by a specimen in a collection. The most important collection for D.R. Congo is BR (www.botanicalcollections.be). Specimens in other collections were retrieved by GBIF. The accepted names follow the APD, or POWO for taxa not covered in the former reference.

Presence outside of cultivation

Herbarium labels were systematically screened for locality and habitat information. First, presence outside of cultivation was verified by exhaustive screening of collecting information recorded. Specimens collected from cultivated plants were discarded (herbarium label explicitly mentioning “cultivé/cultivated”, “planté/planted”, “introduit/introduced”). Collections made in botanic gardens (Kisantu, Eala, University of Kisangani), arboreta (L’Etoile at Lubumbashi), and agronomic research stations of INEAC (Yangambi, etc.) were also discarded, unless the collecting information on the label clearly indicated that the specimen was taken from a plant escaped from cultivation (“subspontané/ spontaneous”, “échappé/escaped”, “naturalisé/naturalised”, “envahissant/invasive”). Any species reported by FAC as “subspontané” (i.e., escaped) or naturalised was included. For GloNAF and GRIIS species without specimens outside of cultivation, an extensive literature search was conducted to trace the origin of the record.

Alien vs. native species; region of origin

Criteria defined by Essl et al. (2018) were used to check alien status. For many species with pantropical and Afro-American distribution, the native range is often difficult to determine (Chevalier 1931, 1951; Wild 1978; Alpern et al. 2008; Essl et al. 2019). American species have been introduced to Africa by transatlantic navigation well before colonisation of Africa by Europeans (Wild 1978; Alpern et al. 2008; Gallagher 2016).

Different sources of information were used to assess the status of species in D.R. Congo, i.e., POWO, APD, FAC, ISC, Flora Zambesiaca and Flora of Tropical east Africa. The status proposed by the majority of these sources was accepted. When the status was unclear e.g., when different sources give contradictory information (disregarding obvious material errors), the species has been included in the alien list as "cryptogenic" (Pagad et al. 2018).

Naturalisation and invasiveness

A preliminary attempt was made to assign each species to a particular stage in the invasion process. Naturalised species are those that form self-replacing populations independently of direct human intervention (Richardson et al. 2000, 2011; Blackburn et al. 2011). First, we considered as naturalised, any species previously reported as such in FAC, or other published floristic and vegetation studies, acknowledging that naturalisation can be effective only locally. Second, we accepted as being naturalised species fulfilling at least one of the following criteria: i) represented by large numbers of specimens in collections, ii) not restricted to anthropogenic habitats, iii) collected repeatedly from the same locality or the same region over an extended period.

Other aliens are referred to as "casuals". These comprise both deliberately introduced species occasionally escaping from cultivation but not maintaining self-sustainable populations and unintentionally introduced species observed as isolated specimen mostly in anthropogenic habitats.

Naturalised species were assessed for invasiveness, based on Richardson et al. (2000) criteria, i.e., "invasive species are a subset of naturalised species that produce reproductive offspring often in very large numbers at considerable distances from the parents and/or site of introduction, and have the potential to spread over long distances". Our assessment was based on previous reports in the literature, and on the number of specimens in the collections. However, this criterion must be considered with caution because some species which have experienced recent and/or regional expansion could be underrepresented in collections.

Life form

Life form, (i.e., annual herbaceous, perennial herbaceous, tree, shrub, climber and aquatic), and region of origin were obtained from floras and POWO.

Number of specimens

The number of specimens in collections has been counted. Residence time in D.R. Congo was estimated from the collecting date of the earliest specimen in collections (Ahern et al. 2010). We have examined if the number of specimens in collections is correlated to the residence time.

Occurrence and distribution within D.R. Congo

Based on locality data on specimen label, species occurrence in the different phytogeographic regions of D.R. Congo was determined.

The data were analysed using Microsoft Office Excel 2016, PAST v.3.25 (Hammer et al. 2001).

Results

Our revised checklist of alien seed plants in D.R. Congo (Supplementary Information S1) includes 436 species i.e., 189 casuals (43%), 247 naturalised (57%) of which 80 (18% of aliens) are invasive. These are represented by ca. 21478 specimens in collections. The 20 most widespread species are listed in Table 1. The precise identity of a few taxa is uncertain (*Bellucia* cf. *pentamera*, *Cecropia* cf. *pachystachya*, *Gnaphalium* cf. *pensylvanicum*, *Taraxacum* sp., *Vicia sativa* s.l.) and further taxonomic work is needed. Seven species in literature records or previous databases, not supported by voucher specimens, could not be checked for taxonomic correctness and were therefore considered as "awaiting confirmation" (Supplementary Information S2 and S3).

Table 2 compares the revised checklist with previous databases. Only 194 out of 397 species in GRIIS list and 253 of 522 species in GloNAF list are confirmed by herbarium specimens as occurring outside of cultivation in D.R. Congo. Many species in previous databases have been excluded for different reasons. First, for a total of 170 species (149 species in GRIIS and 154 species in GloNAF), all specimens in collections appear to have been collected in botanic gardens, agronomic experimental stations, amenity gardens or otherwise cultivated specimens (Supplementary Information S2 and S3). In particular, BR collections comprise many specimens collected in the botanic gardens of Kisantu and Eala. For those cultivated species, literature has been thoroughly explored. No evidence for naturalisation of

any of those 170 species in D.R. Congo was found. For 125 species, literature supporting occurrence outside of cultivation was found (Supplementary Information S2). In most cases, only one reference was found (Pauwels 2014) but, oddly enough, the voucher specimens cited by this author are from cultivated plants, and the status of the species is reported in a rather ambiguous way. For 45 species, literature indicates that the species do not occur outside of cultivation (Supplementary Information S3).

