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# A preliminary assessment of the extent and potential impacts of alien plant invasions in the Serengeti-Mara ecosystem, East Africa

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This article provides a preliminary list of alien plant species in the Serengeti-Mara ecosystem in East Africa. The list is based on broad-scale roadside surveys in the area and is supplemented by more detailed surveys of tourist facilities in the Masai-Mara National Reserve and adjoining conservancies. We encountered 245 alien plant species; significantly more than previous studies, of which 62 (25%) were considered to have established self-perpetuating populations in areas away from human habitation. These included species which had either been intentionally or accidentally introduced. Of the 245 alien plants, 212 (including four species considered to be native to the region) were intentionally introduced into gardens in the National Reserve and 51 (24%) had established naturalised populations within the boundaries of these tourism facilities. Of the 51 naturalised species, 23 (11% of the 212 alien species) were recorded as being invasive within the ecosystem, outside of lodges and away from other human habitation. Currently, the Serengeti-Mara ecosystem is relatively free of widespread and abundant invasive alien plants, with a few exceptions, but there are extensive populations outside of the ecosystem, particularly to the west, from where they could spread. We address the potential impacts of six species that we consider to pose the highest risks (*Parthenium hysterophorus*, *Opuntia stricta*, *Tithonia diversifolia*, *Lantana camara*, *Chromolaena odorata* and *Prosopis juliflora*). Although invasive alien plants pose substantial threats to the integrity of the ecosystem, this has not yet been widely recognised. We predict that in the absence of efforts to contain, or reverse the spread of invasive alien plants, the condition of rangelands will deteriorate, with severe negative impacts on migrating large mammals, especially wildebeest, zebra and gazelles. This will, in turn, have a substantial negative impact on tourism, which is a major economic activity in the area.

**Conservation implications:** Invasive alien plants pose significant threats to the integrity of the Serengeti-Mara ecosystem and steps will need to be taken to prevent these impacts. The most important of these would be the removal of alien species from tourist facilities, especially those which are known to be naturalised or invasive, the introduction of control programmes aimed at eliminating outlier invasive plant populations to slow down the spread, and the widespread use of biological control wherever possible.

## Introduction

The establishment and management of a network of protected areas is a key component of global strategies to protect biodiversity and to conserve a representative sample of the Earth's ecosystems. Proclamation of protected areas is in itself no guarantee that the ecosystems therein will not become degraded, as they face a host of threats, including chronic shortages of management funds, legal and illegal resource use, climate change, pollution and invasion by alien species. Ongoing active management will therefore be needed to address these threats. Invasive alien species can pose significant threats to protected area ecosystems worldwide (Foxcroft et al. 2013a), and one report (De Poorter 2007) identified 487 protected areas where invasive alien species were recorded as a threat. In Africa (with the notable exception of South Africa), very little is known about invasive alien species across the continent's protected areas (Foxcroft, Witt & Lotter 2013b). A lack of information on the extent of these invasions, and the problems that they cause, ultimately translates into a failure to adequately provide for their management. As a starting point, therefore, it would be important to record the extent of the threats posed by invasive alien species to individual protected areas and to assess the options for achieving effective control (Van Wilgen et al. 2016).

In this article, we report on the findings of surveys of invasive alien plants in the Serengeti-Mara ecosystem in East Africa. Prior to our survey, the only available information on alien plants in the area was from Henderson (2002) who found 41 'problem' plants in the Ngorongoro Crater, 8 of which were considered to be native; a report by Bukombe et al. (2012) who recorded 13 alien plant species in the Serengeti National Park, including two species, *Senna didymobotrya* (Fresen.) H.S. Irwin & Barneby (Fabaceae) and *Ricinus communis* L. (Euphorbiaceae), which are often considered to be native; and a report by Clark, Lotter and Runyoro (2010) who listed 147 invasive alien and indigenous 'weedy' species in the Ngorongoro Conservation Area. Our surveys subsequently revealed that many of the alien species listed by Clark et al. (2010) are not invasive. Here, we provide an updated list of the introduced, naturalised and invasive alien plant species present. We then focus on six taxa that are expected to generate the largest impacts and review the degree to which they may be expected to impact the integrity of the Serengeti-Mara ecosystem. We also make recommendations regarding the management interventions that would be required to prevent or reduce these impacts.

# Methods

## Study site

The Serengeti-Mara ecosystem is a trans-border area that covers ± 100 000 km$^2$ in the northwest of Tanzania and southwest of Kenya (Figure 1). The core conservation areas consist of the Masai-Mara National Reserve in Kenya which covers ± 1500 km$^2$, while the Serengeti National Park in Tanzania covers 14 750 km$^2$. Both of these protected areas are surrounded by buffer zones such as inner and outer group ranches or conservancies in Kenya and the Ngorongoro Conservation Area, Loliondo Game Controlled Area and the Maswa, Grumeti and Ikorongo Game Reserves in Tanzania.

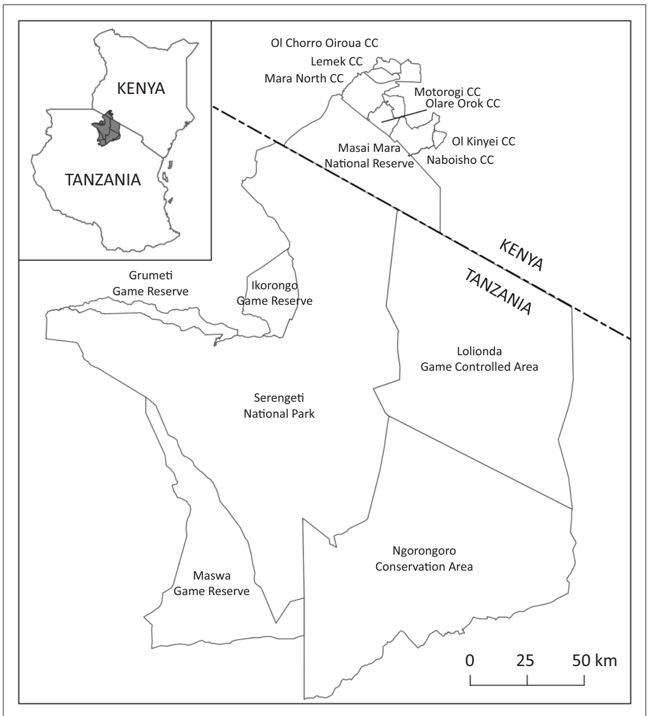



**FIGURE 1:** Location of the Masai-Mara National Reserve, the Serengeti National Park, and surrounding protected areas in East Africa.

The area has varied vegetation and topography, including savanna, grassland, riverine forests, inselbergs (characteristic rock outcrops which rise suddenly above a plain) and wetlands. The mean annual rainfall is around 1000 mm, ranging from 508 mm on the plains to 1200 mm near Lake Victoria in the west, with a short rainy season in October and November and a longer rainy season from March to May. The ecosystem is well known for the migration of 2 million animals (mainly wildebeest, zebras and gazelles), which range between the Serengeti National Park and surrounding conservation areas and the Masai-Mara National Reserve and the adjoining conservancies, and the area is an important tourist destination. The area has a relatively large number of tourist roads and tracks, especially in the Masai-Mara National Reserve, and several lodges have been built, starting in the 1960s; these lodges and other tourist facilities, such as camping sites, can accommodate thousands of tourists, and many more staff and community members reside permanently within the ecosystem.

