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A Preliminary Assessment of Hedge Plant Species and Their Distribution in Rural Eastern Africa and Their Potential Role in Driving Invasions

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ABSTRACT

Alien plant species are widely utilised for ornament, agro-forestry, or even for restoration and are more likely to be introduced multiple times and disseminated widely across a landscape. Here we report on the native and alien species used for hedging purposes in rural and peri-urban eastern Africa and undertake a preliminary assessment to determine whether the use of alien species may be contributing to current invasions. We undertook roadside surveys and recorded the presence of all species used as hedges or barriers, excluding vines or climbers. We recorded 110 such plant species (taxa recorded at genus level excluded) but only report on 54 species recorded at five or more localities, and provide a more detailed analysis of the ten most widely used species. Nine of the 54 species grown as hedges were native to eastern Africa and 45 were alien, of which 73% were known to be invasive. Native *Euphorbia tirucalli* and the alien species *Dovyalis afra*, *Lantana camara*, *Agave sisalana*, *Caesalpinia decapetala*, *Cascabela thevetia*, and *Tithonia diversifolia* were the most widely grown hedge plant species. *Lantana camara* was recorded as invasive in 38% of grid cells (~55 × 55 km), followed by *T. diversifolia* (24%), *C. decapetala* (13%), and *A. sisalana* (9%). The study supports findings that propagule pressure in the form of alien plants used as hedges may contribute to their spread. However, species such as *D. afra* and *C. thevetia* contradict these findings, lending credence to the important role of species traits as drivers of plant invasions. Propagule pressure, species traits, and the characteristics of the recipient environment all contribute to plant invasions; no generalisations can be made.

1 | Introduction

Plant species have been intentionally moved around the world by people for centuries (Mack and Lonsdale 2001). They have been introduced for use as ornamentals, medicinal purposes, agro-forestry, timber, fuelwood, nitrogen-fixation, restoration, crop production, or as hedges or barriers (Groves 1992; Haysom and Murphy 2003). These introductions can have beneficial, neutral, or detrimental effects (Mack and Lonsdale 2001). Previous studies estimated that less than 1% of these introduced or alien species become problematic or invasive in their adventive range (Williamson and Fitter 1996). However, this has been disputed by several authors (Jarić and Cvijanović 2012; Jeschke and Pyšek 2018). Pfadenhauer and Bradley (2024) found that invasion rates, that is the percentage of alien plant species that establish and have negative impacts is highly variable across the globe ranging from 7.2% to 33.8%. These plant invasions threaten crop and pasture production, human and animal health, water resources, economic development and biodiversity (Pimentel 2001; Vilà et al. 2011; Paini et al. 2016; Pyšek et al. 2020; Diagne et al. 2021; Zenni et al. 2021). For example, invasive alien plants and animals play a key role in 60% of global plant and animal extinctions and cost the global economy more than US$ 423 billion (IPBES 2023).

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Because of the significant impacts of invasive alien plant species (IAPS) much research has focussed on trying to understand why some alien species become invasive and others not (Crawley 1987; Richardson and Pyšek 2006; Pyšek and Richardson 2007; Dawson et al. 2015; Milanović et al. 2020). Studies have examined the traits of successful invaders (Elton 1958; Rejmánek 1996; Rejmánek and Richardson 1996) and the types of communities most susceptible to invasion (Levine and D'Antonio 1999; Milanović et al. 2020). The likelihood of an introduced species becoming invasive is essentially a function of propagule pressure, the abiotic characteristics of the invaded ecosystem and the characteristics of the recipient community and invading species (Catford et al. 2009). Propagule pressure is the number of individuals introduced at any one time multiplied by the temporal frequency of these introductions (Eppstein and Molofsky 2007). The size and numbers of propagules and the temporal and spatial patterns of propagule arrival are important factors in determining invasion success or failure (Simberloff 2009). By producing high numbers of propagules, alien plants can overcome the impacts of environmental stochasticity while repeated and widespread introductions can mitigate against the expected genetic bottleneck when few individuals are introduced (Simberloff 2009). Repeated introductions increase genetic variability, enabling species to invade new habitats (Lavergne and Molofsky 2007; Pairon et al. 2010). This may explain the delay between establishment and spread commonly known as the lag phase (Kowarik 1995; Binggeli 2001).

Although many of these introductions have been accidental a much greater proportion of naturalised plants have been introduced intentionally (Hulme et al. 2018; Guo et al. 2019). At least 75% and 93% of the 13,168 alien plant species planted in domestic and botanic gardens, respectively are known to be naturalised (van Kleunen et al. 2018). In eastern Africa most of the species which have been recorded as invasive were intentionally introduced as ornamentals (46%) or used as barriers/hedges (15%), or as agricultural crops (Witt et al. 2018). It is highly probable that the repeated introduction and dissemination of alien plant species throughout eastern Africa is increasing propagule pressure and driving invasions (Muturi et al. 2012). These species may become invasive through propagule pressure alone, but their success may also be influenced by shared attributes that facilitate invasions (Baker 1965; Rejmánek and Richardson 1996; Rejmánek 1996; Kolar and Lodge 2001; Catford et al. 2009), or the characteristics of the recipient environment (Rejmánek 1989; Levine and D'Antonio 1999; Mack et al. 2000; Pyšek and Richardson 2007; Catford et al. 2009; Milanović et al. 2020). Baker (1974) was the first to posit the concept of an 'ideal weed' as one that had high phenotypic plasticity, flexible germination cues, general dispersal and pollination mechanisms, life history traits that allowed for reproduction from a single individual (vegetative reproduction), rapid growth, and high continuous seed output. Richardson and Rejmánek (2004) found that the most important characteristics that separated non-invasive and invasive *Pinus* species were mean seed mass, minimum juvenile period, and mean interval between large seed crops. Small seed mass is usually associated with high seed production, improved dispersal, high initial germinability, and shorter chilling period needs to overcome dormancy while short juvenile period may be related to fast growth (Rejmánek and Richardson 1996).