Secondly, a total of 89 species in previous databases are native to D.R. Congo (28 in GRIIS, 84 in GloNAF) (Supplementary Information S4). For 18 species, the native range is not known with certainty and these have been accepted in the alien list as "cryptogenic" (Supplementary Information S1).

Thirdly, for 31 taxa, we found no evidence for occurrence in D.R. Congo, and previous records were apparently based on wrongly geolocalised specimens, or specimens from neighbouring countries (Rwanda and Burundi), or taxonomic and nomenclatural issues (Supplementary Information S5).

Surprisingly, 241 species accepted in our list were not recorded in GRIIS, and 180 not in GloNAF, and 166 species were reported in neither list. However, not all of these are new to the alien flora of D.R. Congo because they had previously been reported as alien in D.R. Congo by POWO and/or FAC. Forty-one species had apparently never been reported in D.R. Congo hitherto, of which seven are naturalised (Supplementary Information S6).

Taxonomic assemblage

Seventy-seven families are represented among aliens. The six most species-rich families are Fabaceae (68 species; 16%), Asteraceae (47; 11%), Solanaceae (40; 9%), Poaceae (36; 8%), Convolvulaceae and Amaranthaceae (20; 5%) comprising together > 50% of alien species (Fig. 1). The proportion of naturalised species is larger in Asteraceae compared to the whole alien flora (70% vs. 56%); the proportions of invasive species vary among the top 6 families (χ^2_{obs} = 19.17, d.f. = 10, $P < 0.05$) with Asteraceae (15 invasive species i.e., 32% of all introduced Asteraceae) much overrepresented among invasive species (32%) i.e., a much larger proportion than in the whole alien flora (19% invasive). The most species-rich genera are *Solanum* (19 species), *Ipomoea* (10), *Senna* (10), *Euphorbia* (10), *Amaranthus* (8), *Paspalum* (7) (Supplementary Information S1).

Life forms

Annual herbaceous species are the most frequent life form (163 species, 37%), followed by perennial herbaceous (94 species, 22%) (Fig. 2). Aquatic species (4) comprise the smallest group. The proportions of naturalised species vary significantly among life forms (χ^2_{obs} = 25.38, d.f. = 10, P < 0.01) being markedly larger for annual herbaceous species (58%) and perennial herbaceous (63%) species compared to trees and shrubs (46% together).

Phytogeographic assemblage

The Americas are by far the most frequent source continent (65%), far ahead of all other continents (Fig. 3). The proportion of naturalised and invasive species varies among source continents (χ^2_{obs} = 40.93, d.f. = 10, P < 0.001). 26 % of American aliens in D.R. Congo are invasive i.e., a much larger proportion than for all other origins (5%). Seventy-two invasive species in D.R. Congo are from the Americas vs. only 8 invasive aliens from other regions.

Number of specimens and earliest record date

The number of specimens in collection ranges from 1 to 553 (*Ageratum conyzaeoides*). The earliest collection date is 1869 (*Schwenckia americana*) and the most recent new record is 2010 (*Stachytarpheta cayennensis*) (Supplementary Information S1). The number of specimens increases significantly with time since first record (Fig. 4). When controlling for time, invasive species tend to have larger numbers of specimens compared to the rest of aliens.

The cumulated number of species has increased regularly in the first half of the 20th century, reaching a plateau after 1960 (Fig. 5). As few as 32 new species have been added to the alien flora after 1960.

Distribution within D.R. Congo

Fig. 6 shows the number of aliens in the ten phytogeographic districts of D.R. Congo. The Forestier Central (district VI), Haut-Katanga (district XI) and Bas-Congo (district III) stand out as the most species-rich (> 250 species each). No surprisingly, the smallest districts tend to host fewer aliens.

Discussion

We provide a revised checklist of alien seed plants in D.R. Congo, based on the critical examination of an estimated 30,000 herbarium specimens, representing ca. 700 species, an unaffordable task without access to digitised collections. Our new checklist shows striking discrepancies with previous databases. We first examine the origin of these discrepancies. Thereafter, we explore the taxonomic, phytogeographic and life history patterns in the alien flora, and occurrence in the different phytogeographic regions.

Discrepancies with previous databases

We found 436 alien seed plant species in D.R. Congo, of which 247 are naturalised i.e., considerably fewer than GloNAF (522 species). Only 49% of GloNAF and GRIIS species are confirmed by herbarium specimens collected outside of cultivation. First, an important difficulty in the assemblage of the list is cultivated species. Herbarium collections from D.R. Congo comprise many specimens collected from plants cultivated in botanic gardens, agronomic and forestry research stations. In particular, the two largest botanic gardens created in D.R. Congo during colonial times, i.e. Kisantu, and Eala (Kimbelo 1996), but also smaller botanic gardens (University of Kisangani, arboretum of l'Etoile at Lubumbashi) and agronomic research stations of Institut National pour l'Etude agronomique du Congo belge (INEAC) (Yangambi, etc.) used to collect herbarium voucher specimens of their living collections, with duplicates deposited in BR. Specimens from botanic gardens and from the wild are not kept separately in BR. Apart from botanic gardens, many alien species have been introduced to D.R. Congo for ornamental purposes or for human food. Tracing the origin of a specimen (planted or escaped) requires critical examination of collecting data. For 170 species in previous checklists, no specimen collected outside of cultivation was found in collections. For all those species, literature provides no evidence for naturalisation. Field observations are needed to clarify the status of those species.

Specimens in collections provide the only reliable, verifiable evidence for effective presence and status (cultivated/wild) in D.R. Congo. A substantial number of records in previous lists are not supported by voucher materials. A few of these are material errors, including specimens collected in neighbouring countries (Burundi, Rwanda). Due to specimen mislabelling, several species have long been included in the flora of D.R. Congo while they were in fact collected in China (Robbrecht et al. 2021). Specimens in collections allowed us to

detect several identification errors and wrong geolocalisation (Supplementary Information S5). Quite a few native species were also included in error in previous lists (Supplementary Information S4).