## Species surveys

Species surveys were undertaken in the Serengeti-Mara ecosystem during or just after the rains, in order to facilitate plant identification, because actively growing and flowering plants are easier to identify. An initial series of field surveys was carried out in the Masai-Mara National Reserve between 04 and 11 April 2011. During this time, we drove along most of the roads and some of the jeep tracks in an area known as the 'Mara Triangle', the National Reserve Central Plains, the National Reserve East and Ol Derikesi and conservancies to the north (Mara North, Lemek, Ol Choro, Enonkishu) and along the periphery of conservancies to the east (Isaaten and Siana) (Figure 2), with one observer recording the species seen, its status and approximate location. Coordinates, at or within 1 km, of each locality where an alien species was found to be present or naturalised, or invasive and spreading (as defined by Pyšek et al. 2004), were recorded using a hand-held global positioning system (GPS) receiver. The methodology used was similar to that described by Henderson (2007) and Rejmánek et al. (2017). Where we could not immediately identify a species, herbarium specimens were collected or photographs taken for later identification by taxonomists. In August 2016, we undertook a further road survey to record the extent of *Parthenium hysterophorus* L. (Asteraceae) (a species that is currently spreading rapidly, but that is also actively being managed in the 'Mara Triangle') to assess both the degree of spread between 2011 and 2016 and the effectiveness of management interventions.

Similar vehicle-based observations were undertaken during two trips en transit through the Serengeti National Park and Ngorongoro Crater in 2012. In addition, we conducted vehicle-based surveys in land adjacent to the protected areas, especially to the west of the Serengeti National Park, where small-scale farming and pastoralism are the main land-use practices. Finally, we consolidated our list with those of Bukombe et al. (2012), Clark et al. (2010) and Henderson (2002), based on the surveys they undertook

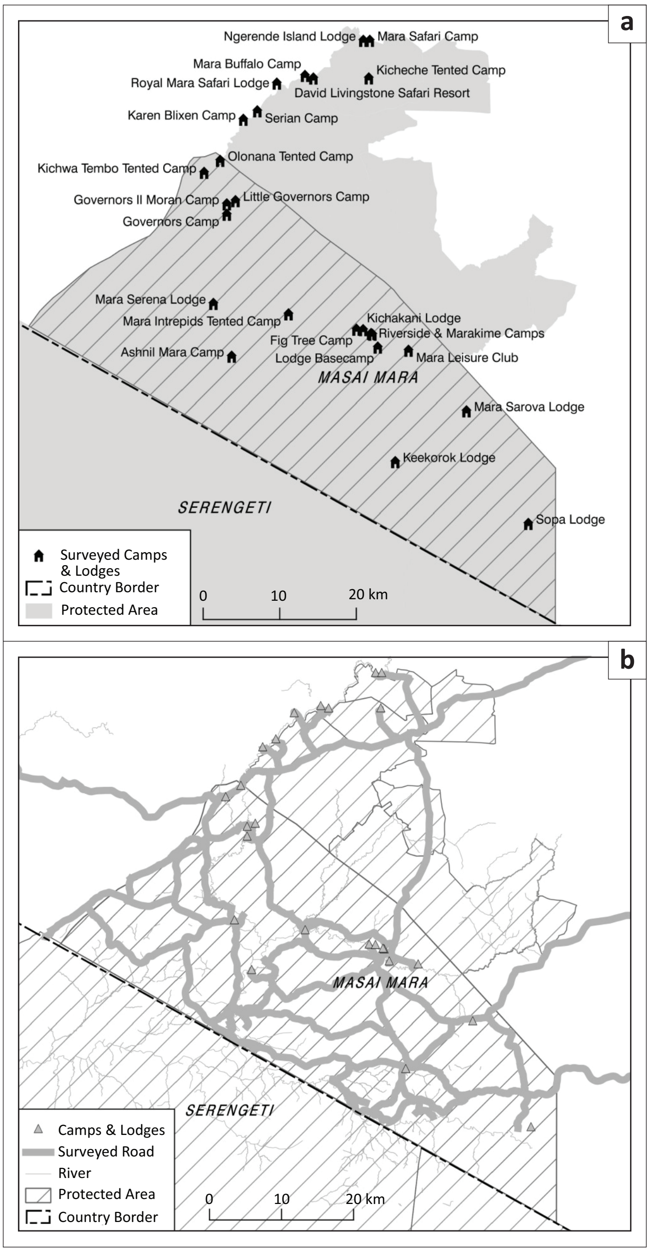



**FIGURE 2:** (a) Location of tourist nodes (lodges and other accommodation) in the Masai-Mara National Reserve and adjacent conservation areas that were surveyed for the occurrence of alien plant species and (b) roads in the area that were surveyed for the occurrence of alien plant species.

in the Ngorongoro Conservation Area and the Serengeti National Park.

## Tourism facilities as pathways of alien plant introductions

Tourist facilities in protected areas can be an important source of invasive alien species. For example, Foxcroft, Richardson and Wilson (2008) surveyed 36 tourist camps and staff villages in the Kruger National Park, South Africa, and identified 258 alien plant species, several of which subsequently became important invaders of the surrounding ecosystem. We therefore surveyed the grounds of 24 tourist facilities (lodges or other accommodation sites, which often included relatively large, fenced grounds covered by natural vegetation) in the Masai-Mara National Reserve (Figure 2). We noted all alien plant species present, and recorded whether the species had established naturalised populations within the tourism facilities and whether they had become invasive. Species were regarded as naturalised if they were considered to have been reproducing consistently, sustaining populations over many life cycles without direct intervention by humans (Richardson et al. 2000). Species were recorded as invasive if they were found to be spreading beyond the fences or outside of the tourism facilities or other human habitation.

## Evidence of impact of selected important species

Although many alien species have established in the Serengeti-Mara ecosystem, a relatively small number poses disproportionate threats, as they spread rapidly, have the potential to invade large areas and can generate large impacts. According to Clark et al. (2010), it has been suggested that *Acacia mearnsii* De Wild, *Leucaena leucocephala* (Lam.) de Wit (Fabaceae), *Caesalpinia decapetala* (Roth) Alston (Fabaceae), *Parkinsonia aculeata* L. (Fabaceae), *Melia azedarach* L. (Meliaceae), *Jacaranda mimosifolia* D. Don (Bignoniaceae), *Eucalyptus* spp. (Myrtaceae), *Lantana camara* (L.) (Verbenaceae), *Datura stramonium* L. (Solanaceae), *Lonicera japonica* Thunb. (Caprifoliaceae) and *Azolla filiculoides* Lam. (possibly *Azolla cristata* Kaulf.) (Salviniaceae) pose the biggest threat to the Ngorongoro Conservation Area. However, we are of the opinion that of these 11 species, only *L. camara* and five others, not listed by any previous studies, pose an even bigger threat to the whole ecosystem based on their recorded impacts elsewhere in the region or on the continent and their current and potential distribution in the region, especially in the Serengeti-Mara ecosystem (Illori et al. 2010; Maundu et al. 2009; McConnachie et al. 2011; Shackleton et al. 2017; Shackleton et al. in press). All of these are known to be aggressively invasive and have the potential to substantially reduce the ability of rangelands to support grazing mammals, and several have other impacts, being allelopathic or toxic, or having an ability to affect the health of livestock or wildlife. The species were:

- *Chromolaena odorata* (L.) R.M. King & H.Rob. (Asteraceae), a shrub from Central America
- *Lantana camara*, a shrub from Central and South America
- *Opuntia stricta* (Haw.) Haw. (Cactaceae), a spinescent stem succulent from Central America
- *Parthenium hysterophorus* L. (Asteraceae), an annual herb from tropical America
- *Prosopis* species and hybrids (Fabaceae), trees and shrubs from North, South and Central America
- *Tithonia diversifolia* (Hemsl.) A. Gray (Asteraceae), a shrub from Central America.

For each species, we located published accounts on the nature and extent of impacts associated with the species, and summarised this information in brief accounts intended to illustrate the potential of the species to impact on the conservation value of the Serengeti-Mara ecosystem.