Dispersal of seeds by birds, bats or primates may also be an important attribute of invasive plant species (Rejmánek and Richardson 1996). High seed production and improved dispersal are attributes that may not be that critical if a plant species is, for example, a popular hedge or barrier plant that is being moved and grown by many people within a country or region. Factors such as self-pollination, breakdown of pollinator specificity and vegetative reproduction can also be important in the initial stages of invasion (Baker 1967; Parrish and Bazzaz 1978). Vegetative reproduction is essential for establishment and short-distance dispersal of many species in terrestrial environments (Auld et al. 1983; Andersen 1995; Thompson et al. 1995; Pyšek 1997). Rapid root growth (Hulbert 1955), shade tolerance (Jones and McLeod 1990; Lososová et al. 2007), resistance to browsing (Ledgard 1988), and production of allelochemicals (Lawrence et al. 1991) all contribute to invasiveness. If people select for similar traits in a hedge plant species, they may inadvertently be driving invasions. The ideal hedge is one that is dense and bushy and preferably armed with spines (impenetrable), unpalatable to livestock, responds well to pruning, evergreen, long-lived, easily propagated, grows fast, resistant to drought and cold, is disease or pest free, and adaptable to a wide range of climatic conditions (Howes 1946; Henderson 1983). These attributes are shared by many invasive plant species in eastern Africa (Witt and Luke 2017; Witt et al. 2018) and globally (Pyšek and Richardson 2007). As such, many plant species used as barriers or hedges could be regarded as 'conflict species' because they have benefits and costs (Shackleton et al. 2015; Novoa et al. 2016).

Introductions of plants for use as hedges or barriers were already initiated in the 1800s (CABI 2019). More than 500 plant species were already being used as hedges or living fences in the warmer parts of the world, with many already naturalised (Howes 1946). For example, Cleghorn (1850) reports on the use of cactus species as hedges in India that grew rapidly in 'sterile soils' and that were 'spreading and impoverishing' the land. Of the 524 tree species recorded in the Forestry Compendium (CABI 2005) as being used either for hedges, windbreaks, or shelterbelts, 94 (18%) were either invasive, aggressive, or tended to become weeds. Of the 1175 full invasive plant datasheets reviewed in the Invasive Species Compendium (CABI 2018), 140 (12%) species were recorded as being introduced or used as 'boundary, barrier or support' species. Of the 428 plant species recorded as having been used as barriers in South Africa, 62% were aliens, and of these, 26% were naturalised or invasive (Henderson 1983). Milimo et al. (1994) listed ten hedge species that were widely used in semi-arid East Africa, nine of which were alien, of which eight are known to be naturalised and/or invasive.

In this study we identify the main plant species grown as hedges in five countries in eastern Africa, assess their distribution and provide information on some of the biological attributes of the eight most widely grown alien hedge plant species. We hypothesise that the use of many of these introduced species as hedges has driven invasions because of propagule pressure. However, by considering the biological traits of the most popular species we hope to ascertain if propagule pressure alone is sufficient in driving invasions or if the attributes of the species may curtail or even inhibit invasions despite the species being widely grown across the region.

2 | Methods

2.1 | Distribution of Hedge Plants in Eastern Africa

Alien plant species were recorded during roadside surveys in five eastern African countries (Ethiopia, Kenya, Rwanda, Tanzania and Uganda) (Figure 1; Witt and Luke 2017; Witt 2017; Witt et al. 2018). The plant species used as hedges in rural and peri-urban areas were also recorded during these surveys. We did not record hedge species in urban areas. We recorded localities using a hand-held GPS unit, and noted whether the species used in hedges were native or alien, and if alien whether they were naturalised or invasive in the area (see Witt and Luke 2017; Witt 2017; Witt et al. 2018). We did not differentiate between garden and security hedges as defined by Henderson (1983) and did not record creepers or vines growing over wire fences or other hedge plants. We broadly defined hedges as a typically linear arrangement of closely planted shrubs or trees around a property or part thereof (Blanusa et al. 2019); not windbreaks. Our inability to accurately differentiate between native *Vachellia*, *Senegalia* and *Aloe* species, or alien *Bougainvillea*, *Eucalyptus*, *Rosa* and *Stachytarpheta* species, resulted in these taxa being recorded at genus level only.

