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South African plants growing wild in Mexico: patterns and the uncertainty of native areas

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Background and aim: Understanding floristic exchanges between regions helps predict introduction and invasion processes. Of the about 700 introduced angiosperm species in Mexico, most are from the Old World, including Africa. This study focuses on the plants that migrated from South Africa to Mexico, two megadiverse countries of the Global South with comparable climates. It addresses the problems of determining native species, and also explores patterns of habit, life cycle, use categories and times of arrival.

Methods: An exhaustive literature review identified the South African species growing wild in Mexico. A decision diagram outlines the inclusion/exclusion criteria; reasons for the decision on each species are provided. Data on habit, life cycle, uses and earliest herbarium specimen dates were compiled and analysed.

Results and conclusion: Of the 129 species listed in databases and literature as native South African species in Mexico, only 43 were confirmed. Poaceae contributed 53% of the species. Perennial forbs and grasses dominated; there was only one shrub and no trees. Uses were documented for 88% of species, mainly as forage and ornamental. Few species used as food or medicine in South Africa were utilised similarly in Mexico. Most South African species arrived during the 20th century, likely via the USA and South America. The lack of secondary uses in Mexico suggest commercial introductions as the primary reason for arrival. The workflow proposed here could assist other countries of the Global South with the identification of the causes of species introductions, aiding prevention.

Keywords: estimated time of arrival, exotic species, intentional introduction, native species, non-native species

Introduction

An alien, introduced, non-native or exotic species is one that arrived in a given region with the direct or indirect help of humans (Pyšek & Richardson 2006; Richardson et al. 2010; Soto et al. 2024). In contrast, a species is considered native if it occurs naturally in a region. This means it arrived from its area of origin by its own means and humans did not intervene (Courchamp et al. 2020; Roy et al. 2023). It is also adapted to the biotic and abiotic environment in its native region and has a co-evolutionary history with coexisting species (Hill & Hadly 2018). Some authors refer to a species as native to a specific region if, in addition to these characteristics, it has been present in an area since the end of the last glacial period (Usher 2000).

Some introduced species become naturalised, meaning they can reproduce without human intervention and form self-sustaining populations in the wild (Richardson et al. 2000). A few naturalised species are considered invasive because they cause serious ecological, economic or health problems (Pyšek & Richardson 2006; DOF 2016). Over the last 150 years, the increased movement of people and goods, regulatory failures at borders and the lack of awareness among the population and decision-makers have all contributed to the arrival and proliferation of unwanted plants (Meyerson & Mooney 2007). The problems caused by these plants are generally the result of several factors: the absence of predators or natural enemies, the physiological, genetic and reproductive characteristics of the species, climatic conditions, intentional selection and breeding, the absence of related species, and available niches, among others (Van Kleunen et al. 2015; Koleff et al. 2021; Gioria et al. 2023).

The exchange of plant species between distant regions is a well-known phenomenon, however, it has not been addressed comparatively until recently (Van Kleunen et al. 2015; Pyšek et al. 2017; Seebens et al. 2021). Over the last decade, a major effort has been made to identify and quantify the plant species exchanged worldwide. The first version of the Global Naturalized Alien Flora (GloNAF, a publicly accessible database; Van Kleunen et al. 2019) was compiled between 2011 and 2015. The first estimate reported 13 168 naturalised plant species globally, a figure representing 3.9% of the known world flora (Van Kleunen et al. 2015). The last update in 2021 had 13 939 species.

These studies have mostly used a geographic division based on continents, as suggested by the Taxonomic Databases Working Group (TDWG; Brummitt 2001). Van Kleunen et al. (2015) showed that North America and Europe have accumulated the largest number of naturalised species, with Asia and Europe as the main species donors. They proposed that species exchange has not occurred mainly between the Old and New Worlds, but rather between the northern and southern hemispheres. However, the underlying data may not always be reliable. Also, recent molecular work on some species has changed the evidence on origins considerably (e.g., Barres et al. 2011; Hyldgaard et al. 2017).

A clear understanding of the native and alien status of species has direct implications for the scientific knowledge of biological invasions and for public policy regarding eradication, control and conservation efforts (Hill & Hadly 2018). However, determining the area of origin, the native distribution area and the introduced range of species can be problematic. For many widespread species, information on their region of origin and migration history is lacking or contradictory. Some migrations may be ancient – earlier than the emergence of human beings, or recent, but undocumented; human intervention is sometimes difficult to prove (Usher 2000).

Identifying migration patterns is helpful for dealing with these organisms (Hierro et al. 2005). We consider the South Africa–Mexico species movement to be an interesting model for such a comparison. Both countries are considered a part of the Global South (Quiroga-Garza et al. 2022) as they have a history as European colonies, and share some socioeconomic and political characteristics. Besides, the countries have, in part, similar climates, are megadiverse for plants (Mittermeier et al. 1997) and have a culturally diverse population. The documentation of their native and alien flora, and its ethnobotany, is relatively advanced compared to neighbouring regions. However, they are located in different continents and hemispheres, and have had relatively little direct contact historically.

In Mexico, most research in the field of alien plants has focused on their distribution and impacts (Espinosa-García et al. 2004; Morales-Romero et al. 2019). The number of alien species in general and those with invasive behaviour is relatively low in Mexico compared to other regions of the world. This may be due to the long history of agriculture and human disturbance in the region, which has led to the development of a very diverse native weed flora (Vibrans, 2016); many of its members are now naturalised or invasive elsewhere in the tropics. However, there are some alien species that are causing problems and have gained attention in recent years (Espinosa-García & Villaseñor 2017; Koleff et al. 2021). The notable importance of species originating from Africa, particularly grasses, has previously been highlighted (Rzedowski & Rzedowski 1990).