Our new list comprises many species that were not included in previous databases. Not all of these, however, represent additions to the alien flora of D.R. Congo, because they had already been recorded as alien in D.R. Congo in Plants of the World Online. Extensive data mining from collections guided by literature search has allowed us to uncover 41 species that had apparently never been reported for D.R. Congo hitherto (Supplementary Information S6).

Alien species richness

Based on the 522 naturalised species in GloNAF Pyšek et al. (2017) estimated the proportion of alien species in the flora of D.R. Congo to be 4.5%. Based on our revised checklist, the proportion of naturalised species is 2.2% (3.9% when including casuals). The naturalised flora of D.R. Congo appears to be relatively species-poor, in comparison to global patterns. First, based on the species richness – area relationship in Pyšek et al. (2017), the expected number of naturalised species in D.R. Congo is ca. 1000 species i.e., four-fold the actual number (two-fold when including casuals). Second, based on the correlation between species richness in the alien and the native flora (Pyšek et al. 2017), the expected number of naturalised species is 457 species (for 11,000 native species), higher than the actual number (247), even when including casuals (436). D.R. Congo is apparently not a hotspot of alien species richness. These figures fit in well with the generally low alien species richness in tropical regions (Fine 2002). Higher intrinsic resistance of tropical ecosystems could be due to “fewer available free ecological niches, faster recovery of vegetation after disturbance or a lower introduction rate” (van Kleunen et al. 2015). Factors accounting for relatively low number of invasive species in African savannas were discussed by Foxcroft et al. (2010). The low level of economic development and the poor transport infrastructure in D.R. Congo are certainly also limiting factors (Essl et al. 2019).

However, our alien list is likely conservative for different reasons. First, some species, represented in collections only as specimens from cultivation, may actually also exist as garden escapes. Botanic gardens potentially represent important sources of alien plant introduction, especially in the tropics (Dawson et al. 2008). Naturalisation from botanic gardens in D.R. Congo has been circumstantially reported (Kembelo 1996; Binggeli 2011). Field observations in Congolese botanic gardens and neighbouring areas could reveal many more naturalised

409 species than accepted here. Second, herbarium collections have poor coverage of recent
410 decades, a well-known sampling bias in central Africa (Meyer et al. 2016). The cumulated
411 number of alien species shows a plateau in the last three decades (Fig. 5), with few additions
412 after 1960. This contrasts with the lack of saturation in the accumulation of alien species
413 worldwide (Seebens et al. 2018). This could be accounted for by decreasing sampling effort.
414 However, the same pattern of saturation was found for Ghana (Ansong et al. 2019), and Sudan
415 (Omer et al. 2021), even though the alien checklists in these countries are based on recent field
416 observations by local experts. Therefore, the saturation is not necessarily an artifact and could
417 reflect decreasing rates of new introductions in developing countries of tropical Africa.
418
419 Native vs. alien; naturalisation and invasiveness
420
421 Our assessment of naturalisation is likely conservative. Evidence for naturalisation cannot be
422 derived from herbarium specimens. Specimen number is not always a reliable indicator of
423 naturalisation success, because a species can be naturalised only locally. Several alien species
424 appear to have naturalised in botanic gardens, from which they have expanded to neighbouring
425 regions (*Musa acuminata, Cecropia* sp., *Rivina humilis, Petiveria alliacea* …). On the other
426 hand, some species represented by large number of specimens in collections are still not
427 considered as naturalised by recent floras e.g., *Solanum aethiopicum* (Bikandu et al. 2020).
428 Interestingly, a few species that were explicitly reported as being naturalised locally have not
429 been collected for a very long time, suggesting that such species have gone extinct or have
430 failed to spread from their naturalised population. On the contrary, other species naturalised in
431 botanic gardens, have spread quickly to neighbouring regions (e.g., *Cecropia* cf. *pachystachya*
432 in the region of Eala (Hauman 1948)). The (past and present) role of botanic gardens in the
433 introduction of alien species in D.R. Congo deserves further investigation.
434 In contrast to the relatively low number of alien species, the number of invasive species
435 (80) appears to be quite high in comparison to expectations (21) based on the number of
436 naturalised species. This could be due to our too inclusive criterion used in this work. However,
437 our estimation is remarkably close to the 84 invasive species in Zimbabwe (Maroyi 2012).
438 Interestingly, most of the species considered here as invasive were already recorded in D.R.
439 Congo over a century ago. This suggests that long residence time is a most important
440 determinant of invasiveness (Ahern et al. 2010; Philips et al. 2010). However, when controlling
441 for time since first record, invasive species tend to have more specimens in collections. This

could indicate that these species indeed have a higher spread rate, or, alternatively, that they were introduced long before the first specimen was collected.

Taxonomic, phytogeographic and life form spectrum

Patterns in the alien flora of D.R. Congo are compared with the global patterns (Pyšek et al. 2017) and with regional patterns in two other sub-Saharan countries i.e., Ghana, in the Guineo-Congolian region (Ansong et al. 2019) and Zimbabwe in the Zambezian region (Maroyi 2012) (Table 3). The alien flora is richer in Fabaceae (16%) and poorer in Poaceae (8%) than global patterns. A prominent contribution of Fabaceae was also found in Ghana by Ansong et al. (2019). The large contribution of Solanaceae (ranking 3d, 9% of aliens) is a striking feature of the alien flora. Many Solanaceae species have been introduced to D.R. Congo as edible plants (leaves and/or fruits) and have often escaped from cultivation (Bikandu et al. 2020). However, in terms of invasive species, Asteraceae stand out with 15 species, most likely due to their relatively high dispersal capacity (anemochory).