2.2 | Biological Traits of Most Popular Alien Hedge Plant Species

For the most frequently used hedge species, most of which are also common IAPS, we provide data on a few selected traits such as size of native range (number of countries) (Rejmánek and Richardson 1996; Pyšek et al. 2015), residence time (Pyšek et al. 2009, 2015; Maurel et al. 2016), palatability (Ledgard 1988; O'Connor and van Wilgen 2020), propagation (Baker 1974; Andersen 1995; Auld et al. 1983; Pyšek 1997; Thompson et al. 1995), seed size (Richardson and Rejmánek 2004), dispersal mechanisms

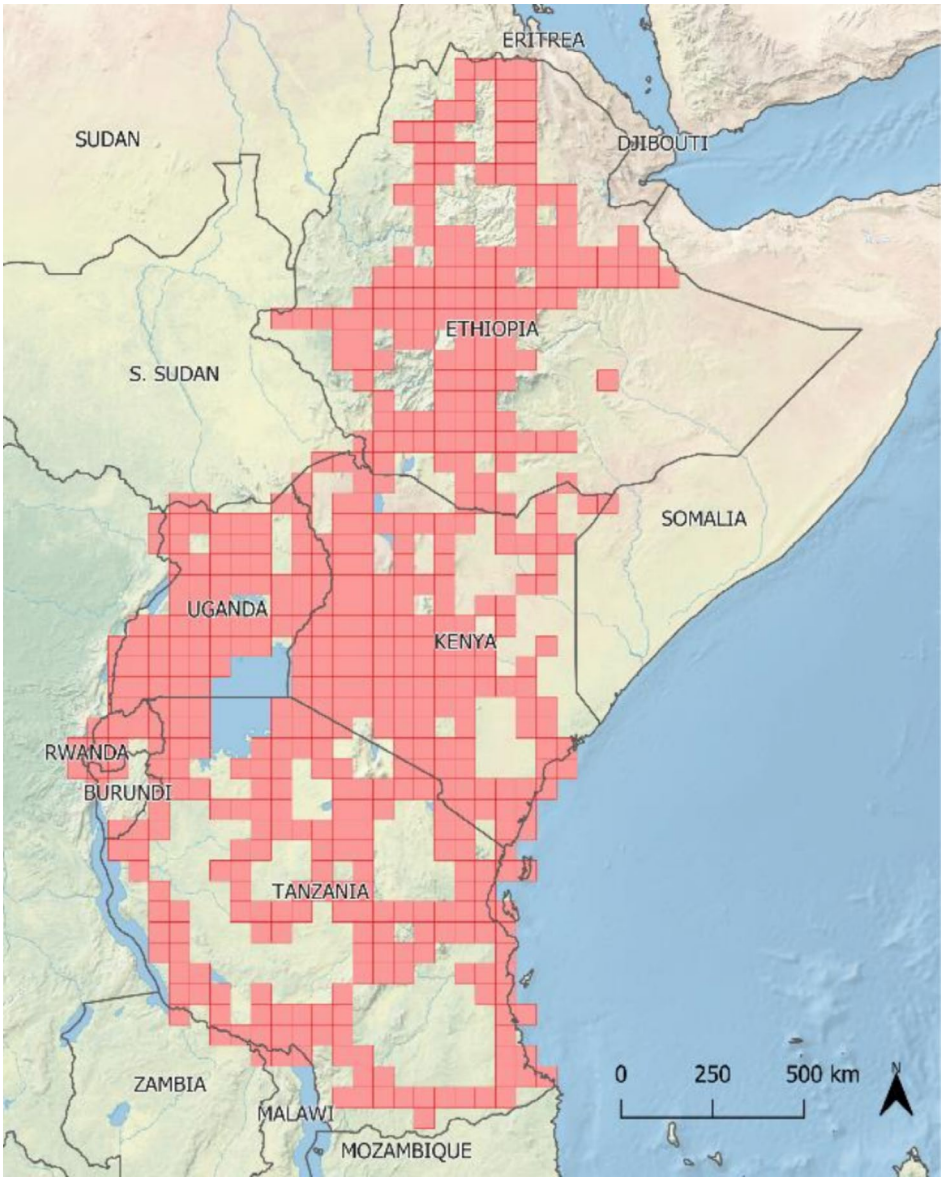


FIGURE 1 | The ½ degree (~55 × 55 km) grid cells surveyed in eastern Africa to determine the distribution of invasive alien plant species and the species used in hedges.

(Rejmánek and Richardson 1996), juvenile period (Richardson and Rejmánek 2004), growth rates (Baker 1974; Dawson et al. 2011; Montesinos 2022), and longevity. Information on the traits of these hedge plant species was obtained from multiple sources, mainly CABI (2025), but also Maundu and Tengnäs (2005), Orwa et al. (2009), Tropical Plants Database (2026), and others. It should be noted that there is often considerable variation in measures of the same traits within a single species from multiple sources.