South Africa has also played a role as a donor of species, many of them invasive, to other parts of the world. Pyšek et al. (2020) reported 80 species native to South Africa and adjacent regions that have invasive behaviour in the areas where they have been introduced. These include *Carpobrotus edulis* (L.) N.E.Br., *Andropogon gayanus* Kunth and *Cenchrus ciliaris* L.

Plant introductions to countries very distant from each other, such as Mexico and South Africa, are often indirect (e.g., in this case through Spain, Brazil or the USA; Rzedowski & Rzedowski 1990). Europeans mediated South Africa's trade with other parts of the world for centuries through their colonies (De Vega 2011). Historically, direct connections between Mexico and (South) Africa have been few, though there were some: from the 16th century onwards, Spaniards brought many Africans, mainly from Western Africa, as slaves to the Caribbean islands and the main seaports (Veracruz, Acapulco and Campeche) in Mexican territory (Mondragón-Barrios 2009; Velázquez & Iturralde-Nieto 2012). The first records of South African inhabitants in Mexico were Boer or Afrikaans groups that arrived in the north of the country as refugees after the war with Britain at the end of the 19th century (De Vega 2011).

In this study, we present criteria and a workflow to identify the species of plants likely native to South Africa and introduced to Mexico, using the available literature and other resources. Also, the problems encountered in the literature in determining the native and introduced ranges of species are analysed for every species.

We hope these tools will be a useful model for similar studies in other regions. Then we determined if there were patterns in terms of habit, life cycle, use categories and times of arrival of the wild-growing South African plant species in Mexico. We show that this more detailed analysis of plant origin, plant characteristics and migration patterns between these two countries of the Global South without much direct human or commercial exchange improves the understanding of the reasons for species migration, and thus enables more efficient predictions and prevention measures.

Methods

The study area

Mexico is located in the northern hemisphere, between parallels 14°32′ and 32°43′ N, and meridians 86°42′ and 118°27′ W. Although in terms of geography, the country is mostly a part of North America and has a medium-income status, Mexico is considered part of the Global South due to its socioeconomic conditions and history of colonialism (Quiroga-Garza et al. 2022).

Mexico's extension and physiographic conditions allow for a large variety of climates and ecosystems throughout the territory, including climate types A (warm), B (dry), C (temperate) and E (cold). The distribution of these climates in general terms is: 1) dry in practically the entire northern half of the country, 2) warm on the Pacific Ocean and Gulf of Mexico slopes, 3) temperate in the mountain regions and central plains and 4) cold on the high mountain peaks, according to the Köppen climate classification modified by Enriqueta García (García 2004). There is also much local and regional variation in temperature, seasonality and precipitation due to the mountainous terrain. These characteristics contribute in part to the high diversity of plant species and the number of endemics in the country (Villaseñor 2016). The human population arrived mainly towards the end of the last glacial period, 15 000 to 10 000 years ago, although some groups may have arrived earlier (McCaa 2000; García-Ortiz et al. 2021), and went on to create one of the centres of origin of agriculture from 10 000 BP onwards.

Determination of South African species introduced to Mexico and information gathering

First, plant species introduced into Mexico were identified (Figure 1). We reviewed scientific articles and other sources on the allochthonous flora of Mexico (Villaseñor & Espinosa-García 2004; Espinosa-García & Villaseñor 2017) or that included information on their migratory status (Ocampo-Acosta 2002; Rzedowski et al. 2003; Rzedowski & Rzedowski 2005; Villaseñor et al. 2012; Sánchez-Ken 2019). Standard databases were consulted for relevant information: Global Register of Introduced and Invasive Species – Mexico (González-Martínez et al. 2020), Global Invasive Species Database (GISD; https://www.iucngisd.org/gisd), and The Global Naturalized Alien Flora Database (GloNAF; https://glonaf.org). The collected information was sorted, duplicate records were removed, and valid scientific names were verified. Scientific names followed primarily Plants of the World Online (POWO; https://powo.science.kew.org). Some other databases were also consulted for synonymies: World Flora Online (https://www.worldfloraonline.org), the International Plant Names Index (https://www.ipni.org), and Tropicos (https://www.tropicos.org/home). The resulting list was compared with the species reported as native to South Africa by the South African National Biodiversity Institute (SANBI 2016). We used the SANBI database from 2016 (https://ipt.sanbi.org.za/resource?r=brahms_online) as a starting point for the South African species, as it distinguished between native and alien species. In March 2025, the database moved to the 'Botanical Database of Southern Africa (BODATSA): Botanical Collections' at https://www.gbif.org/dataset/d0963cee-1a29-47a2-b9bf-fb0e7690077c. It now includes additional information, such as a list of herbarium specimens with some associated data. However, it lost the information on the native/alien classification due to the homogenisation with GBIF data fields.

Species not reported as native to South Africa in this database were omitted from further analysis. Those recorded as native were subjected to a literature review to corroborate this fact. As a general principle, we considered a plant species to be native to South Africa, if the biogeographic region where it had its main distribution area was either the Capense kingdom or the Sudano-Zambezian biogeographic region ('biogeographic region' definition sensu Takhtajan 1986). This initial decision could then be modified, if the available genetic, phylogenetic, ecological, palaeobotanical, archaeological and ethnohistorical information pointed to human-mediated migration and not natural expansion. The treatment of contradictions and uncertainty is discussed below.