Concerning life forms, the contribution of annuals (38%) is markedly higher than global patterns (23%) and very similar to Zimbabwe (37%); in Ghana, the bias towards to annuals is much less marked (Table 3). Trees and shrubs comprise 28% of aliens, very similar to Zimbabwe. The large contribution of annuals in Zimbabwe and D.R. Congo could be accounted for by the long dry season in the Zambezian ecoregion (southern D.R. Congo). The bias towards annuals is even more striking for invasive species, with 40 invasive annuals vs. only 15 invasive trees and shrubs. However, as pointed out by Bordbar and Meerts (2020), life history patterns are strongly family-specific in the alien flora of D.R. Congo, with trees and shrubs much overrepresented among alien Fabaceae, and annuals much overrepresented among alien Asteraceae, reflecting contrasting introduction pathways (i.e., deliberate introduction for forestry purposes for Fabaceae, vs. accidental introduction of weeds for Asteraceae).

Concerning the region of origin, the overwhelming contribution of the Americas (65%), much larger compared to the global scale (30%) is in line with Ghana and Zimbabwe. This is accounted for by a long history of transatlantic exchanges of crops (and contaminant seed) between Africa and the Americas, dating back to the 16th century (Wild 1978) and possibly even earlier (Gallagher 2016). The Americas are even more overrepresented among the most widespread species (Table 1) and among invasive species (Fig. 3), as found in Ghana.

Considering the history of European colonisation, the virtual lack of European species is striking, as previously found in Ghana (Ansong et al. 2019). Climatic mismatch is likely the

cause. This hypothesis is supported by the observation that quite a few cryptogenic species with a mostly temperate distribution, occur in D.R. Congo only at high elevation (Afromontane belt in the Albertine Rift.). Whether such populations are native or were introduced by humans is difficult to ascertain without evidence from molecular markers. Some of these mostly high-altitude species in D.R. Congo also have ruderal populations at lower elevation (e.g., *Poa annua)*, certainly of recent anthropogenic origin. Such species are therefore accepted as aliens, as recommended by Pagad et al. (2018).

Conclusions

Massive digitisation and online release of images of herbarium specimens offers excellent opportunities to improve checklists of alien species in tropical Africa. For D.R. Congo, many previous records are not confirmed by voucher materials collected outside cultivation and await confirmation. Conversely, extensive search in online collections made it possible to discover many previously unknown species for the alien flora of D.R. Congo.

The alien flora of D.R. Congo is relatively species-poor considering the large area of the country and its rich native flora. The overwhelming contribution of American species, of annual Asteraceae, woody Fabaceae, Solanaceae are striking features of the alien flora.

Field work is urgently needed to assess the status of many alien species, and to ensure better coverage of recent introductions. Botanic gardens and protected nature areas are priority targets in this research agenda.

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749 **Table 1** The 20 most abundant alien species in the flora of D.R. Congo

750

Species	Family	Number of specimens in BR	Life form	Origin	Earliest record
Ageratum conyzoides L.	Asteraceae	553	Annual	America	1888
Setaria sulcata Raddi	Poaceae	444	Perennial	America	1879
Bidens pilosa L.	Asteraceae	370	Annual	America	1888
Mimosa pigra L.	Fabaceae	318	Shrub	America	1888
Erigeron bonariensis L.	Asteraceae	288	Annual	America	1910
Hilleria latifolia (Lam.) H.Walter	Petiveriaceae	281	Perennial	America	1895
Alternanthera sessilis (L.) R.Br. ex DC.	Amaranthaceae	272	Annual	Multiple	1888
Eclipta prostrata (L.) L.	Asteraceae	271	Annual	America	1888
Spermacoce pusilla Wall.	Rubiaceae	265	Annual	Asia	1888
Hyptis lanceolata Poir.	Lamiaceae	264	Perennial	America	1886
Physalis angulata L.	Solanaceae	263	Annual	America	1887
Euphorbia hirta L.	Euphorbiaceae	247	Annual	America	1888
Senna occidentalis (L.) Link	Fabaceae	244	Perennial	America	1888
Sida cordifolia L.	Malvaceae	243	Annual	Multiple	1886
Paspalum conjugatum P.J.Bergius	Poaceae	231	Perennial	America	1888
Scoparia dulcis L.	Plantaginaceae	225	Annual	America	1888
Piper umbellatum L.	Piperaceae	219	Shrub	America	1888
Amaranthus cruentus L.	Amaranthaceae	216	Annual	America	1888
Oxalis corniculata L.	Oxalidaceae	212	Perennial	America	1895
Imperata cylindrica (L.) P.Beauv.	Poaceae	189	Perennial	Multiple	1888

751

752 **Table 2** Alien seed plants in D.R. Congo: Comparison of the new checklist with previous
753 checklists. GRIIS (Global Register of Introduced and Invasive Species); GloNAF (Global
754 Naturalized Alien Flora database). Confirmed aliens: taxa in previous lists that are accepted in
755 the new list; awaiting confirmation: alien taxa in previous lists without voucher specimens
756 outside of cultivation; native: taxa native to D.R. Congo; other taxa excluded: wrong
757 identifications, geolocalisation errors, synonyms. New alien taxa: alien taxa collected outside
758 cultivation, not included in previous checklists
759