# Results

## Species surveys

During our roadside surveys, we encountered 62 alien plant species that had established adventive populations in the Serengeti-Mara ecosystem (Table 1). These included ruderal weeds such as *Bidens pilosa* L. (Asteraceae), *Alternanthera pungens* Kunth (Amaranthaceae), *Gomphrena celosioides* Mart (Amaranthaceae), *Cirsium vulgare* (Savi) Ten. (Asteraceae), *Flaveria bidentis* (L.) Kuntze (Asteraceae), *Conyza* spp. (Asteraceae) and others, which were probably all accidentally introduced or had moved unaided into the ecosystem from adjoining areas. These species were mainly confined to roadsides or other man-made disturbances and were not

**TABLE 1:** Alien plant species, including some native plant species which may be growing outside of their natural range, recorded in the Serengeti-Mara ecosystem and immediate surrounds (excluding vegetable crops and grains).

| Species | Family | Number of tourist facilities where species was cultivated | Naturalised within tourist facilities | Invasive outside of tourist facilities |
|---|---|---|---|---|
| *Brillantaisia lamium* (Nees) Benth. | Acanthaceae | 3 | Yes | No |
| *Hypoestes aristata* (Vahl) Roem. & Schult. | Acanthaceae | 1 | No | No |
| *Hypoestes phyllostachya* Baker | Acanthaceae | Clark et al. (2010) | | |
| *Odontonema tubaeforme* (Bertol.) Kuntze | Acanthaceae | 1 | No | No |
| *Ruellia simplex* C. Wright | Acanthaceae | 1 | No | No |
| *Sanchezia parvibracteata* Sprague & Hutch. | Acanthaceae | Clark et al. (2010) | | |
| *Thunbergia grandiflora* (Roxb. ex Rottl.) Roxb. | Acanthaceae | 2 | No | No |
| *Thunbergia mysorensis* (Wight) T. Anderson | Acanthaceae | 1 | No | No |
| *Sambucus nigra* L. ssp. *canadensis* (L.) R. Bolli | Adoxaceae | 1 | No | No |
| *Agave attenuata* Salm-Dyck | Asparagaceae | 3 | No | No |
| *Agave americana* L. | Asparagaceae | 12 | Yes | No |
| *Agave angustifolia* Haw. var. *angustifolia* | Asparagaceae | 3 | Yes | Yes |
| *Agave sisalana* Perrine | Asparagaceae | 12 | Yes | No |
| *Furcraea foetida* (L.) Haw. | Asparagaceae | 1 | Yes | No |
| *Carpobrotus edulis* (L.) N.E. Br. | Aizoaceae | 1 | No | No |
| *Mesembryanthemum cordifolium* L.f. [Syn.: *Aptenia cordifolia* (L.f.) Schwantes] | Aizoaceae | 9 | No | No |
| *Amaranthus hybridus* L. | Amaranthaceae | 0 | Yes | Yes |
| *Alternanthera pungens* Kunth | Amaranthaceae | 0 | Yes | Yes |
| *Gomphrena celosioides* Mart. | Amaranthaceae | 0 | Yes | Yes |
| *Iresine diffusa* Humb. & Bonpl. ex Willd. | Amaranthaceae | Clark et al. (2010) | | |
| *Iresine herbstii* Hook. | Amaranthaceae | 2 | No | No |
| *Agapanthus praecox* Willd. | Amaryllidaceae | 3 | No | No |
| *Allium neapolitanum* Cirillo [Syn.: *Nothoscordum inodorum* (Aiton) G. Nicholson] | Amaryllidaceae | 3 | Yes | Yes |
| *Clivia miniata* (Lindl.) Bosse | Amaryllidaceae | 1 | No | No |
| *Hymenocallis littoralis* (Jacq.) Salisb. | Amaryllidaceae | 1 | No | No |
| *Tulbaghia fragrans* Verd. | Amaryllidaceae | 5 | No | No |
| *Tulbaghia violacea* Harv. | Amaryllidaceae | 1 | No | No |
| *Mangifera indica* L. | Anacardiaceae | 2 | No | No |
| *Schinus molle* L. | Anacardiaceae | 8 | No | No |
| *Schinus terebinthifolius* Raddi | Anacardiaceae | 4 | No | No |
| *Annona montana* Macfad. | Annonaceae | Clark et al. (2010) | | |
| *Polyalthia longifolia* (Sonn.) Thwaites | Annonaceae | Clark et al. (2010) | | |
| *Calotropis gigantea* (L.) Dryand. | Apocynaceae | 0 | No | Yes |
| *Cascabela thevetia* (L.) Lippold [Syn.: *Thevetia peruviana* (Pers.) K. Schum.] | Apocynaceae | 2 | No | Yes |
| *Catharanthus roseus* (L.) G. Don | Apocynaceae | 11 | Yes | Yes |
| *Plumeria rubra* L. | Apocynaceae | 4 | No | No |
| *Nerium oleander* L. | Apocynaceae | 7 | No | No |
| *Vinca major* L. | Apocynaceae | Clark et al. (2010); Henderson (2002) | | |
| *Aglaonema commutatum* Schott | Araceae | Clark et al. (2010) | | |
| *Alocasia* sp. | Araceae | 2 | No | No |
| *Anthurium andraeanum* Linden | Araceae | 2 | No | No |
| *Anthurium* sp. | Araceae | Clark et al. (2010) | | |
| *Colocasia esculenta* (L.) Schott | Araceae | 1 | No | No |
| *Dieffenbachia maculata* (Lodd.) Sweet | Araceae | 4 | No | No |
| *Epipremnum aureum* (Linden & André) G.S. Bunting | Araceae | Clark et al. (2010) | | |
| *Epipremnum pinnatum* (L.) Engl. | Araceae | Clark et al. (2010) | | |
| *Monstera deliciosa* Liebm. | Araceae | 8 | No | No |

*Source*: The list was compiled from three sources: (1) surveys within the grounds of tourist accommodation facilities in the Masai-Mara National Reserve, (2) extensive road surveys throughout the region, and (3) species recorded in the Ngorongoro Conservation Area by Henderson (2002) and Clark et al. (2010)

Table 1 continues on the next page →

**TABLE 1: (Continues...)** Alien plant species, including some native plant species which may be growing outside of their natural range, recorded in the Serengeti-Mara ecosystem and immediate surrounds (excluding vegetable crops and grains).