3 | Results

3.1 | Distribution of Hedge Plants in Eastern Africa

We recorded hedges at 2075 localities in Kenya, followed by 1953, 1392, 691 and 254 in Tanzania, Ethiopia, Uganda and Rwanda respectively. Of the 110 species being used as hedges or barriers only 54 (excludes native *Aloe*, *Senegalia*, and *Vachellia* species, and alien *Bougainvillea*, *Eucalyptus*, *Rosa* and *Stachytarpheta* species that were only recorded to genus level) were recorded at five or more localities (Supporting Information). Species that were recorded at fewer localities have not been included here because they are not considered to be important hedge plant species across the region. Of these 54 species, 45 (83%) were alien species with 31 of these being native to Tropical America. Just over three-fifths (61%) of all of the hedge plant species recorded at five or more localities in eastern Africa were alien and invasive; three-quarters (73%) of the alien species were invasive. Most of the species recorded as hedge plant species belonged to the family Fabaceae ($n = 12$ species), followed by Euphorbiaceae ($n = 7$ species) and Cactaceae ($n = 5$ species). Most taxa in the latter two families exhibit vegetative reproduction, making them easier to propagate as hedge plants. Of the ten most frequently used species eight were alien and two, *Euphorbia tirucalli* and *E. ingens* were native, both in the family Euphorbiaceae (Supporting Information). At a country level *E. tirucalli* was recorded at more localities in Ethiopia ($n = 239$), Rwanda ($n = 100$) and Tanzania ($n = 375$) than any other species. The most recorded alien plant species used in hedges in each country in the region were *Caesalpinia decapetala* (Fabaceae) in Ethiopia ($n = 193$), *Dovyalis afra* (Salicaceae) ($n = 380$) in Kenya, *Lantana camara* (Verbenaceae) in Rwanda ($n = 20$), *Agave sisalana* (Agavaceae) in Tanzania ($n = 289$) and *Cascabela thevetia* (Apocynaceae) in Uganda ($n = 161$). *Cascabela thevetia* and *Tithonia diversifolia* (Asteraceae) were not recorded as hedges in Ethiopia (the latter was only recorded at one locality and not in a hedge). According to Tadesse (2004), *T. diversifolia* was only known from a single plant at Alemaya University Experimental Farm. *Agave sisalana* (Agavaceae) and *Austrocylindropuntia subulata* (Cactaceae) were rarely or never recorded as hedge plants in Rwanda and Uganda and *E. ingens* was not seen as a hedge or barrier in Rwanda. The succulent *Opuntia ficus-indica* (Cactaceae) was not recorded as a hedge in Uganda (Figure 2). Succulents such as *Agave*, *Euphorbia* and *Opuntia* species are well adapted to growing in arid and semi-arid areas and as such are widely used in Ethiopia, Kenya and Tanzania and less so in Rwanda or Uganda where the climate is more tropical throughout, suitable for the growing of tropical hedge plant species. Being native, *E. tirucalli* has been used as a hedge plant throughout the region for many centuries, prior to the introduction of alien species, hence its continued popularity in all countries.