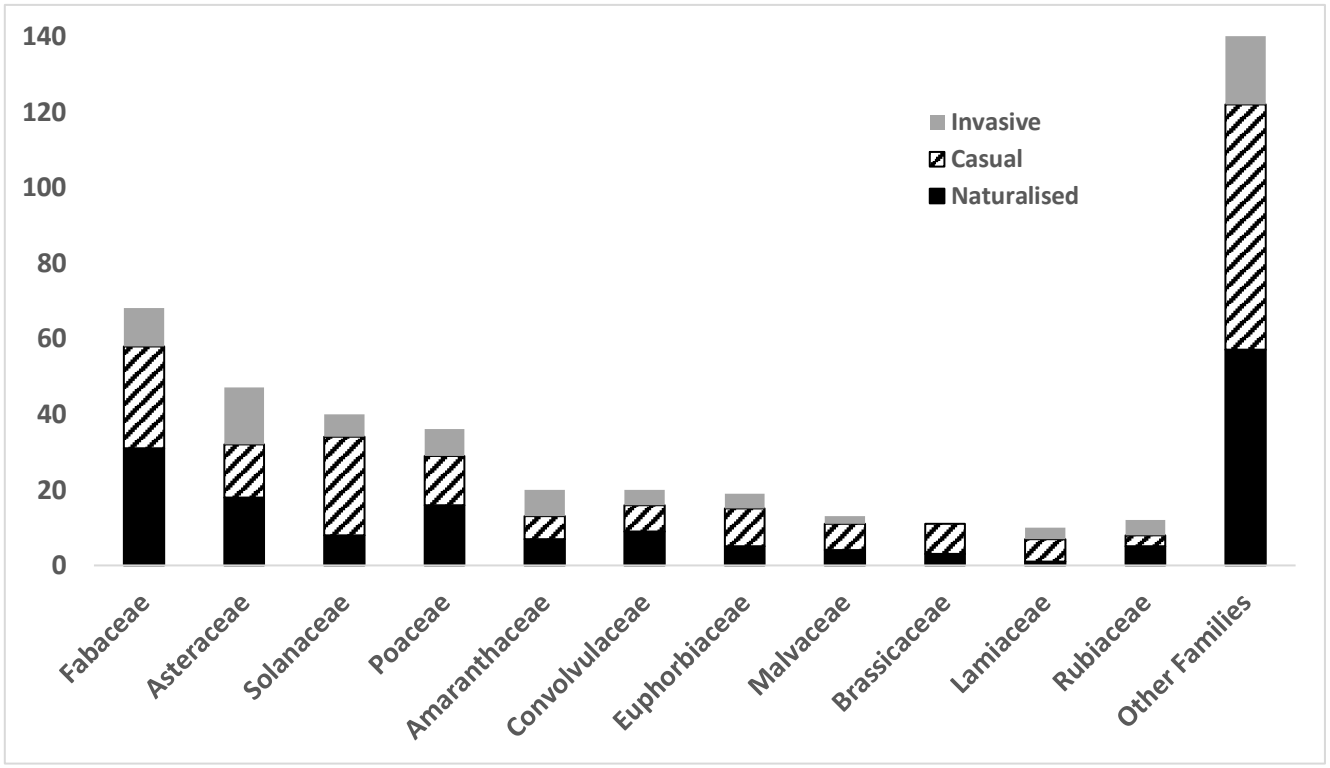
	GRIIS	GLoNAF
Taxa included in previous checklists	397	522
Aliens confirmed outside of cultivation	194 (108 naturalised)	253 (151 naturalised)
Awaiting confirmation		
Positive evidence from literature	124	118
Negative evidence from literature	29	40
Rejected		
Native	28	84
Other taxa excluded	22	27
New aliens	241 (139 naturalised)	180 (96 naturalised)

760 **Table 3** Patterns in the alien flora of D.R. Congo, compared with global patterns, and with
761 two other sub-Saharan Africa countries (N: naturalised; A: alien; I: invasive: C: casual)
762

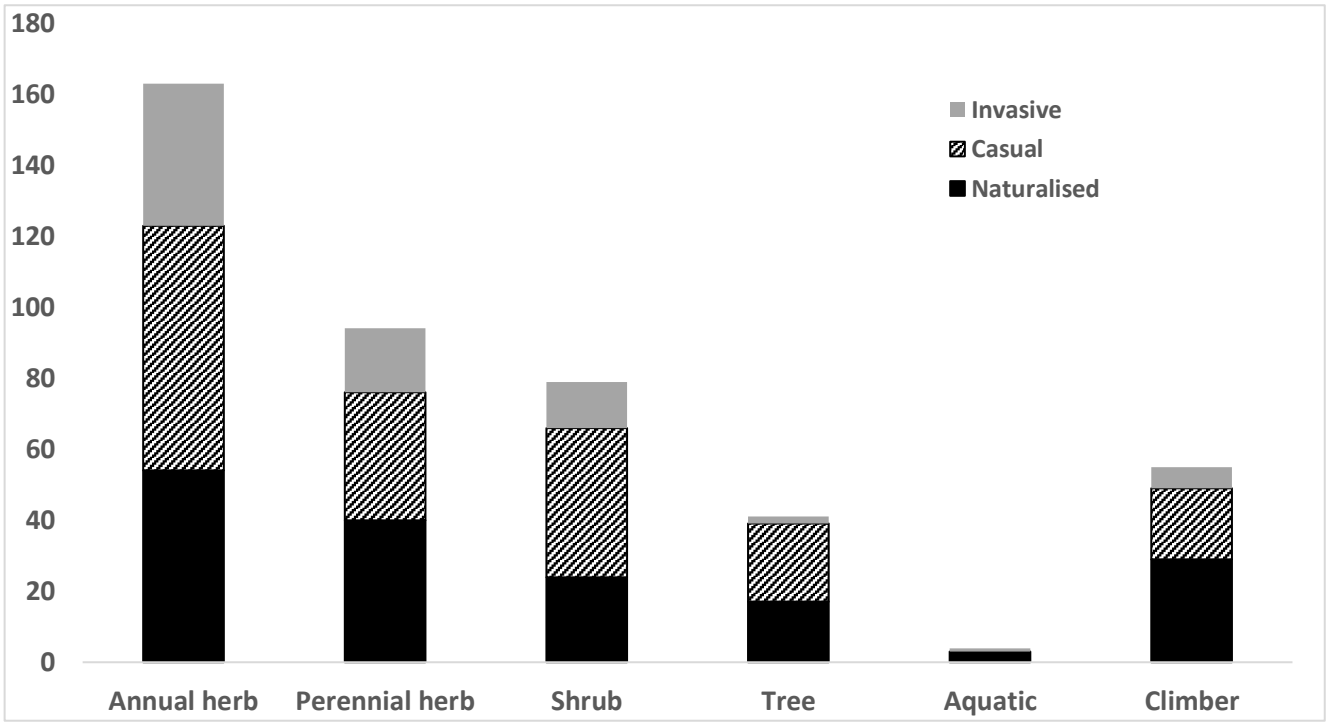
	Global Pyšek et al. (2017)	Zimbabwe Maroyi (2012)	Ghana Ansong et al. (2019)	D.R. Congo (This work)
Aliens (A)		391 A	--	436 A
Casuals (C)		153 C	--	189 C
Naturalised (N)	13168 N	154 N	291 N	167 N
Invasive (I)		84 I	25 I	80 I
Fabaceae	9%	13%	22%	16%
Asteraceae	10%	14%	8%	11%
Poaceae	10%	12%	6%	8%
Annuals	22%	37%	24%	37%
Herbaceous perennials	39%	24%	25%	22%
Trees and shrubs	32%	21%	40%	28%
Origin: America	30%	49.6%	54%	65%
Origin: Asia	32%	23.8%	28%	18%
Origin: Europe	15%	24%	1%	<1%