| Species | Family | Number of tourist facilities where species was cultivated | Naturalised within tourist facilities | Invasive outside of tourist facilities |
|---|---|---|---|---|
| *Pistia stratiotes* L. | Araceae | 1 | Yes | Yes |
| *Syngonium podophyllum* Schott | Araceae | 1 | No | No |
| *Hedera helix* L. | Araliaceae | 1 | No | No |
| *Schefflera actinophylla* (Endl.) Harms | Araliaceae | 3 | No | No |
| *Araucaria heterophylla* (Salisb.) Franco | Araucariaceae | Clark et al. (2010) | | |
| *Dypsis leptocheilos* (Hodel) Beentje & J.Dransf. | Arecaceae | Clark et al. (2010) | | |
| *Phoenix canariensis* Chabaud | Arecaceae | 1 | No | No |
| *Syagrus romanzoffiana* (Cham.) Glassman | Arecaceae | 1 | No | No |
| *Phytelephas tenuicaulis* (Barfod) A.J. Hend. | Arecaceae | 1 | No | No |
| *Roystonia regia* (Kunth) Cook | Arecaceae | 1 | No | No |
| *Asparagus setaceus* (Kunth) Jessop | Asparagaceae | 2 | No | No |
| *Chlorophytum comosum* (Thunb.) Jacques | Asparagaceae | 4 | No | No |
| *Chlorophytum bracteatum* Hua | Asparagaceae | 2 | No | No |
| *Chlorophytum capense* (L.) Voss | Asparagaceae | 3 | No | No |
| *Chlorophytum* sp. | Asparagaceae | Clark et al. (2010) | | |
| *Dracaena draco* (L.) L. | Asparagaceae | 1 | No | No |
| *Liriope* sp. | Asparagaceae | 1 | No | No |
| *Liriope muscari* (Decne.) L.H. Bailey | Asparagaceae | 1 | No | No |
| *Sansevieria trifasciata* Prain | Asparagaceae | 1 | Yes | No |
| *Yucca aloifolia* L. | Asparagaceae | 3 | No | No |
| *Acanthospermum hispidum* DC. | Asteraceae | 0 | Yes | Yes |
| *Ageratum conyzoides* (L.) L. | Asteraceae | 0 | Yes | Yes |
| *Bidens pilosa* L. | Asteraceae | 0 | Yes | Yes |
| *Bidens schimperi* (native) | Asteraceae | Henderson (2002) | | |
| *Chromolaena odorata* (L.) King & H.E. Robins | Asteraceae | 0 | No | Yes |
| *Cirsium vulgare* (Savi) Ten. | Asteraceae | 0 | No | Yes |
| *Conyza bonariensis* (L.) Cronq. | Asteraceae | 0 | Yes | Yes |
| *Conyza sumatrensis* (Retz.) E. Walker | Asteraceae | 0 | Yes | Yes |
| *Conyza* sp. | Asteraceae | Clark et al. (2010) | | |
| *Dahlia imperialis* Roezl ex Ortgies | Asteraceae | Clark et al. (2010) | | |
| *Euryops chrysanthemoides* (DC.) B. Nord. | Asteraceae | 2 | Yes | No |
| *Flaveria bidentis* (L.) Kuntze | Asteraceae | 0 | Yes | Yes |
| *Galinsoga parviflora* Cav. | Asteraceae | Henderson (2002) | | |
| *Gazania rigens* (L.) Gaertn. | Asteraceae | 1 | No | No |
| *Helichrysum petiolare* Hilliard & B.L. Burtt | Asteraceae | 1 | No | No |
| *Parthenium hysterophorus* L. | Asteraceae | 0 | No | Yes |
| *Senecio cylindricus* (A.Berger) Jacobsen | Asteraceae | 3 | No | No |
| *Schkuhria pinnata* (Lam.) Kuntze ex Thell. | Asteraceae | 0 | Yes | Yes |
| *Sonchus oleraceus* (L.) L. | Asteraceae | 0 | Yes | Yes |
| *Sphagneticola trilobata* (L.) Pruski | Asteraceae | 3 | No | No |
| *Tagetes minuta* L. | Asteraceae | 1 | Yes | Yes |
| *Tridax procumbens* (L.) L. | Asteraceae | 0 | Yes | Yes |
| *Tithonia diversifolia* (Hemsl.) A.Gray | Asteraceae | 1 | Yes | Yes |
| *Tithonia rotundifolia* (Mill.) S.F. Blake | Asteraceae | 0 | No | Yes |
| *Xanthium strumarium* L. | Asteraceae | 0 | No | Yes |
| *Zinnia peruviana* (L.) L. | Asteraceae | 1 | Yes | Yes |
| *Impatiens walleriana* Hook.f. | Balsaminaceae | 2 | No | No |
| *Anredera cordifolia* (Ten.) Steenis | Basellaceae | 2 | Yes | No |
| *Begonia semperflorens* Link & Otto | Begoniaceae | 1 | No | No |
| *Begonia* hybrids | Begoniaceae | Clark et al. (2010) | | |
| *Jacaranda mimosifolia* D. Don | Bignoniaceae | 5 | Yes | No |
| *Podranea ricasoliana* (Tanfani) Sprague | Bignoniaceae | Henderson (2002) | | |
| *Pyrostegia venusta* (Ker Gawl.) Miers | Bignoniaceae | 5 | Yes | Yes |
| *Spathodea campanulata* Pal. | Bignoniaceae | 2 | No | No |
| *Tecoma capensis* (Thunb.) Lindl. | Bignoniaceae | 1 | Yes | No |
| *Tecoma stans* (L.) Juss. ex Kunth | Bignoniaceae | 6 | Yes | Yes |
| *Capsella bursa-pastoris* (L.) Medik. | Brassicaceae | Clark et al. (2010); Henderson (2002) | | |
| *Raphanus raphanistrum* L. | Brassicaceae | 0 | Yes | Yes |
| *Bromelia* sp. | Bromeliaceae | 2 | No | No |

*Source*: The list was compiled from three sources: (1) surveys within the grounds of tourist accommodation facilities in the Masai-Mara National Reserve, (2) extensive road surveys throughout the region, and (3) species recorded in the Ngorongoro Conservation Area by Henderson (2002) and Clark et al. (2010)

Table 1 continues on the next page →

**TABLE 1: (Continues...)** Alien plant species, including some native plant species which may be growing outside of their natural range, recorded in the Serengeti-Mara ecosystem and immediate surrounds (excluding vegetable crops and grains).