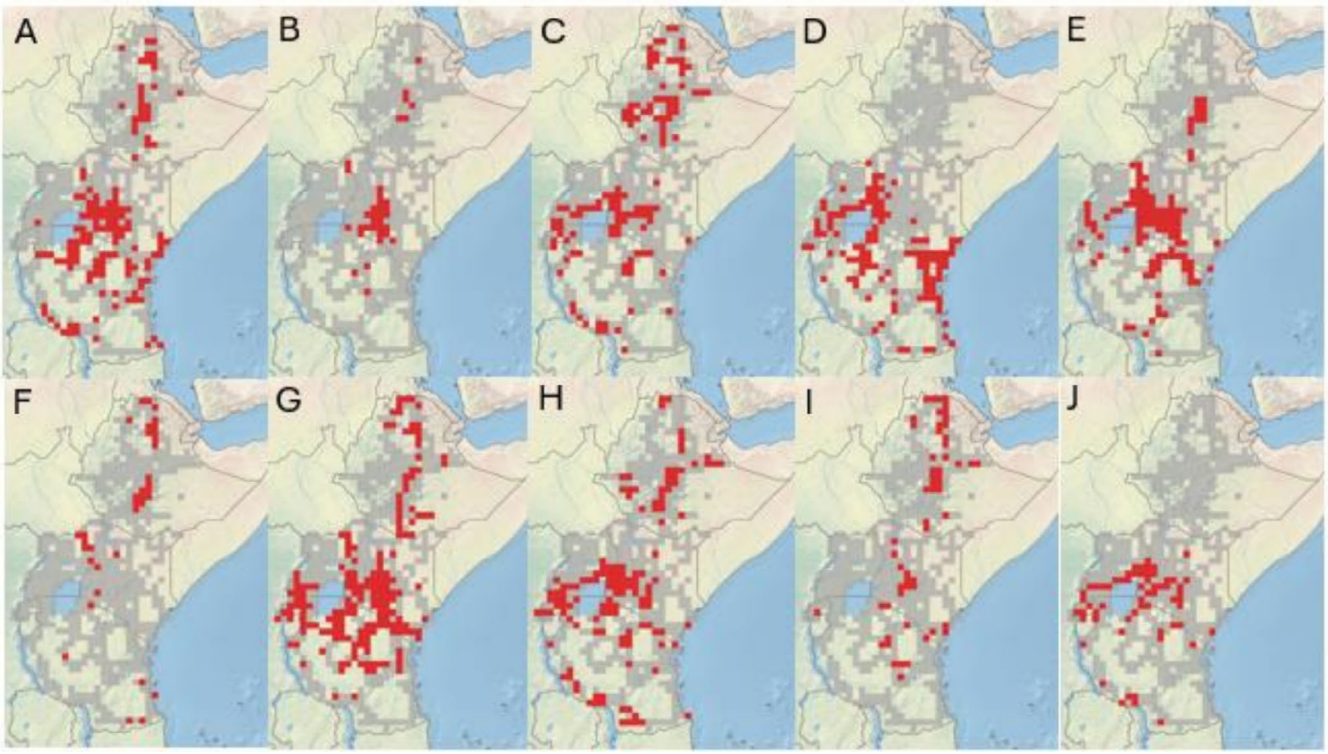


FIGURE 2 | Half degree grid cells (~55 × 55 km) in which *Agave sisalana* (A), *Austrocylindropuntia subulata* (B), *Caesalpinia decapetala* (C), *Cascabela thevetia* (D), *Dovyalis afra* (E), *Euphorbia ingens* (F), *E. tirucalli* (G), *Lantana camara* (H), *Opuntia ficus-indica* (I) and *Tithonia diversifolia* (J) hedges or barriers were recorded in eastern Africa.

The species which were most often recorded as hedges or barriers, and invasive in the same grid cells, were *L. camara* in Ethiopia, Kenya, Tanzania and Uganda, and *T. diversifolia* in Rwanda (Table 1). *Tithonia diversifolia* was recorded as invasive in all grid cells in Rwanda, 85% in Kenya, 80% in Tanzania, and 75% in Uganda where it was being grown as a hedge or barrier (Table 1). *Cascabela thevetia* and *D. afra* were often grown as hedges or barriers in eastern Africa yet were only occasionally found to be invasive in Kenya in the same grid cells in which they were being grown as hedges (Table 1). They were less invasive than would be expected considering their widespread use as ornamentals and hedges in eastern Africa.

3.2 | Biological Traits of Most Popular Alien Hedge Plant Species

Of the 10 most widely grown hedge or barrier plant species, six were from Tropical America, one from Tropical Asia and three from Africa, two of these native to eastern Africa (Supporting Information). *Lantana camara* has a large native distribution, being present in 40 countries, and as such is likely to be well adapted to grow over a wide range of climatic regimes. The species with the 2nd largest native distribution is *C. thevetia* ($n = 17$ countries), followed by *C. decapetala* ($n = 13$) and *T. diversifolia* ($n = 9$) (CABI 2025). However, presence in multiple countries does not necessarily equate to a large native range; a species may be present in many small countries or one large country or only be present in a small area within a large country, or widespread throughout a large or small country. *Lantana camara* is also invasive in more countries (93) than any of the other hedge or barrier plant species used, followed by *T. diversifolia*, which has been recorded as invasive in 43 countries, 19 of them in Africa (CABI 2025; Table 2). In contrast, species such as *A. sisalana* and *O. ficus-indica*, which have a limited natural distribution in Mexico, have each been recorded as invasive in 17 countries. All the most widely used hedge plant species have been present in eastern Africa between 84 (*A. subulata*) and 133 (*A. sisalana*) years, relatively long residence times, so ample time to spread, either naturally or facilitated by people.

Traits such as seed size, dispersal mechanisms, juvenile period, growth rate and longevity, among others, are important traits that may determine if an introduced species becomes invasive or not. However, very few to no generalisations can be made across all of the eight most widely used introduced hedge plant species (see Table 2). For example, all species are toxic or have spines with the exception of *T. diversifolia*; seed sizes range from small (*T. diversifolia*) to large (*C. thevetia*); seed dispersal is either by animals (*L. camara*) or wind (*T. diversifolia*) and/or water (*C. thevetia*); juvenile periods are variable ranging from a few months (*T. diversifolia*) to 4–5 years (*D. afra*), growth rates are slow (*A. sisalana*) to fast (*T. diversifolia*) and longevity moderate to long (Table 2). All eight species shared the trait of being able to reproduce vegetatively, an important attribute of hedge plants making them easier to propagate. Other important traits of IAPS such as rapid root growth, shade tolerance, and production of allelochemicals were not considered. However, with reference to those traits that were compared there is considerable variability between the species; invasive hedge plant species used in eastern Africa do not all share the same traits.

4 | Discussion

Most plant species used as hedges in rural eastern Africa are alien and invasive, as also found by Milimo et al. (1994). Lowe (2017) listed 85 taxa used as hedges, screens and barriers in East African gardens, of which only 14 were native (assuming that most other taxa listed to genus level only were alien; for example, the genera *Agave*, *Furcraea*, *Neltuma*, and *Opuntia* are alien in Africa). However, a few other genera listed by Lowe (2017) have species native to Africa as well as other continents. If all taxa listed to genus level are excluded, then only eight species in Lowe (2017) are currently known to be invasive in eastern Africa, but this could increase. Maundu and Tengnäs (2005) listed 69 trees and shrubs as 'living fences' in Kenya, of which 51 species were native and 18 alien. This suggests that native species dominate, in contrast to the findings of our study and those of Milimo et al. (1994) and Lowe (2017). However, Maundu and Tengnäs (2005) did not include the widespread alien species *L. camara*, or any of the *Agave* and *Opuntia* species, which are

TABLE 1 | The eight alien plant species most widely used as hedges or barriers in countries in eastern Africa with the percentage (%) of grid cells surveyed in which these species were found being grown as hedges or barriers and in which they were also found to be invasive. *Euphorbia tirucalli* and *E. ingens* have not been included here because they are native.