763
764

765 **Figures**



766 **Fig 1** Taxonomic spectrum of the alien flora of D.R. Congo. The proportions of invasive
767 species vary among the top 6 families (χ^2_{obs} = 19.17, d.f. = 10, P < 0.05)

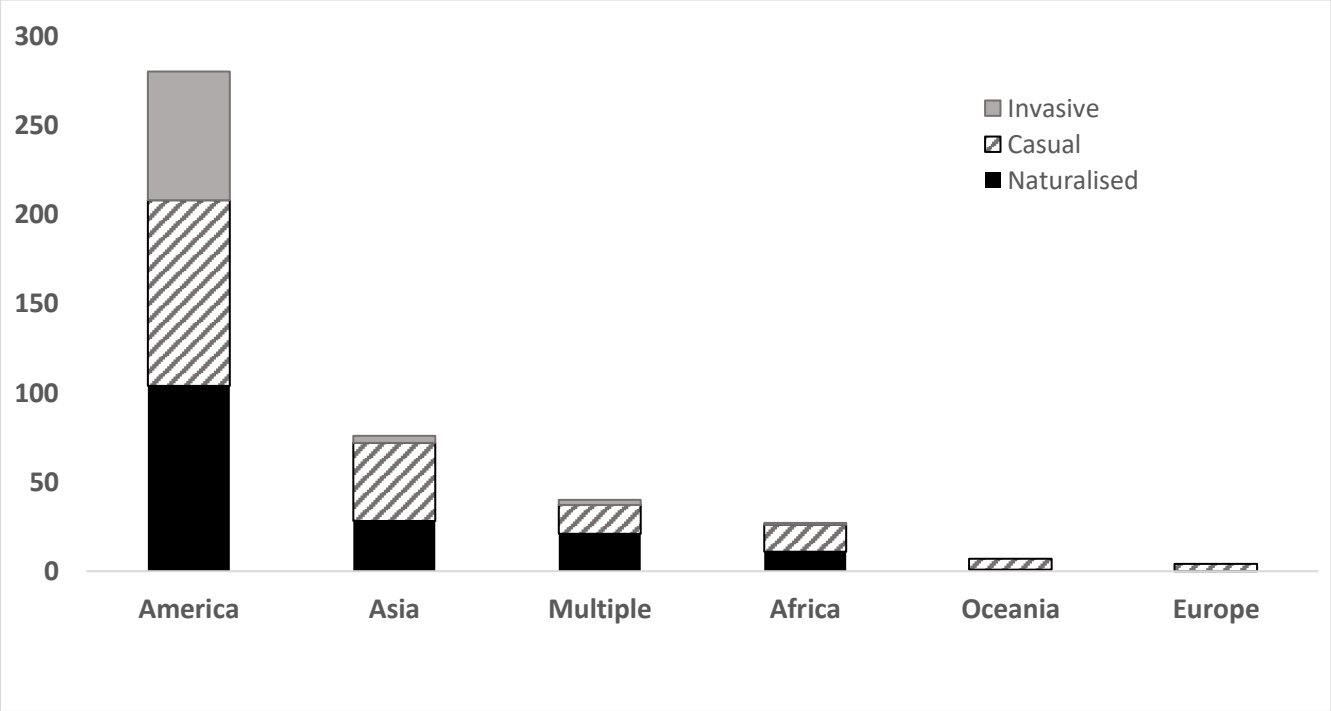


768

769 **Fig 2** Life form spectrum of the alien flora of D.R. Congo. The proportions of naturalised
770 species vary significantly among life forms (χ^2_{obs} = 25.38, d.f. = 10, P < 0.01)