The choice of the delimitations of biogeographic regions involves judgment by authors; biogeographical divisions are currently being widely discussed and reassigned based on the analysis of large datasets and different methods and criteria (e.g., Liu et al. 2023, but also Morrone & Ebach 2022; Qian 2024). The most predictive classifications may differ between plants and other types of organisms (e.g., Linder et al. 2012), or even between life forms (Mucina 2024). For our purposes, the modernised Takhtajan classification proposed by Loidi and Vynokurov (2024) was useful.

For the species supported in the literature as native to South Africa, we verified their presence in the wild in Mexico. Wild-growing meant the specimen was not

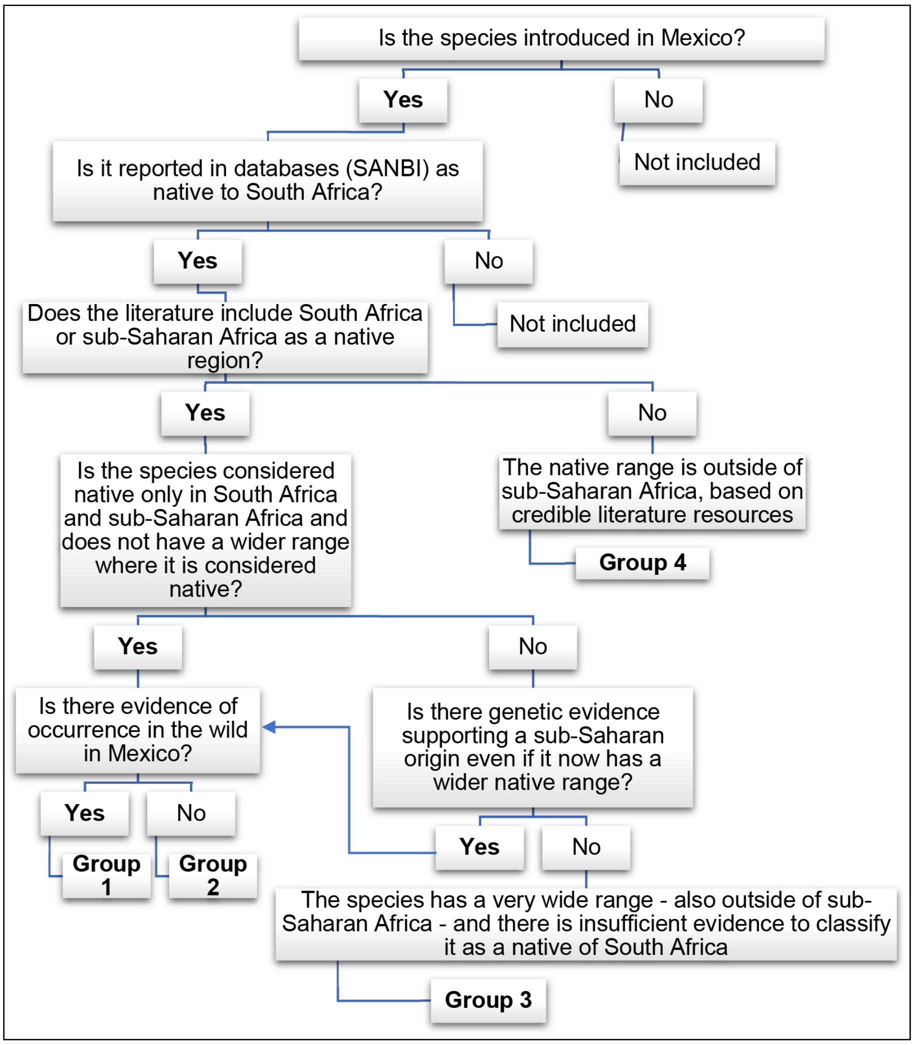

Figure 1. Decision diagram for determining the species native to South Africa that are wild-growing in Mexico. Group 1: plants native to South Africa occurring in Mexico in the wild (includes species that may have originated in other parts of sub-Saharan Africa, particularly the Sudano-Zambezian biogeographic region, or have a wider distribution but evidence points to a sub-Saharan origin, and are considered native to South Africa by the cited literature). Group 2: plants native to South Africa but with no evidence of occurrence in the wild in Mexico. Group 3: plants of doubtful or very extensive provenance, beyond the area of interest. Group 4: plants native to regions other than South Africa and south of the Sahara, but mentioned as African in the SANBI database (https://www.gbif.org/dataset/d0963cee-1a29-47a2-b9bf-fb0e7690077c).

cultivated but grew spontaneously. This had to be stated or be implicit in the specimen label. In this study, we use the terms 'wild growing' or 'present in the wild' instead of 'naturalised', as herbarium specimens typically do not include information on the degree of naturalisation, that is, the permanence of populations.

The verification was based on the already mentioned publications, as well as some additional sources. The descriptions of the website Malezas de México [Weeds of Mexico] (http://www.conabio.gob.mx/malezas-demexico/2inicio/home-malezas-mexico.htm), an online Spanish-language flora on weeds, were examined. We also reviewed the information of the herbarium labels of digitised specimens available online from different herbaria (ASU, BCMEX, HCIB, HEFA, KANU, LL, MEXU, MICH, NY, RSA, SD, SDSU, TAES, TEX, USON, USF; Thiers 2025), that contained in the 'Open Data' site of the National Autonomous University of Mexico (https://datosabiertos.unam.mx/biodiversidad), the Mexican Herbaria Network (https://herbanwmex.net/portal), and Tropicos (https://tropicos.org). In some cases, we relied on photographs published on the iNaturalist website (https://www.inaturalist.org). We only used this site for species that could be easily and accurately identified from photos and considered only specimens with a 'research grade' status in the 'data quality' section. Each determination was based on at least two sources, preferably independent of each other.