	Country				
Species	**Ethiopia**	**Kenya**	**Rwanda**	**Tanzania**	**Uganda**
Lantana camara	74	86	86	83	89
Tithonia diversifolia	0	85	100	80	75
Opuntia ficus-indica	59	54	0	18	0
Caesalpinia decapetala	23	41	0	31	17
Agave sisalana	14	37	0	31	0
Austrocylindropuntia subulata	0	55	0	20	0
Cascabela thevetia	0	7	0	0	0
Dovyalis afra	0	3	0	0	0

TABLE 2 | Origin, countries recorded as invasive, year of first introduction to eastern Africa and some of the key biological traits of the eight most widely grown alien hedge or barrier plants in rural eastern Africa. Sources of information: CABI (2025)[1]; Witt et al. (2018)[2]; Maundu and Tengnäs (2005)[3]; Orwa et al. (2009)[4]. *Euphorbia tirucalli* and *E. ingens* have not been included here because they are native.

Species	Origin (No. of countries)[1]	No. of countries invasive[1]	~Year of 1st introd.[2]	Defence[1]	Propag-ation[1,3]	Seed size[1]	Seed dispersal[1,3,4]	Juvenile period[1,3]	Growth rate[1,3,4]	Longevity[1,3,4]
Agave sisalana (Agavaceae)	North America (1)	Africa (7); Asia (1); Europe (1); North & Central America (4); Oceania (4)	1892	None although leaf terminal spine may deter some herbivores	Suckers & plantlets	Small (only produced once in lifetime)	Wind and water	Long (7–10 years)	Slow (~30 cm/year)	Long (7–10 years; flowers, and then dies)
Cascabela thevetia (Apocynaceae)	North, Central & South America (17)	Africa (6); North & Central America (3); Oceania (10)	1904	Toxic	Stem cuttings & seeds	Large (~35 × 15 mm; 480 mg)	Animals (limited) & water	Short (353–498 days)	Fast (~90 cm/year)	Long (50 years)
Tithonia diversifolia (Asteraceae)	North & Central America (9)	Africa (19); Asia (5); Oceania (10); North & Central America (6); South America (3)	1917	Over-consumption can be toxic	Stem cuttings & seeds	Small (~5–8 mm long; 6–8 mg)	Wind & water	Short (4 months)	Fast (125–143 cm in 18 weeks)	Moderate (> 2 years)
Austrocylindro-puntia subulata (Cactaceae)	South America (2)	Africa (3); Europe (1); Oceania (1)	1941	Spines deter animals	Stems & fruit root	Moderate (~10–12 × 10 mm)	Fruits moved by water	?	Moderate	Long

(Continues)

TABLE 2 | (Continued)

Species	Origin (No. of countries)[1]	No. of countries invasive[1]	~Year of 1st introd.[2]	Defence[1]	Propag-ation[1,3]	Seed size[1]	Seed dispersal[1,3,4]	Juvenile period[1,3]	Growth rate[1,3,4]	Longevity[1,3,4]
Opuntia ficus-indica (Cactaceae)	Central America (1)	Africa (10); Asia (3); North & Central America (2); Oceania (1); South America (1)	1903	Spines deter animals	Stems & fruit root; seeds	Small (~4 ×4 mm; 14 mg)	Animals	3–4 years from seed; faster from cladodes	Moderate	Long
Caesalpinia decapetala (Fabaceae)	Asia (13)	Africa (5); Central & North America (2); Oceania (5)	1895	Toxic pods; hooked thorns deter animals	Stem cuttings; seeds	Moderate (~8–12 ×6–8 mm)	Animals, water	< 12 months	Fast	Long
Dovyalis afra (Salicaceae)	Southern Africa (4)	Africa (1)	1910	Spines deter animals	Stem cuttings; seeds preferred	Small (~5 ×3 mm)	Animals	(3-) 4–5 years	Moderate to fast (~80 cm/year)	Long (20 years)
Lantana camara (Verbenaceae)	Central & South America (40)	Africa (33); Asia (22); Europe (5); North America (6); Oceania (23); South America (4)	1932	Toxic leaves; Prickles deter animals	Stem cuttings; seeds	Small (~1–2 mm long; 12–14 mg)	Animals	~12 months	Fast (90–120 cm/year)	Long

widely used as hedges in Kenya. They also included many native tree species which are used as windbreaks rather than as hedges. We remain confident that our surveys reflect the reality that most species used as hedges in eastern Africa are alien, and that many are invasive.

The most widely used alien hedge or barrier species in eastern Africa were all introduced into the region in the late 1800s to early 1900s. Many of these species were widely promoted during colonial times as hedges with species such as *D. afra* promoted as an 'impenetrable hedge plant, resists drought' and *C. decapetala* as 'a straggling thorn shrub, forms impenetrable hedge' (Kenya Gazette 1927). *Lantana camara* was also widely promoted as a hedge plant because it grows readily from cuttings, has small prickles, is toxic to livestock, and forms a very dense and impenetrable hedge (Howes 1946). The most widely grown hedge, based on our surveys, was the native succulent *E. tirucalli* which is well adapted to dry conditions and poor soils, is easily propagated from cuttings which root easily, and has moderate growth.