| Species | Family | Number of tourist facilities where species was cultivated | Naturalised within tourist facilities | Invasive outside of tourist facilities |
|---|---|---|---|---|
| *Cryptanthus bromelioides* Otto & A. Dietr. | Bromeliaceae | 1 | No | No |
| *Austrocylindropuntia subalata* (Muehlenpf.) Backeb. | Cactaceae | 2 | No | Yes |
| *Cereus jamacaru* DC. | Cactaceae | 5 | No | No |
| *Opuntia ficus-indica* (L.) Mill. | Cactaceae | 4 | Yes | Yes |
| *Opuntia monacantha* (Willd.) Haw. | Cactaceae | 7 | Yes | Yes |
| *Opuntia stricta* (Haw.) Haw | Cactaceae | 0 | No | Yes |
| *Cannabis sativa* L. | Cannabaceae | Clark et al. (2010) | | |
| *Canna indica* L. | Cannaceae | 10 | Yes | No |
| *Canna × generalis* L.H. Bailey & E.Z. Bailey | Cannaceae | 2 | No | No |
| *Cleome gynandra* L. | Capparaceae | 0 | Yes | Yes |
| *Lonicera japonica* Thunb. | Caprifoliaceae | 1 | No | No |
| *Carica papaya* L. | Caricaceae | 1 | Yes | No |
| *Casuarina equisetifolia* L. | Casuarinaceae | Clark et al. (2010) | | |
| *Casuarina* sp. | Casuarinaceae | 2 | No | No |
| *Terminalia mantaly* H. Perrier | Combretaceae | 4 | No | No |
| *Terminalia superba* Engl. & Diels | Combretaceae | Clark et al. (2010) | | |
| *Callisia fragrans* (Lindl.) Woodson | Commelinaceae | 5 | Yes | No |
| *Callisia repens* (Jacq.) L. | Commelinaceae | 3 | Yes | No |
| *Tradescantia pallida* (Rose) D.R. Hunt | Commelinaceae | 2 | Yes | No |
| *Tradescantia zebrina* Bosse | Commelinaceae | 13 | Yes | No |
| *Ipomoea cairica* (L.) Sweet (native) | Convolvulaceae | 2 | Yes | Yes |
| *Ipomoea hildebrandtii* Vatke (native) | Convolvulaceae | 2 | Yes | Yes |
| *Bryophyllum delagoense* (Eckl. & Zeyh.) Druce | Crassulaceae | 12 | Yes | Yes |
| *Bryophyllum fedtschenkoi* (Raym.-Hamet & H. Perrier) Lauz.-March. | Crassulaceae | 11 | No | No |
| *Bryophyllum proliferum* Bowie ex Hook. | Crassulaceae | 8 | Yes | No |
| *Cotyledon orbiculata* L. | Crassulaceae | 1 | No | No |
| *Crassula multiclava* Lem. | Crassulaceae | 5 | Yes | No |
| *Crassula ovata* (Mill.) Druce | Crassulaceae | 9 | ? No | No |
| *Echeveria expatriata* Rose | Crassulaceae | 3 | No | No |
| *Kalanchoe beharensis* Drake | Crassulaceae | 4 | No | No |
| *Kalanchoe blossfeldiana* Poelln. | Crassulaceae | 1 | No | No |
| *Kalanchoe longiflora* Schltr. ex J.M. Wood | Crassulaceae | 1 | No | No |
| *Kalanchoe* sp. 1 | Crassulaceae | 1 | No | No |
| *Kalanchoe* sp. 2 | Crassulaceae | 1 | No | No |
| *Cupressus lusitanica* Mill. | Cupressaceae | 1 | No | No |
| *Cupressus sempervirens* L. | Cupressaceae | Clark et al. (2010) | | |
| *Widdringtonia nodiflora* (L.) E. Powrie | Cupressaceae | Clark et al. (2010) | | |
| *Cyathea australis* (R. Br.) Domin | Cyathaceae | 1 | No | No |
| *Acalypha amentacea* Roxb. | Euphorbiaceae | 1 | No | No |
| *Acalypha wilkesiana* Müll. Arg. | Euphorbiaceae | 3 | No | No |
| *Euphorbia cotinifolia* L. | Euphorbiaceae | 3 | No | No |
| *Euphorbia pulcherrima* Willd. ex Klotzsch | Euphorbiaceae | 6 | No | No |
| *Euphorbia milii var. splendens* (Bojer ex Hook.) Ursch & Leandri (Syn.: *Euphorbia splendens* Bojer ex Hook.) | Euphorbiaceae | 12 | No | No |
| *Hura crepitans* L. | Euphorbiaceae | Clark et al. (2010) | | |
| *Jatropha podagrica* Hook. | Euphorbiaceae | 2 | No | No |
| *Jatropha* sp. | Euphorbiaceae | Clark et al. (2010) | | |
| *Pedilanthus tithymaloides* (L.) Poit | Euphorbiaceae | 3 | No | No |
| *Ricinus communis* L. (? native) | Euphorbiaceae | 4 | Yes | Yes |
| *Acacia mearnsii* De Wild. | Fabaceae | Clark et al. (2010); Henderson (2002) | | |
| *Acrocarpus fraxinifolius* Arn. | Fabaceae | 1 | No | No |
| *Albizia lebbeck* (L.) Benth. | Fabaceae | 1 | No | No |
| *Bauhinia variegata* L. | Fabaceae | 2 | No | No |
| *Caesalpinia decapetala* (Roth) Alston | Fabaceae | 0 | No | Yes |
| *Caesalpinia pulcherrima* (L.) Sw. | Fabaceae | Clark et al. (2010) | | |
| *Calliandra calothyrsus* Meisn. | Fabaceae | 2 | No | No |
| *Chrysanthemum* sp. | Fabaceae | 4 | No | No |
| *Delonix regia* (Hook.) Raf. | Fabaceae | 1 | No | No |
| *Leucaena leucocephala* (Lam.) de Wit | Fabaceae | 7 | Yes | Yes |

*Source*: The list was compiled from three sources: (1) surveys within the grounds of tourist accommodation facilities in the Masai-Mara National Reserve, (2) extensive road surveys throughout the region, and (3) species recorded in the Ngorongoro Conservation Area by Henderson (2002) and Clark et al. (2010)

Table 1 continues on the next page →

**TABLE 1: (Continues...)** Alien plant species, including some native plant species which may be growing outside of their natural range, recorded in the Serengeti-Mara ecosystem and immediate surrounds (excluding vegetable crops and grains).

| Species | Family | Number of tourist facilities where species was cultivated | Naturalised within tourist facilities | Invasive outside of tourist facilities |
|---|---|---|---|---|
| *Mimosa pigra* L. | Fabaceae | 0 | No | Yes |
| *Parkinsonia aculeata* L. | Fabaceae | Clark et al. (2010) | | |
| *Prosopis juliflora* (Sw.) DC. | Fabaceae | 0 | No | Yes |
| *Prosopis* sp. | Fabaceae | 2 | No | No |
| *Senna didymobotrya* (Fresen.) H.S. Irwin & Barneby (native) | Fabaceae | 4 | Yes | Yes |
| *Senna hirsuta* (L.) H.S. Irwin & Barneby | Fabaceae | 0 | No | Yes |
| *Senna obtusifolia* (L.) H.S. Irwin & Barneby | Fabaceae | 0 | Yes | Yes |
| *Senna occidentalis* (L.) Link | Fabaceae | 0 | No | Yes |
| *Senna spectabilis* (DC.) H.S. Irwin & Barneby | Fabaceae | 8 | Yes | Yes |
| *Senna septemtrionalis* (Viv.) H.S. Irwin & Barneby | Fabaceae | 6 | Yes | No |
| *Senna siamea* (Lam.) H.S.Irwin & Barneby | Fabaceae | 2 | No | No |
| *Tipuana tipu* (Benth.) Kuntze | Fabaceae | 2 | No | No |
| *Geranium* sp. | Geraniaceae | 4 | No | No |
| *Pelargonium domesticum* L.H. Bailey | Geraniaceae | Clark et al. (2010) | | |
| *Pelargonium fulgidum* L'Hér. | Geraniaceae | 1 | No | No |
| *Heliconia caribaea* Lam. | Heliconiaceae | Clark et al. (2010) | | |
| *Heliconia rostrata* Ruiz & Pav. | Heliconiaceae | 1 | No | No |
| *Hydrangea macrophylla* (Thunb.) Ser. | Hydrangeaceae | Clark et al. (2010) | | |
| *Dietes grandiflora* N.E. Br. | Iridaceae | 3 | No | No |
| *Iris* sp. | Iridaceae | 2 | No | No |
| *Holmskioldia sanguinea* Retz. | Lamiaceae | 1 | No | No |
| *Plectranthus madagascariensis* (Pers.) Benth. | Lamiaceae | 1 | No | No |
| *Plectranthus scutellarioides* (L.) R.Br. (Syn.: *Coleus hybridus* Cobeau) | Lamiaceae | 2 | No | No |
| *Rosmarinus officinalis* L. | Lamiaceae | 1 | No | No |
| *Salvia coccinea* Buc'hoz ex Etl. | Lamiaceae | 2 | Yes | No |
| *Salvia leucantha* Cav. | Lamiaceae | 2 | No | No |
| *Persea americana* Mill. | Lauraceae | Clark et al. (2010) | | |
| *Michelia fuscata* (Andrews) Blume | Magnoliaceae | 1 | No | No |
| *Ceiba speciosa* (A.St.-Hil.) Ravenna | Malvaceae | 1 | No | No |
| *Hibiscus acetosella* Welw. ex Hiern | Malvaceae | 1 | No | No |
| *Hibiscus rosa-sinensis* L. | Malvaceae | 4 | No | No |
| *Hibiscus vitifolius* L. | Malvaceae | 1 | No | No |
| *Malvaviscus arboreus* var. *mexicanus* Schlectend. | Malvaceae | 3 | No | No |
| *Sida acuta* Burman f. | Malvaceae | 0 | Yes | Yes |
| *Sida cordifolia* L. (uncertain) | Malvaceae | 0 | Yes | Yes |
| *Calathea zebrina* (Sims) Lindl. | Marantaceae | 1 | No | No |
| *Ctenanthe oppenheimiana* (E. Morren) K. Schum. | Marantaceae | 1 | No | No |
| *Maranta leuconeura* E. Morren | Marantaceae | 1 | No | No |
| *Tibouchina heteromalla* (D. Don) Cogn. | Melastomataceae | 2 | No | No |
| *Azadirachta indica* A. Juss. | Meliaceae | 4 | Yes | No |
| *Melia azedarach* L. | Meliaceae | Clark et al. (2010) | | |
| *Artocarpus heterophyllus* Lam. | Moraceae | Clark et al. (2010) | | |
| *Ficus benjamina* L. | Moraceae | 2 | No | No |
| *Ficus elastica* Roxb. ex Hornem. | Moraceae | 2 | No | No |
| *Ficus pumila* L. | Moraceae | 1 | No | No |
| *Ficus* hybrids | | Clark et al. (2010) | | |
| *Morus alba* L. | Moraceae | Clark et al. (2010) | | |
| *Musa* × *paradisiaca* L. | Musaceae | Clark et al. (2010) | | |
| *Musa* sp. | Musaceae | 1 | No | No |
| *Mussaenda erythrophylla* Schumach. & Thonn. | Musaceae | 1 | No | No |
| *Callistemon citrinus* (Curtis) Skeels | Myrtaceae | 3 | No | No |
| *Callistemon lanceolatus* (Sm.) Sweet | Myrtaceae | 3 | No | No |
| *Eucalyptus camaldulensis* Dehnh. | Myrtaceae | Clark et al. (2010) | | |
| *Eucalyptus cladocalyx* F. Muell. (uncertain) | Myrtaceae | Henderson (2002) | | |
| *Eucalyptus globulus* Labill. | Myrtaceae | Clark et al. (2010) | | |
| *Eucalyptus grandis* W.Hill (uncertain) | Myrtaceae | Henderson (2002) | | |
| *Eucalyptus saligna* Sm. | Myrtaceae | Clark et al. (2010) | | |
| *Eucalyptus* sp. | Myrtaceae | 6 | Yes | No |