Contradictory information on species' native regions was considered. When sources disagreed (e.g., one claimed a species was native to South Africa, while others indicated a different region), we assessed the reliability of the sources, their methods, their recency and whether they used genetic data. Species confirmed as South African by the most reliable evidence were classified as native to South Africa. Others were categorised as of doubtful origin, including species with wide distributions beyond the Sudano-Zambezian region and no data on the origin. Species listed by at least two reliable sources as non-South African were grouped as non-native.

The decision diagram of Figure 1 shows the procedure for assigning species to four categories or groups:

1. Plants native to South Africa and growing wild in Mexico (Supplementary Material 1). This group includes species endemic to South Africa and additionally

those with a continuous distribution south of the Sahara (Sudano-Zambezian biogeographic region). The Sudano-Zambezian region has few barriers to plant migration, so species may have colonised this area prehistorically, even if they originated outside southern Africa. This category also included a few widespread species with evidence of a sub-Saharan African origin and considered native by SANBI.

2. Species native to South Africa and cultivated in Mexico, but not documented as growing wild (Supplementary Material 2).
3. Species of unknown/doubtful origin or with a native distribution beyond the area of interest (Supplementary Material 3). Very widespread species (across Africa, southern Asia, Europe and sometimes Australia) may have reached their current distribution either through climate variations before the appearance of modern humans or through undocumented human activities and the spread of agriculture and commerce. Due to these uncertainties, they were placed in group 3 unless evidence showed they originated in sub-Saharan Africa.
4. Species not native in South Africa (Supplementary Material 4).

The first group (plants native to South Africa and present in the wild in Mexico) was the focus of the second part of this research. For these plants, additional information was sought on their habit, life cycle and uses in Mexican and South African literature. We classified the uses into the categories proposed by Burgos-Hernández et al. (2014). Invasive plant status in Mexico was determined based on an official legal norm, the List of Invasive Alien Species for Mexico (DOF 2016). We also extracted the dates of the first collection of each species in Mexico from the specimens reviewed in the herbaria listed above.

Results

Determination of the native range of the species

Group 1 (plants native to South Africa present in the wild in Mexico) contained only 43 species (Table 1; Supplementary Material 1). For group 2 (plants native to South Africa with no evidence of presence in the wild in Mexico), a list of 23 species was obtained. This group consisted mainly of commercial ornamental species but did not include all South African ornamentals present in Mexico, as cultivated plants are not well documented. Also, we observed that only a few of them have naturalised in other parts of the world and are therefore not included in the work of Pyšek et al. (2020) (Supplementary Material 2). Group 3 (plants of doubtful provenance) had 26 species (Supplementary Material 3), and group 4 (plants native to regions other than South Africa and the area south of the Saharan Desert) had 37 species (Supplementary Material 4).

The original databases had indicated 129 South African species present in Mexico. However, we found several discrepancies in the reported native ranges in the literature and databases, and observed various problems. For example, six species were reported as native for both Mexico and South Africa (Table 2).

Table 1. Species native to South Africa and present in Mexico in the wild; specimens from cultivated populations are not included. Comments on their inclusion in this group can be found in Supplementary Material 1. Uses: F = food, AF = animal forage, M = medicinal, O = ornamental, OT = other, NU = no use. Invasiveness according to DOF (2016)

Family	Scientific name	Uses in South Africa	Uses in Mexico	Year of first record in Mexico	Invasive in Mexico
Acanthaceae	*Thunbergia alata* Bojer ex Sims	O, M	O, M	1908	Yes
Aizoaceae	*Carpobrotus edulis* (L.) N.E.Br.	O, M, F	O	1980	Yes
Aizoaceae	*Mesembryanthemum crystallinum* L.	O, M	O	1920	Yes
Aizoaceae	*Mesembryanthemum nodiflorum* L.	O	O	1929	No
Aizoaceae	*Trianthema portulacastrum* L.	M	M	1897	No
Apocynaceae	*Gomphocarpus physocarpus* E.Mey.	O, M	O	1969	No
Araceae	*Zantedeschia aethiopica* (L.) Spreng.	O, M	O	1925	No
Asparagaceae	*Dracaena hyacinthoides* (L.) Mabb. [=*Sansevieria hyacinthoides* (L.) Druce]	O, M	O	1981	No
Asphodelaceae	*Kniphofia uvaria* (L.) Oken	O, M	O	1941	No
Asteraceae	*Arctotheca prostrata* (Salisb.) Britten	O, M	O	2013	No
Asteraceae	*Cotula coronopifolia* L.	NU	NU	1936	No

Table 1. Species native to South Africa and present in Mexico in the wild; specimens from cultivated populations are not included. Comments on their inclusion in this group can be found in Supplementary Material 1. Uses: F = food, AF = animal forage, M = medicinal, O = ornamental, OT = other, NU = no use. Invasiveness according to DOF (2016) (continued)