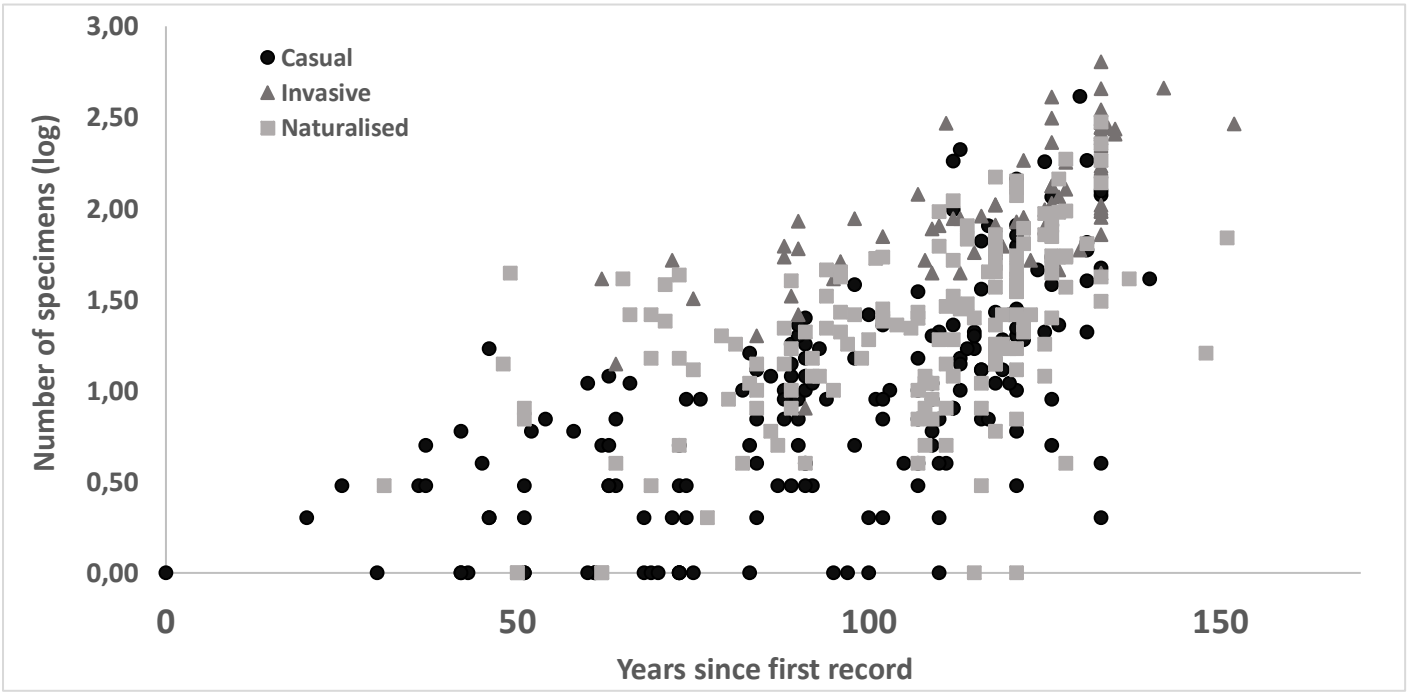
771

772



773

774 **Fig 3** Phytogeographic spectrum of the alien flora of D.R. Congo. The proportion of
775 naturalised and invasive species varies among source continents (χ^2_{obs} = 40.93, d.f. = 10, P <
776 0.001).



777

778 **Fig 4** Number of specimens in collections as a function of time since first record (y = -
779 0.0002x + 0.9429 r^2 = 0.56 P<0.001)