*Source*: The list was compiled from three sources: (1) surveys within the grounds of tourist accommodation facilities in the Masai-Mara National Reserve, (2) extensive road surveys throughout the region, and (3) species recorded in the Ngorongoro Conservation Area by Henderson (2002) and Clark et al. (2010)

Table 1 continues on the next page →

**TABLE 1: (Continues...)** Alien plant species, including some native plant species which may be growing outside of their natural range, recorded in the Serengeti-Mara ecosystem and immediate surrounds (excluding vegetable crops and grains).

| Species | Family | Number of tourist facilities where species was cultivated | Naturalised within tourist facilities | Invasive outside of tourist facilities |
|---|---|---|---|---|
| *Melaleuca armillaris* (Sol. ex Gaertn.) Sm. | Myrtaceae | 2 | No | No |
| *Psidium guajava* L. | Myrtaceae | 3 | Yes | Yes |
| *Syzygium cumini* (L.) Skeels | Myrtaceae | 1 | No | No |
| *Nephrolepis exaltata* (L.) Schott (uncertain) | Nephrolepidaceae | 8 | Yes | No |
| *Bougainvillea spectabilis* Willd. (uncertain) | Nyctaginaceae | Clark et al. (2010) | | |
| *Bougainvillea* sp. | Nyctaginaceae | 10 | Yes | No |
| *Mirabilis jalapa* L. | Nyctaginaceae | 2 | Yes | No |
| *Jasminum polyanthum Franch* | Oleaceae | 1 | No | No |
| *Fuchsia* sp. | Onagraceae | Clark et al. (2010) | | |
| *Ludwigia adscendens* ssp. *diffusa* (Forssk.) P.H. Raven | Onagraceae | Clark et al. (2010) | | |
| *Oxalis latifolia* Kunth | Oxalidaceae | 0 | Yes | Yes |
| *Argemone ochroleuca* Sweet | Papaveraceae | 0 | No | Yes |
| *Argemone mexicana* L. | Papaveraceae | 0 | No | Yes |
| *Passiflora edulis* Sims | Passifloraceae | 1 | No | No |
| *Passiflora subpeltata* Ortega | Passifloraceae | 4 | Yes | Yes |
| *Peperomia obtusifolia* (L.) A. Dietr. (uncertain) | Piperaceae | 1 | No | No |
| *Russelia equisetiformis* Schltdl. & Cham. | Plantaginaceae | 1 | No | No |
| *Plumbago auriculata* Lam. | Plumbaginaceae | 3 | No | No |
| *Pennisetum setaceum* var. *rubrum* (Forssk.) Chiov. | Poaceae | 3 | No | No |
| *Yushania alpina* (K.Schum.) W.C. Lin (Syn.: *Arundinaria alpina* K. Schum.) (uncertain) | Poaceae | 1 | No | No |
| *Arundinaria disticha* Pfitzer (uncertain) | Poaceae | 1 | No | No |
| *Bambusa nutans* Wall. ex Munro | Poaceae | 4 | No | No |
| *Pennisetum setaceum* (Forssk.) Chiov. (native) | Poaceae | 2 | No | No |
| *Pontederia cordata* L. | Pontederiaceae | 2 | Yes | No |
| *Grevillea robusta* A.Cunn. ex R. Br. | Proteaceae | 10 | No | No |
| *Cotoneaster pannosus* Franch. | Rosaceae | 1 | No | No |
| *Eriobotrya japonica* (Thunb.) Lindl. | Rosaceae | 1 | No | No |
| *Malus domestica* Borkh. | Rosaceae | Clark et al. (2010) | | |
| *Prunus persica* (L.) Batsch | Rosaceae | Clark et al. (2010) | | |
| *Rosa rubignosa* L. | Rosaceae | 1 | No | No |
| *Rosa* sp. | Rosaceae | 2 | No | No |
| *Coffea arabica* L. | Rubiaceae | Clark et al. (2010) | | |
| *Hamelia patens* Jacq. | Rubiaceae | 5 | No | No |
| *Citrus limon* (L.) Osbeck | Rutaceae | Clark et al. (2010) | | |
| *Citrus sinensis* (L.) Osbeck | Rutaceae | Clark et al. (2010) | | |
| *Citrus* sp. | Rutaceae | 2 | No | No |
| *Azolla filiculoides* Lam. (possibly *Azolla cristata* Kaulf.) | Salvinaceae | Clark et al. (2010) | | |
| *Bergenia ciliata* (Haw.) Sternb. | Saxifragaceae | 1 | No | No |
| *Brugmansia suaveolens* (Humb. & Bonpl. ex Willd.) Bercht. & J. Presl | Solanaceae | 1 | Yes | No |
| *Brunfelsia uniflora* (Pohl) D. Don [Syn.: *Brunfelsia hopeana* (Hook.) Benth.] | Solanaceae | 1 | No | No |
| *Capsicum annuum* L. (Syn.: *Capsicum frutescens* L.) | Solanaceae | Clark et al. (2010) | | |
| *Cestrum aurantiacum* Lindl. | Solanaceae | Clark et al. (2010) | | |
| *Cestrum elegans* (Brongn. ex Neumann) Schltdl. | Solanaceae | 1 | No | No |
| *Cestrum nocturnum* L. | Solanaceae | 1 | No | No |
| *Cyphomandra betacea* (Cav.) Sendtn. (unresolved name) | Solanaceae | Clark et al. (2010) | | |
| *Datura stramonium* L. | Solanaceae | 0 | No | Yes |
| *Lycianthes rantonnei* (Carrière) Bitter (Syn.: *Solanum rantonnetii* Carrière) | Solanaceae | 1 | No | No |
| *Nicandra physalodes* (L.) Gaertn. | Solanaceae | 0 | Yes | Yes |
| *Nicotiana glauca* Graham | Solanaceae | Clark et al. (2010) | | |
| *Nicotiana tabacum* L. | Solanaceae | Clark et al. (2010) | | |
| *Solanum campylacanthum* A. Rich (native) | Solanaceae | 0 | Yes | Yes |
| *Solanum mauritianum* Scop. | Solanaceae | 7 | Yes | Yes |
| *Solanum seaforthianum* Andrews | Solanaceae | 2 | Yes | No |
| *Withania somnifera* (L.) Dunal | Solanaceae | Clark et al. (2010) | | |
| *Strelitzia reginae* Banks | Strelitziaceae | 5 | No | No |
| *Talinum paniculatum* (Jacq.) Gaertn. | Talinaceae | 1 | Yes | No |