Family	Scientific name	Uses in South Africa	Uses in Mexico	Year of first record in Mexico	Invasive in Mexico
Asteraceae	*Senecio inaequidens* DC.	NU	NU	1992	Yes
Cucurbitaceae	*Cucumis anguria* L.	M, F	M, F, AF	1921	No
Cucurbitaceae	*Momordica balsamina* L.	M, F	M, F	1986	No
Cyperaceae	*Cyperus esculentus* L.	F, M	F	1886	No
Cyperaceae	*Cyperus involucratus* Rottb.	NU	NU	1938	No
Iridaceae	*Gladiolus dalenii* Van Geel	O, M, F	O	1992	No
Lamiaceae	*Leonotis nepetifolia* (L.) R.Br.	O, M, OT	O, M, OT	1906	Yes
Malvaceae	*Sida rhombifolia* L.	M	M	1892	No
Oxalidaceae	*Oxalis pes-caprae* L.	O, M, F	O, M, F	1969	Yes
Poaceae	*Andropogon gayanus* Kunth	AF	AF	1987	Yes
Poaceae	*Cenchrus ciliaris* L.	AF, M	AF	1956	Yes
Poaceae	*Digitaria eriantha* Steud.	AF, M	AF	1972	No
Poaceae	*Digitaria milanjiana* (Rendle) Stapf	NU	NU	1935	No
Poaceae	*Echinochloa colona* (L.) Link	AF	AF	1898	No
Poaceae	*Echinochloa pyramidalis* (Lam.) Hitchc. & Chase	AF	AF	1969	No
Poaceae	*Ehrharta erecta* Lam.	AF	AF	2007	No
Poaceae	*Eragrostis ciliaris* (L.) R.Br.	AF, M	AF	1984	No
Poaceae	*Eragrostis curvula* (Schrad.) Nees	AF, O	AF	1959	Yes
Poaceae	*Eragrostis echinochloidea* Stapf	NU	NU	2001	No
Poaceae	*Eragrostis lehmanniana* Nees	AF, OT	AF, OT	1976	No
Poaceae	*Eragrostis superba* Peyr.	AF, OT	AF, OT	1962	No
Poaceae	*Eragrostis viscosa* (Retz.) Trin. [= *Eragrostis amabilis* (L.) Wight & Arn.]	AF	AF	1910	No
Poaceae	*Hyparrhenia cymbaria* (L.) Stapf	AF	AF	2011	No
Poaceae	*Hyparrhenia hirta* (L.) Stapf	AF, M	AF	1888	Yes
Poaceae	*Hyparrhenia rufa* (Nees) Stapf	AF	AF	1963	Yes
Poaceae	*Hyparrhenia variabilis* Stapf	AF	AF	2006	No
Poaceae	*Hyperthelia dissoluta* (Nees ex Steud.) Clayton	AF	AF	1910	No
Poaceae	*Megathyrsus maximus* (Jacq.) B.K.Simon & S.W.L.Jacobs (= *Panicum maximum* Jacq.)	AF, M	AF	1931	No
Poaceae	*Melinis minutiflora* P.Beauv.	AF	AF	1953	Yes
Poaceae	*Melinis repens* (Willd.) Zizka (= *Rhynchelytrum repens* (Willd.) C.E.Hubb.)	O, OT	O	1927	Yes
Poaceae	*Setaria sphacelata* (Schumach.) Stapf & C.E.Hubb. ex M.B.Moss	AF	AF	1965	No
Poaceae	*Tricholaena monachne* (Trin.) Stapf & C.E.Hubb. (= *Panicum coloratum* L.)	NU	NU	1986	No

Table 2. Species reported to be native and alien in both Mexico and South Africa

Family	Scientific name	Native range
Cyperaceae	*Cyperus compressus* L.	Unknown if native to Mexico or South Africa. Germishuizen and Meyer (2003) consider it native to South Africa and González-Elizondo et al. (2018) to Mexico. Other sources (e.g., POWO) indicate a 'native area' spanning various continents.
Fabaceae	*Mucuna pruriens* (L.) DC.	Native to south and southeast Asia based on recent genetic data (Tripathi et al. 2018; Misra et al. 2021) but reported as native in Mexico (Villaseñor 2016) and South Africa (SANBI 2016).
Malvaceae	*Waltheria indica* L.	Native distribution unknown. There are references based on historical records, taxonomic revisions and checklists; however, they are contradictory and name several regions, including the countries of interest in this work (Verdoorn 1981; Germishuizen & Meyer 2003; Baudilio-Rondon 2008).
Sapindaceae	*Cardiospermum grandiflorum* Sw.	Native to Central America (including Mexico) and South America based on ecological and historical data (Gildenhuys et al. 2013). It was reported as native in South Africa (SANBI 2016) but is now considered alien and invasive (Foster et al. 2019). Other sources (e.g., POWO) indicate a 'native area' that included all tropical and subtropical regions of America and Africa.
Sapindaceae	*Cardiospermum halicacabum* L.	There is still debate about the origin of this species, but it is probably native to America based on ecological and historical data (Gildenhuys et al. 2013) and introduced to South Africa (Foster et al. 2019).
Verbenaceae	*Phyla nodiflora* (L.) Greene	Native distribution unknown and highly contradictory in the literature. It may be native to the Americas based on genetic and biogeographical data (Gross et al. 2017).

South African species wild-growing in Mexico

The 43 South African species present in Mexico belong to 29 genera from 14 families (Figure 2). Of these, 13 species (30%) are registered in the List of Invasive Alien Species for Mexico (DOF 2016), although others, such as *Hyparrhenia variabilis* Stapf., *Megathyrsus maximus* (Jacq.) B.K.Simon & S.W.L.Jacobs and *Sida rhombifolia* L. are invasive but not included in the official list.

Poaceae emerged as the main donor of introduced South African plants, accounting for 53% of the species,

Figure 2. Some of the South African plants growing wild in Mexico; A, *Leonotis nepetifolia*; B, *Cenchrus ciliaris*; C, *Senecio inaequidens*; D, *Melinis repens*.