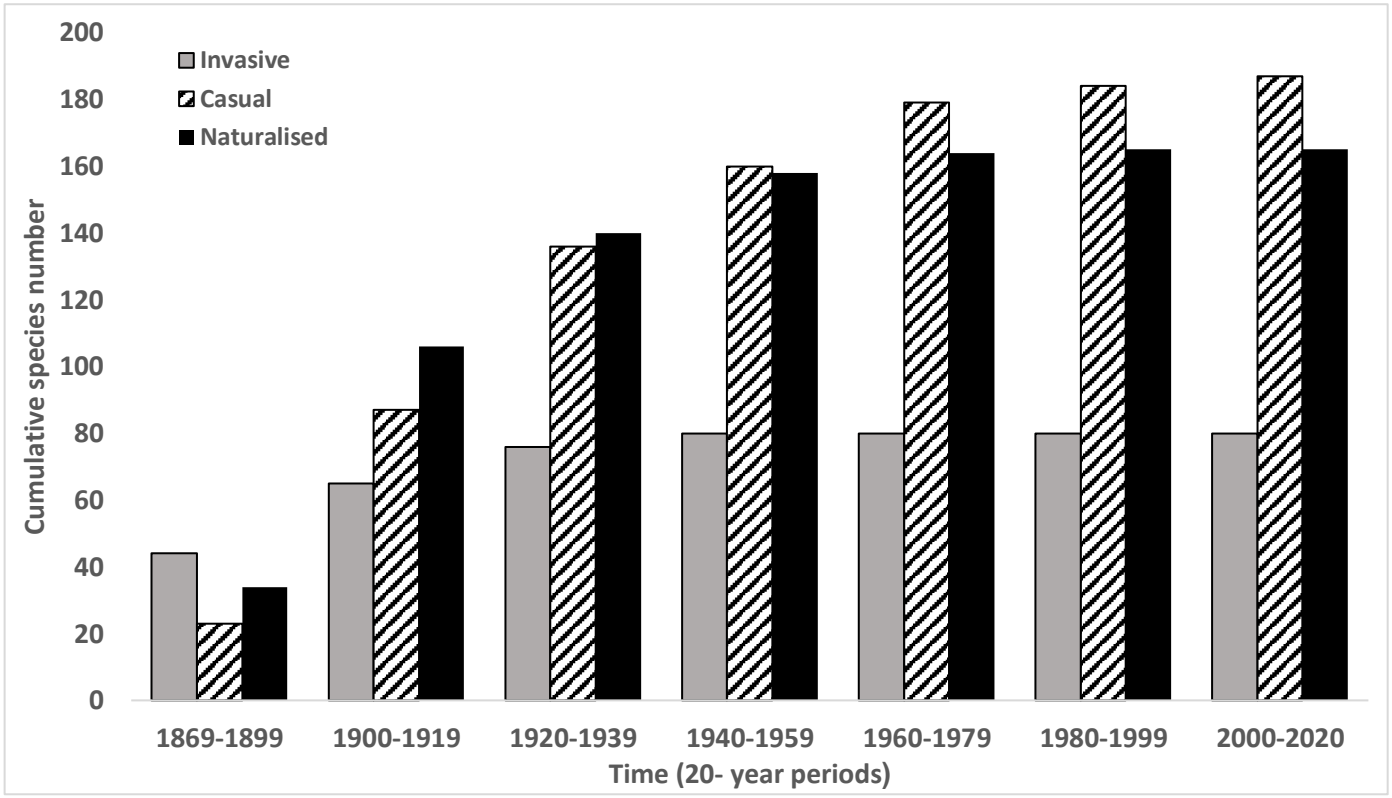
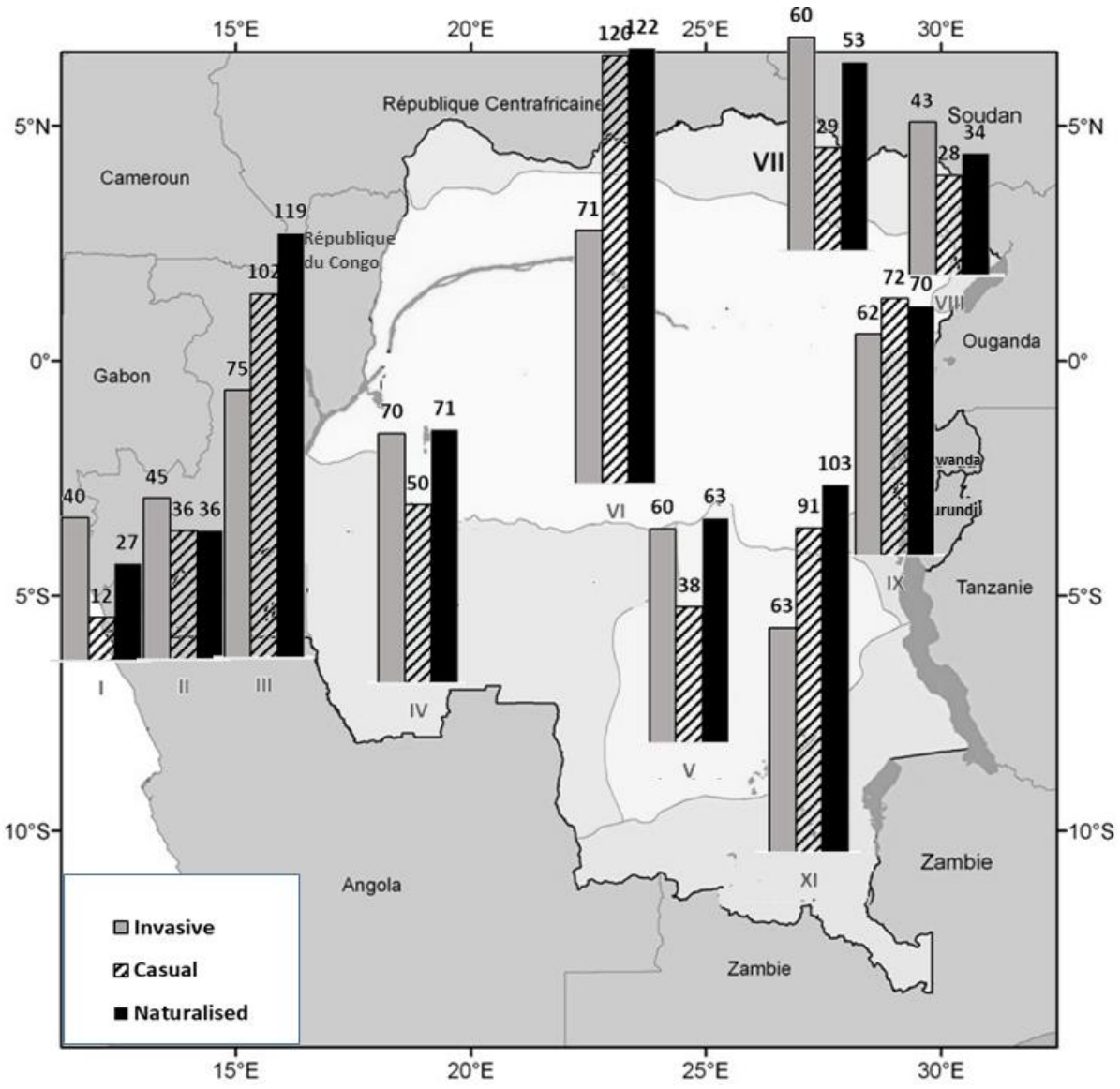


Fig 5 Number of species recorded as a function of time



794 **Fig 6** Alien species richness in the phytogeographic regions of D.R. Congo. I. Côtier, II.
795 Mayombe, III. Bas-Congo, IV. Kasaï, V. Bas-Katanga, VI. Forestier Central, VII. Ubangi-
796 Uele, VIII. Lac Albert, IX. Lacs Edouard et Kivu. XI. Haut-Katanga
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Supplementary Information

S1: List of alien species, with their status in previous databases, number of voucher specimens, date of earliest and latest record, life form, continent of origin and proposed status

S2: Species in GRIIS and/or GLoNAF list, without herbarium specimens outside of cultivation. Literature reference supporting occurrence outside of cultivation is indicated

S3: Species in GRIIS and/or GloNAF list, without herbarium specimens outside of cultivation, with literature refuting occurrence outside cultivation, or without literature

S4: Native species included in GRIIS and /or GloNAF, excluded from new checklist

S5: Species in GRIIS and/or GloNAF databases, excluded from the alien flora of D.R. Congo

S6: New records for the alien flora of D.R. Congo: Alien species not previously recorded outside of cultivation (APD, GBIF, GloNAF, GRIIS, ISC, POWO, Flore d'Afrique Centrale).