*Source*: The list was compiled from three sources: (1) surveys within the grounds of tourist accommodation facilities in the Masai-Mara National Reserve, (2) extensive road surveys throughout the region, and (3) species recorded in the Ngorongoro Conservation Area by Henderson (2002) and Clark et al. (2010)

Table 1 continues on the next page →

**TABLE 1: (Continues...)** Alien plant species, including some native plant species which may be growing outside of their natural range, recorded in the Serengeti-Mara ecosystem and immediate surrounds (excluding vegetable crops and grains).

| Species | Family | Number of tourist facilities where species was cultivated | Naturalised within tourist facilities | Invasive outside of tourist facilities |
|---|---|---|---|---|
| *Tropaeolum majus* L. | Tropaeolaceae | Henderson (2002) | | |
| *Aloysia citriodora* Palau [Syn.: *Lippia citriodora* (Palau) Kunth] | Verbenaceae | 1 | No | No |
| *Duranta erecta* L. | Verbenaceae | 11 | No | No |
| *Lantana camara* L. | Verbenaceae | 12 | Yes | Yes |
| *Lantana montevidensis* (Spreng.) Briq. | Verbenaceae | 1 | No | No |
| *Lantana* hybrids | Verbenaceae | 1 | No | No |
| *Petrea volubilis* L. | Verbenaceae | 2 | No | No |
| *Verbena bonariensis* L. | Verbenaceae | 1 | Yes | Yes |
| *Verbena hybrida* Groenl. & Rumpler | Verbenaceae | 1 | No | No |
| *Verbena officinalis* L. | Verbenaceae | 2 | No | Yes |
| *Aloe* sp. | Xanthorrhoeaceae | 5 | No | No |
| *Bulbine asphodeloides* (L.) Spreng. | Xanthorrhoeaceae | 1 | No | No |
| *Bulbine latifolia* (L.f.) Spreng. (Syn.: *Bulbine natalensis* Baker) | Xanthorrhoeaceae | 2 | No | No |
| *Dianella tasmanica* Hook.f. | Xanthorrhoeaceae | 1 | No | No |
| *Hemerocallis fulva* (L.) L. | Xanthorrhoeaceae | 1 | No | No |
| *Phormium tenax* J.R. Forst. & G. Forst. | Xanthorrhoeaceae | 1 | No | No |
| *Alpinia purpurata* (Vieill.) K.Schum. | Zingiberaceae | 1 | No | No |
| *Alpinia zerumbet* (Pers.) B.L. Burtt & R.M. Sm. | Zingiberaceae | 1 | No | No |
| *Curcuma zedoaria* (Christm.) Roscoe | Zingiberaceae | Clark et al. (2010) | | |
| *Zingiber neglectum* Valeton | Zingiberaceae | Clark et al. (2010) | | |
| *Tribulus terrestris* L. | Zygophyllaceae | 0 | Yes | Yes |
| Unknown sp. A – H (8 spp.) | Unknown | 1 | No | No |

*Source*: The list was compiled from three sources: (1) surveys within the grounds of tourist accommodation facilities in the Masai-Mara National Reserve, (2) extensive road surveys throughout the region, and (3) species recorded in the Ngorongoro Conservation Area by Henderson (2002) and Clark et al. (2010)

regarded as being transformers as described by Richardson et al. (2000), in that they probably have negligible impacts on biodiversity or ecosystems over a large area. However, other species such as *P. hysterophorus*, which were probably also accidentally introduced or moved into the ecosystem unaided, are already widespread and abundant and pose a significant threat to biodiversity. A large number of alien species have also been intentionally introduced. Of the 245 alien plant species seen and recorded in the ecosystem (including *Ipomoea hildebrandtii* Vatke [Convolvulaceae], *Ipomoea cairica* [L.] Sweet, *S. didymobotrya* and *R. communis* which are native to the region but may have been intentionally introduced into the ecosystem as ornamentals, and excluding the additional species recorded by Clark et al. [2010] and Henderson [2002]), 212 species were considered to have been intentionally introduced, mainly as ornamentals, in tourism accommodation facilities (Table 1). Of those 212 alien ornamental plant species seen in tourist facilities, 51 were considered to be naturalised in that they had spread and established self-perpetuating populations within the tourist compounds, often in natural vegetation. Species such as *Callisia repens* (Lindl.) Woodson (Commelinaceae) had established large populations in woodland understoreys of some lodges together with *Tradescantia zebrina* (Rose) D.R. Hunt (Commelinaceae), while climbers or creepers such as *Pyrostegia venusta* (Ker Gawl.) Miers (Bignoniaceae), *Tecoma capensis* (Thunb.) Lindl. (Bignoniaceae), *Solanum seaforthianum* Andrews (Solanaceae) and others had invaded woodlands, scrambling or climbing over native trees and contributing to canopy collapse. Of these naturalised ornamentals, 23 species appeared to have spread beyond the facility fences or other human habitation, where they were also being cultivated, and established populations in the adjacent natural vegetation (Table 1). These included species such as *Catharanthus roseus* (L.) G. Don (Apocynaceae), *Zinnia peruviana* (L.) L. (Asteraceae), *T. diversifolia*, *Solanum mauritianum* Scop. (Solanaceae), *Senna spectabilis* (DC.) H.S. Irwin & Barneby (Fabaceae), *L. camara* and *Tecoma stans* (L.) Juss. ex Kunth. (Bignoniaceae). Although the cactus species *Opuntia monacantha* (Willd.) Haw. (Cactaceae) and *Austrocylindropuntia subalata* (Muehlenpf.) Backeb. were present in lodge gardens in the Masai-Mara National Reserve, and adjoining conservancies, they were not found to be invasive, unlike the situation within the Serengeti National Park and surrounding conservation areas where the former had escaped cultivation and established populations in the wild. *Opuntia stricta* and *C. decapetala* were not seen in any tourism facilities but were widely grown, especially as living fences, in villages within and immediately adjacent to the Serengeti-Mara ecosystem from where they have established populations in the natural vegetation. Another species that is probably not cultivated but nevertheless abundant on the edge of the ecosystem is *C. odorata*.

Our second roadside survey of the extent of *P. hysterophorus* in the Masai-Mara National Reserve revealed a significant densification of *P. hysterophorus* infestations within the National Reserve Central Plains and the establishment of numerous new infestations to the east (Figure 3). However, intensive management in the form of ongoing control of *P. hysterophorus* over several years, using manual (hand-pulling) and chemical (Tordon 101 containing the active ingredients Picloram and 2,4-D) control interventions in the adjacent 'Mara Triangle' resulted in a reduction in the