Table 3. Plant families of South African species wild-growing in Mexico and number of species registered in the List of invasive species for Mexico (DOF 2016)

Family	Number of wild-growing species	Number of invasive species
Poaceae	23	7
Aizoaceae	4	2
Asteraceae	3	1
Cucurbitaceae	2	0
Cyperaceae	2	0
Asparagaceae	1	0
Araceae	1	0
Lamiaceae	1	1
Apocynaceae	1	0
Acanthaceae	1	1
Iridaceae	1	0
Malvaceae	1	0
Oxalidaceae	1	1
Asphodelaceae	1	0

Table 4. Habit and life cycle of South African species present in the wild in Mexico

Habit	Life cycle	Number of species
Grass	Annual	3
Grass	Perennial	19
Grass	Annual or perennial	1
Forb	Annual	3
Forb	Perennial	14
Forb	Annual or perennial	2
Shrub	Perennial	1

followed by Aizoaceae (9%) and Asteraceae (7%). Nine families were represented by only one species (Table 3). The genera with the highest number of species were *Eragrostis* (6 spp.) and *Hyparrhenia* (4 spp.).

Most species (76%) were perennial forbs and grasses. Only one shrub (*Sida rhombifolia*; Table 4) and no trees were recorded.

Uses of African species

A large proportion of the plant species of Group 1 had human uses. In both Mexico and South Africa, uses have been reported for 88% of the species. No uses were found for *Cotula coronopifolia* L., *Cyperus involucratus* Rottb., *Eragrostis echinochloidea* Stapf, *Senecio inaequidens* DC. and *Tricholaena monachne* (Trin.) Stapf & C.E. Hubb in either country.

The main use categories, 'forage' (including fodder) and 'ornamental', had similar proportions in both countries. Medicinals showed the largest difference with 21 species recorded as medicinal for South Africa, but only 7 for Mexico (Table 5). Differences were also found in the proportion of multipurpose species: in South Africa, 55% of the species had at least two different use types, whereas in Mexico, only 16% did. Only one South African plant had a new use in Mexico that was not recorded for South Africa (*Cucumis anguria* L., used as forage in Mexico; Lira & Caballero 2002).

Arrival date of the species

The first herbarium record for just over half of the species (24) was 75 years or older (see Supplementary Material 1). The oldest records of wild populations belonged to *Cyperus esculentus* L. from 1886 and *Hyparrhenia hirta* (L.) Stapf from 1888. Five species appear to be recent introductions to Mexico but have naturalised very quickly and now behave as alien weeds: *Eragrostis echinochloidea* from 2001, *Hyparrhenia variabilis* from 2006, *Ehrharta erecta* Lam. from 2007, *Hyparrhenia cymbaria* (L.) Stapf from 2011,

Table 5. Use categories of South African species present in the wild in Mexico, in South Africa and Mexico

Use category	Number of species per use category in South Africa	Number of species per use category in Mexico
Medicinal	21	7
Forage/fodder	20	21
Ornamental	14	14
Food	5	4
Other (erosion control)	4	2
Other (honey production)	1	1

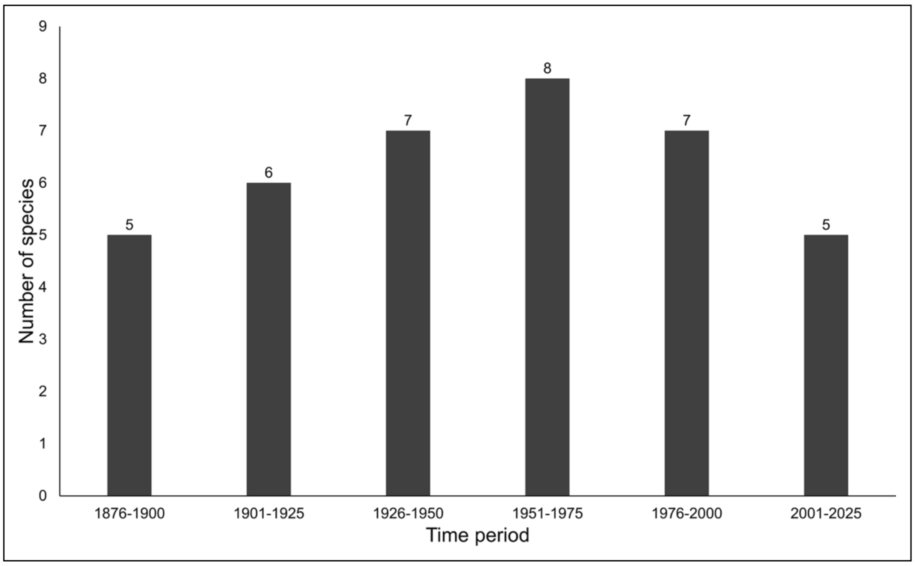

Figure 3. The dynamics of arrival of South African plant species in Mexico: year of the first documented herbarium specimens, by quarter-centuries.

and *Arctotheca prostrata* (Salisb.) Britten from 2013. A peak is observed in the middle of the last century (Figure 3).

Discussion

Determination of the status of species as native or alien

The number of species native to South Africa and also found in Mexico was much lower than the number reported in the primary global database, GloNAF (Van Kleunen et al. 2019). This discrepancy is due to the information sources on the native ranges of these species gathered in databases. These databases and their sources are prone to errors due to conceptual, informational and human inconsistencies (McGeoch et al. 2012; Villaseñor 2016). Here, we made an effort to: a) standardise the categorisation process and explain it in detail, and b) identify the problems associated with these categorisations. Determining the native area caused the most difficulties, as evident in the justifications for the individual species in the Supplementary Material. This was due to the following factors:

1. The lack of consistent concepts for native and exotic species. This is one of the major issues in determining the native range of species and a major reason for the differences found in the literature (Pyšek et al. 2004; Courchamp et al. 2020). Authors frequently appear to assume that terms such as 'native', 'exotic', 'introduced' and 'allochthonous' are universally understood and fail to define them (Richardson et al. 2000). There is a clear need for coherent and consistent definitions, and methods on how to determine if a species is native or alien (Soto et al. 2024).
2. Lack of explanations for how authors categorise species, complicating efforts to standardise these decisions. In most sources, especially older ones, there is little indication of why a species was considered native or not. Some documents explicitly state that all species without documented evidence of introduction to the area of interest were considered native (Germishuizen & Meyer 2003; Villaseñor 2016).
3. Use of current distribution areas, if they are more or less continuous, interchangeably with native ranges. For example, *Cyperus iria* L. is considered native to South Africa by SANBI (2016), not by POWO (2024), but has a wide Old-World distribution. It is likely that this species is native to a region within this wide distribution area, but it probably spread to its current area associated with rice cultivation (Kraehmer et al. 2016). Additionally, sources employ terms like 'pantropical' or 'cosmopolitan' (Rzedowski & Rzedowski 1990), which is often shorthand for 'it has a wide distribution but we don't know where it is native' (Pociecha et al. 2016). Plant dispersal between the Old and New World independent of humans is theoretically possible, but it does not appear to be common (Renner 2004) and should have evidence when alleged.
4. Misquotations, particularly of older sources – in several cases, the original sources either did not mention the species of interest or reported a different native distribution, or were based on misidentifications. Such errors perpetuate in databases and then influence decisions due to their perceived reliability (Villaseñor 2016).
5. Large databases rely on information from herbaria, floras, scientific articles, books and other sources. Sometimes native ranges are generalised to large regions, such as continents, for easier data

management (Van Kleunen et al. 2015). Contradictory information in the sources for the native range of a species is sometimes 'solved' in the databases by simply adding all the areas instead of further investigation (Randall 2017). POWO (2024), for example, shows two or three disjunct 'native areas' for several species. One of these cases is that of *Stenotaphrum secundatum* (Walter) Kuntze, which is shown as native to countries of Central Africa, South America and to southeastern Mexico, but introduced in northern Mexico; this case could not be resolved. *Cardiospermum grandiflorum* Sw. has been reported as native from both Africa (Germishuizen & Meyer 2003) and America (Villaseñor 2016), but recent molecular and niche model data point to an American origin (Gildenhuys et al. 2013) and historical data confirms that it arrived in South Africa 100 years ago (Foster et al. 2019). A number of other species considered native to South Africa were found to be from other continents, such as *Atriplex patula* L., which is native from Europe and is unlikely to have arrived in South Africa without human assistance (Bassett & Munro 1987). The list of native species published by SANBI (South African National Biodiversity Institute 2016) was derived from other local listings that confounded native and current distribution areas. Similar problems were observed in databases such as World Flora Online (http://www.worldfloraonline.org) and the GRIN database (Germplasm Resources Information Network, https://www.ars-grin.gov).

In this study, some contradictions in the literature were resolved and the species assigned to our groups. We also observed that species in Group 1, besides being widely accepted as South African natives (Pyšek et al. 2020), also tended to be abundant in the country. Group 4 species were generally less abundant in southern Africa compared to their probable native regions. In some cases, it was possible to identify a specific native region within Africa (e.g., *Dactyloctenium aegyptium* (L.) Willd., Cerrato et al. 2021). In this work, these were considered alien to South Africa, and our main references agreed.

Some of our decisions for the assignment of species to the groups may be controversial. For example, we used a biogeographic region and a barrier, the Sahara Desert and the Arabian Sea, to delimit South African species. Most of South Africa is part of the paleotropical floristic kingdom, and there is a continuous area of dry tropical conditions that ranges from southern through eastern Africa to the sub-Saharan region, without notorious biogeographic barriers, generally recognised as the Sudano-Zambezian biogeographic region as mentioned above (Werger 1978). Thus, the likelihood of autonomous expansion is relatively high. This is not true of species originating in the Cape Floristic Kingdom, which rely on more humid conditions with a winter-rainfall regime (Loidi & Vynokurov 2024).

South African species in Mexico

A relatively small proportion of Mexico's alien plant flora is of South African origin. The 43 wild-growing species native to South Africa documented here represent about 6.1% of all known alien species in Mexico (approximately 700; Espinosa-García & Villaseñor 2017). Previous estimates have suggested that 20% of alien species originate from the African continent, including North Africa (Villaseñor & Espinosa-García 2004), so other African regions need to be analysed. However, we identified several patterns within this group.

The composition of the South African plants in Mexico was unusual, particularly the absence of trees and of plants used for food or fibre, which usually accompany migrating people or disperse through seed contamination. Main uses were similar in both countries, with fewer secondary uses in Mexico. This, together with the dominance of herbaceous ornamentals and forage plants, appear to indicate that most introductions were deliberate, though not necessarily direct: the commercially relevant information travelled with the plants, but information from folk culture, such as use as medicine, did not. The introduced flora of the United States also appears to derive mainly from such deliberate introductions (Mack & Erneberg 2002).

The introductions were concentrated in a use category not well represented in the native Mexican flora: tropical forage grasses and also, as everywhere, ornamentals. The movement of ornamental species is a major pathway for plant introduction, and subsequent naturalisation and invasion (Van Kleunen et al. 2018). Poaceae stands out as the largest contributor of alien species to Mexico in general (that is, from all origins; Espinosa-García & Villaseñor 2017). Approximately 27% of Mexico's alien species are grasses, occupying extensive areas (Pérez-Postigo et al. 2021). Our findings for South African species support this, with grasses contributing the largest proportion of naturalised species (58%). Of the 224 alien grass species in Mexico, South African grasses contribute 11%, with some of them being among the most widespread (*Andropogon gayanus, Cenchrus ciliaris, Megathyrsus maximus, Melinis repens*; Sánchez-Ken et al. 2019). Concerns about the naturalisation of African grasses in Mexico have been raised for decades (Rzedowski & Rzedowski 1990). Recent years have seen arrivals such as *Hyparrhenia cymbaria* and *Hyparrhenia variabilis*, which now cover extensive areas in western Mexico (Vibrans et al. 2014).