The alien species grown in hedges are now widespread throughout rural eastern Africa with *L. camara* recorded in 54% of grid cells surveyed, followed by *C. thevetia* (49%), *C. decapetala* (36%), *T. diversifolia* (29%), *O. ficus-indica* (18%), *A. sisalana* (18%), *A. subulata* (12%), and *D. caffra* (12%) (Witt and Luke 2017; Witt et al. 2018). Increased propagule pressure through the growing of hedges, and also as ornamentals, would have created many opportunities to form foci for invasion across the landscape and as expected *L. camara* was found to be invasive in more than half (38%) of the grid cells in which it was seen, followed by *T. diversifolia* in 24%, and *C. decapetala* in 13% (Witt et al. 2018). In contrast, *D. afra* (<1%) and *C. thevetia* (6%) were invasive in comparatively few grid cells (Witt et al. 2018) despite being widely used as hedges (Table 2), and often grown as ornamentals in gardens.

Differences in the biological attributes of these species may explain some of this variability in invasion success, even if they are widely distributed across the landscape. Introduced species with short juvenile periods, short reproduction intervals, small seed masses, and large native range sizes are more likely to become invasive (Roy et al. 1991; Rejmánek 1995; Rejmánek and Richardson 1996; Pyšek et al. 2009; Hui 2009; Moodley et al. 2013). Plants used as hedges such as *L. camara*, *T. diversifolia* and others have very small seeds and are also highly invasive in eastern Africa (Witt and Luke 2017). Despite being widely grown as a hedge, especially in Kenya and Tanzania, *C. thevetia* was rarely recorded as being invasive despite having a native range encompassing 17 countries and a short juvenile period. We postulate that the large seeds of *C. thevetia* may limit dispersal. In eastern Africa it has may been found to be invasive in riparian areas or dry riverbeds, an indication that fast-moving water may be critical for dispersal, hence its comparatively limited invasion status. Hydrochory is known to play a major role in the dispersal of *C. thevetia* seeds (Bebawi et al. 2016). In Australia 57% of all seeds are predated by birds which may also limit its invasiveness (Bebawi et al. 2016). However, there are no records of seed predation or dispersal by animals in eastern Africa.

Analysis of 40 invasive woody plant species revealed that the seeds of the majority are dispersed by birds, bats or primates (Rejmánek and Richardson 1996). Most of the seeds of the invasive species used as hedges in eastern Africa are also dispersed by animals, especially birds, except for *T. diversifolia* and *A. sisalana* which have wind-dispersed seeds. However, *A. sisalana* rarely produces seeds, and then only at the end of its lifespan. Low and infrequent seed production in *A. sisalana* may also partly explain that despite being widely grown as a hedge plant it is not as invasive as one would expect. This could be attributed to the fact that it mainly spreads via suckers and bulbils; in other words, opportunities for long-distance dispersal through seeds are limited. This is supported by Kloot (1987) who found that despite *Agave americana* being widely grown as a hedge in South Australia for over a century, it has 'hardly spread'. The potential for spread by *A. subulata* may also be limited because it is not known if it produces viable seeds. In addition, the fruit has a thick and hard exocarp enclosing the seeds, preventing access to potential dispersers. No feeding activity on fruits was recorded in eastern Africa (A. Witt *pers. obs*.). Long-distance dispersal would therefore also be limited for this species; hence its clumped distribution in the landscape and its 'dependence' on people for long-distance dispersal as a hedge plant, although stem fragments and fruits can be moved by water, explaining the occurrence of some invasions along riverbeds, some distance from source plants. *Austrocylindropuntia subulata* is one of five of the eight most widely used alien hedges in eastern Africa capable of vegetative reproduction, a trait which is important especially in the early stages of invasion (Baker 1967; Parrish and Bazzaz 1978; Kolar and Lodge 2001). Vegetative reproduction is significantly more common in invasive plants, with 44% of invaders in California reproducing vegetatively compared to only 23% of non-invaders (Reichard 1996). Species exhibiting vegetative reproduction are also easier to grow, especially as a hedge. All the eight most frequently used alien hedge plant species in eastern Africa can be grown from cuttings, plantlets or cladodes.

Self-pollination and breakdown of pollinator specificity are also important traits, especially in the initial stages of invasion (Baker 1967; Parrish and Bazzaz 1978). Species that cannot reproduce vegetatively and depend on the production of seeds are dependent on pollination by animals such as insects and wind-pollination, although some are self-pollinated. Species capable of autonomous seed production are more likely to become invasive because they don't require the services of pollinators (van Kleunen and Johnson 2007). This is supported by Rambuda and Johnson (2004) who found that of the 17 invasive alien species studied in South Africa, all were either self-compatible or apomictic. Dioecious plants are also less likely to become invasive than monoecious species (Van Etten et al. 2017), and this may partly explain why *D. afra*, despite being widely grown as a hedge plant, being a fast grower (Howes 1946) and 'extremely tough and drought resistant' (Lowe 2017), is not significantly invasive in eastern Africa. This is also evident from where it has been introduced and grown in Australia, West Indies, California, Philippines, and Sri Lanka, where it does not seem to have 'run wild' or become 'troublesome anywhere' (Howes 1946), although there are some reports of it being invasive along the coast of New South Wales, Australia.

Resistance to browsing can also be an important trait of IAPS (Ledgard 1988). O'Connor and van Wilgen (2020) noted that many IAPs in rangelands in South Africa are unpalatable. Some

plant species also possess anti-herbivore mechanical defences such as thorns, spines or prickles (Grubb 1992; Gowda 1996; Milewski and Madden 2006), often in association with pathogenic bacteria (Halpern et al. 2007). All the most popular species used in hedges in eastern Africa have some form of resistance to browsing in the form of spines, thorns, or prickles or being toxic except for *T. diversifolia* which is often promoted as livestock fodder and *A. sisalana* which can be eaten by livestock although this was never observed in eastern Africa. *Agave sisalana* lacks the sharp spines which are found on the edge of the leaves of many other *Agave* spp. Other plant traits such as rapid root growth (Hulbert 1955), shade tolerance (Jones and McLeod 1990), and production of allelochemicals (Lawrence et al. 1991) also contribute to invasiveness but were not assessed in this study.

The characteristics of the recipient environment are also an important factor contributing to plant invasions. Although this study did not determine the characteristics of the recipient environments in eastern Africa, it is widely accepted that many invasions take place in human- and/or naturally disturbed habitats (Mack 1989; Hobbs and Huenneke 1992; Rejmánek 1989; Whitemore 1991). Land degradation affects 51%, 23% and 22% of the land area in Tanzania, Ethiopia and Kenya, respectively (Kirui and Mirzabaev 2014) and may be a significant driver of plant invasions in the region. In addition, hedges are grown in areas that may already have significant levels of anthropogenic disturbance. Our findings that widely used alien hedge plant species do not necessarily lead to invasions support those of Davis et al. (2000), Catford et al. (2009), Simberloff (2009), and Duncan et al. (2014) that invasions are not a result of propagule pressure alone (Britton-Simmons and Abbott 2008; Simberloff 2009) but most likely as a result of a combination of multiple factors including the characteristics of the recipient environment and the traits of the plant species themselves. For example, the presence of an alien species in hedges across the landscape will not necessarily result in increased invasions, as demonstrated by *C. thevetia* and *D. afra*, which possess some traits which inhibit invasion. Species such as *C. thevetia* and *A. subulata* are also more likely to become invasive if planted in hedges in areas prone to flooding or adjacent to water channels. This supports the findings by van Kleunen et al. (2015) and Lau and Funk (2023) that no generalisations can be made across all invasive plant species. That said, we are of the opinion that some alien species grown in hedges in eastern Africa contribute significantly to propagule pressure, increasing the risk of invasions. In addition, many alien hedge species share many of the attributes evident in IAPS. However, the study has clearly demonstrated that some widely grown alien hedge plant species are not invasive and that many native plant species possess the same or similar attributes of alien hedge species, making them suitable candidate hedge species.

5 | Recommendations and Conclusions

Managing invasions in rangelands and elsewhere without addressing the source of those invasions in hedges will not be effective or sustainable. This can possibly be addressed by promoting the use of native species which are already being used and were recorded at five or more localities such as *E. tirucalli*, *E. ingens*, *Draceana afromontana*, *Artemisia afra*, *Aloe* spp., *Buddleja polystachya*, *Justicia schimperiana*, *Vachellia* and *Senegalia* spp., and *Solanum aculeastrum* or relatively benign alien species such as *D. afra*. It is critical that a suite of native and benign alien species be identified that could grow and flourish in different climatic regimes across the region. For this to be achieved, adoption must be feasible, practical, and beneficial, with species that are easy to plant, free to obtain, and unpalatable (Dolbeare 2016). The lack of labour and water in many localities is a major constraint and needs to be a serious consideration in the selection of species.

However, even if alternative and easy-to-grow native species are made available it is not known if landowners will voluntarily remove IAPS in hedges. In the Eastern Cape, South Africa, only 33% of rural respondents were willing to contemplate removal compared to 76% in urban areas with the condition that they were removed at no cost to themselves, and benign replacement species were provided (Sifanele and Shackleton 2025). Respondents in the Eastern Cape valued the invasive species in their hedges, with many stating that they caused no harm. This demonstrates that there is a real need to increase awareness as to the threats posed by using invasive hedge plant species, and the need to remove and replace them with other species if they want to ensure that the landscapes in which they reside remain productive. It is also imperative that legislation be developed and implemented making it illegal to sell and grow these IAPS in eastern Africa.

Author Contributions

A.B.R.W. conceived and undertook the study, analysed the data and wrote the paper. T.B. curated the data and developed the maps. Both authors approved the final copy of the paper.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in GBIF dataset at https://www.gbif.org/dataset/23ec2d04-c0eb-4ca4-afb8-a8710e38f641.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Hedge plant species recorded at five or more locations in eastern Africa with information on region of origin (POWO 2026), number of localities where the species was recorded as a hedge, and status in eastern Africa, in Africa outside of eastern Africa, and outside of Africa as in CABI (2026) unless otherwise indicated. 1 = Witt and Luke (2017).