The high percentage of South African grasses in Mexico may be attributed to similar abiotic conditions in both countries, including semi-dry temperate and tropical climates, vast plains where grasses can easily spread and the influence of fire (García 2004; Engelbrecht & Engelbrecht 2016). Also, tropical Mexico lacked large herbivores after the last glacial age, and thus, the coevolved plant species (Stebbins 1981; Charles-Dominique et al. 2016). The growth of cattle ranching in Mexico encouraged the introduction of adapted grasses from Africa (Rzedowski & Rzedowski 1990). Most species were introduced initially for grazing purposes and then escaped; some may have arrived with contaminated seed imports (Stokes et al. 2011; Marshall et al. 2012). Several of these alien grass species have arrived via the United States of America (USA) (Marshall et al. 2012), both intentionally and through natural expansion.

Aizoaceae ranked second in South African species that arrived in Mexico and became wild growing. This family's naturalisation and potential for invasion in Mexico has been noted since the early 1990s (Rzedowski & Rzedowski 1990). Two species from this family are legally considered invasive in Mexico (DOF 2016), indicating their ability to displace native vegetation. They were possibly introduced accidentally or intentionally through the USA where wild populations have been recorded near the Mexican border for decades (D'Antonio 1993).

Thirteen South African species are listed as invasive in Mexico (DOF 2016), a relatively high proportion, although this official list has shortcomings. For example, it misclassifies some native species such as *Argemone mexicana* L., as an invasive alien species, while omitting other clearly invasive species like those mentioned above (Villaseñor & Espinosa-García 2004; Vibrans et al. 2014; Espinosa-García & Villaseñor 2017). The list is considered official but requires revisions, particularly of the definitions and species classification.

The data for the first documented herbarium specimen of a wild-growing population for these alien species shows a peak in the middle of the past century. Though the absolute numbers are low and the data should be treated with some caution, they do permit a parsimonious interpretation. The middle of the last century was a time of intense commerce and purposeful introduction of plant species from around the world, but this exchange was not yet seen as problematic. Recent regulations may have reduced the number of newly introduced species, though the lower numbers of the last 50 years may also reflect the time many species need to establish wild-growing populations (i.e., lag phase; Gioria et al. 2023). However, we do not think the peak from 1950 to 1975 is a documentation artefact, as the main period of plant collection in Mexico was from the 1980s to the 1990s.

Practical implications

The study shows that the large majority of South African plants growing wild in Mexico were introduced as ornamentals or forage plants. This result can guide future biosecurity threat assessments for Mexico. The work also shows that a more detailed analysis of the species exchange between regions, the native areas of plants, and their characteristics can yield concrete results that can inform public policy and private action. The workflow summarised in Figure 1 can be adapted to other regions.

Limitations of this study

Although we attempted to use standardised criteria, some species may be reclassified in the future, either as native or alien, particularly those of Group 3. The limitations of the literature, including the lack of clear definitions for concepts and their applications, along with the vastness of 'native' areas and existing controversies around some species, suggest that modifications are likely as new data, especially molecular ones, become available. However, the general trend of our results will probably persist.

Recommendations

Molecular techniques have helped identify the area of origin and the time at which some groups diverged (Hyldgaard et al. 2017; Jiang et al. 2022). They are also useful for reconstructing the routes of introduction and invasion of species, as they allow inferring from which population (or populations) they dispersed and when (North et al. 2021). This type of genetic data can be associated with fossil, archaeological, historical and biogeographical data to identify the area of origin of species and even infer where else and when they might have been introduced (Gildenhuys et al. 2013; Cristescu 2015). For many species, especially those with a very wide distribution range, population genetic studies are urgently needed.

Conclusion

The introduction of South African species into Mexico has been driven primarily by their commercial utility as forage or ornamental plants. Human migrations or accidental introductions are less likely to have been a major pathway of the species we analysed. Therefore, monitoring commercial ornamental and forage species from South Africa is important to avoid future invasions.

The work highlights the importance of having well-documented lists of species with their native and introduced ranges, as this information is relevant for decision-making in public policy and outreach, as well as control and management. Our standardised method could be applied to corroborate species exchanges between other regions.

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Competing interests

The authors declare no competing interests.

Authors' contributions

JLS gathered and analysed the data and wrote the first draft in Spanish. HV contributed to the analysis and wrote the English-language manuscript in collaboration with JLS. All authors contributed to the project design and concepts and also to the review of the manuscript.

Competing interests

The authors declare that they have no financial or personal relationship(s) that may have inappropriately influenced them in writing this article.

Ethical considerations

This study was literature-based and did not require ethical clearances.

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Supplementary material

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Supplementary Material 1: Species native to South Africa, present in Mexico in the wild, including a justification of their inclusion as South African natives and their classification in Mexico.

Supplementary Material 2: South African native species that are present in Mexico, but for which no evidence for wild-growing populations in Mexico was found.

Supplementary Material 3: Species present in Mexico that are considered by the South African National Biodiversity Institute (SANBI) to be native to South Africa but have a 'native' distribution that extends beyond sub-Saharan Africa; the available literature does not allow the determination of a more circumscribed native region or region of origin.

Supplementary Material 4: Species present in Mexico that are considered to be native to South Africa by the South African National Biodiversity Institute (SANBI), but the literature indicates a different native region.