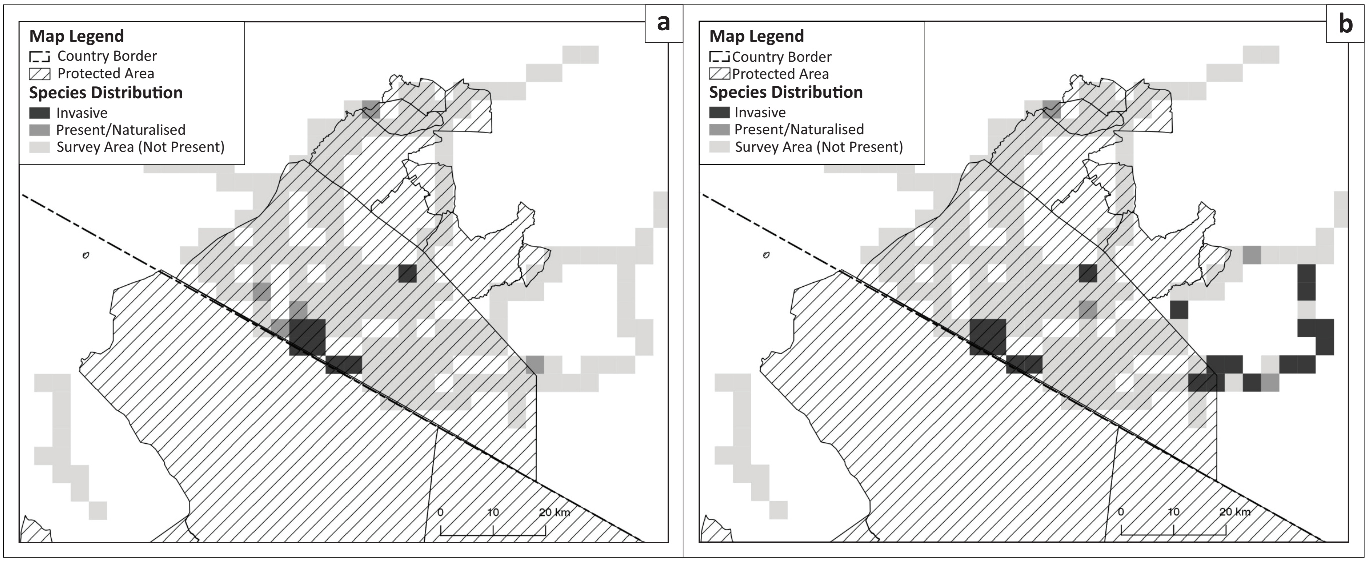



**FIGURE 3:** Successive surveys in (a) 2011 and (b) 2016 of *Parthenium hysterophorus* in the Masai-Mara National Reserve and surrounding areas in Kenya, showing the establishment of new populations to the east of the Reserve by 2016.

distribution and abundance of this noxious weed. This provides an illustration of what can potentially be achieved with focussed management programmes, especially when infestations are still small and localised. These efforts need to be expanded because much of this conservation area is under threat from further *P. hysterophorus* invasions.

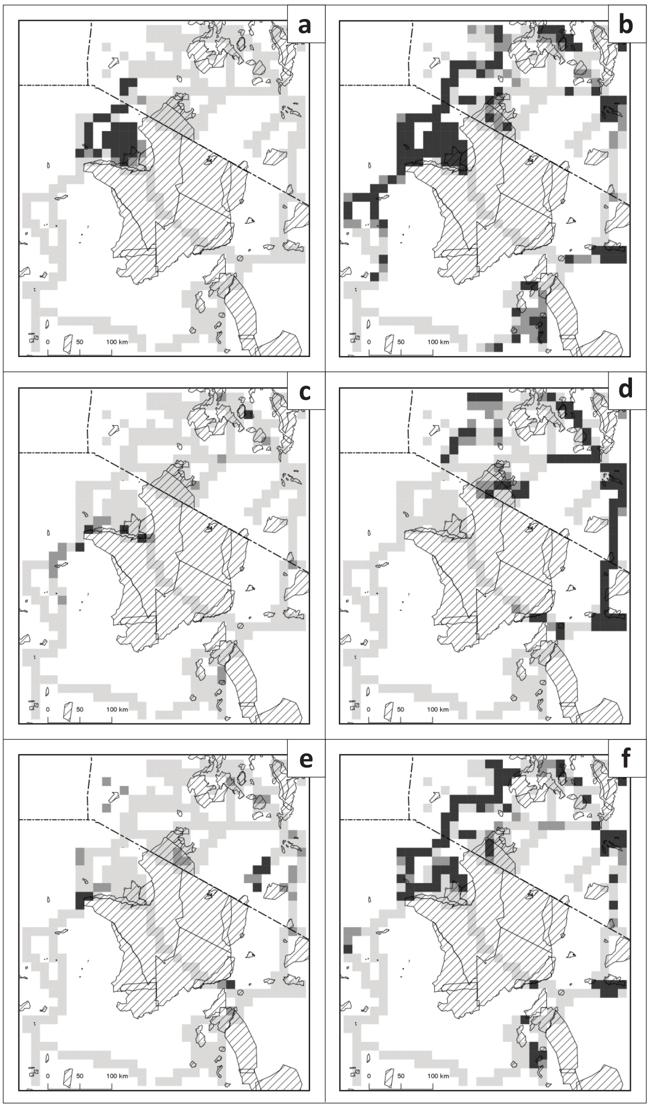
Overall, our extensive roadside surveys revealed that the Serengeti-Mara ecosystem is currently relatively free of transforming invasive alien plants, with the exception of relatively small localised populations of *L. camara*, *T. diversifolia*, *O. stricta*, *Opuntia ficus-indica*, and *O. monacantha*, with more extensive and widespread infestations of *P. hysterophorus* in the Masai-Mara National Reserve and adjoining conservancies (Figure 4). Unless they are managed, these infestations are likely to expand, as the results of our second survey on *P. hysterophorus* in 2016 clearly demonstrated. This is very likely considering that climate suitability maps, developed by Kriticos et al. (2015) and McConnachie et al. (2011), indicate that most of the Serengeti-Mara ecosystem is climatically suitable for the establishment of *P. hysterophorus*, especially the northwestern section (Figure 5). Other invasive plant species such as *C. odorata* and *Prosopis juliflora*, which are currently abundant outside of the ecosystem, within predominantly communal lands to the west (Figure 4), are also likely to spread into the ecosystem in the foreseeable future, if steps are not taken to prevent this.

## Evidence of impact of selected important species

Our review of available literature on the impacts of six selected taxa revealed that each poses substantial threats to the Serengeti-Mara ecosystem, should they be allowed to spread and densify within the ecosystem or invade it from adjacent areas. Evidence for the main impacts are summarised below.

*Opuntia stricta* is a succulent shrub that was introduced from Central America, and it is regarded as a transformer species in savannas and arid grasslands (Henderson 2001). The species is highly invasive and forms dense stands, impeding movement and access across the landscape. In Madagascar, *O. stricta* has invaded land used for crop and pasture production, and has encroached on villages and roads, impeding human mobility (Larsson 2004). Here, the cactus has had a negative impact on native grasses and herbs, and affects trees by inhibiting their growth and regeneration (Larsson 2004). The small spines (known as glochids) on the fruit, when consumed by livestock, lodge in their gums, on their tongues or in their gastrointestinal tracts, causing bacterial infections, while the hard seeds may cause rumen impaction, which can be fatal and which often leads to excessive, enforced culling of affected animals (Ueckert et al. 1990). Similar impacts have been recorded in Laikipia County, Kenya, where pastoralists have lost significant numbers of livestock (Shackleton et al. in press). People who consume the fruits develop diarrhoea and may suffer from serious infections caused by the spines (Larsson 2004). In Kenya, *O. stricta* infestations have resulted in the abandonment of land (A.B.R. Witt pers. observ.).

*Lantana camara* is an invasive shrub or scrambling plant introduced from Central and South America. The species invades forest edges, savannas and degraded rangelands, where it forms dense, impenetrable thickets (Henderson 2001). The species reduces biodiversity and threatens a host of rare and endangered species. In Australia, Turner and Downey (2010) identified 275 native plant species and 24 native animal species that were threatened by *L. camara*. In crop production systems in Southeast Asia, lantana has both reduced yields and increased management costs incurred by growers of durian, pineapples, bananas and rubber (Waterhouse 1993). *Lantana camara* is also toxic to livestock, causing pastoral losses that were estimated at Aus$ 7.7 million in Queensland, Australia, in 1985, and which included

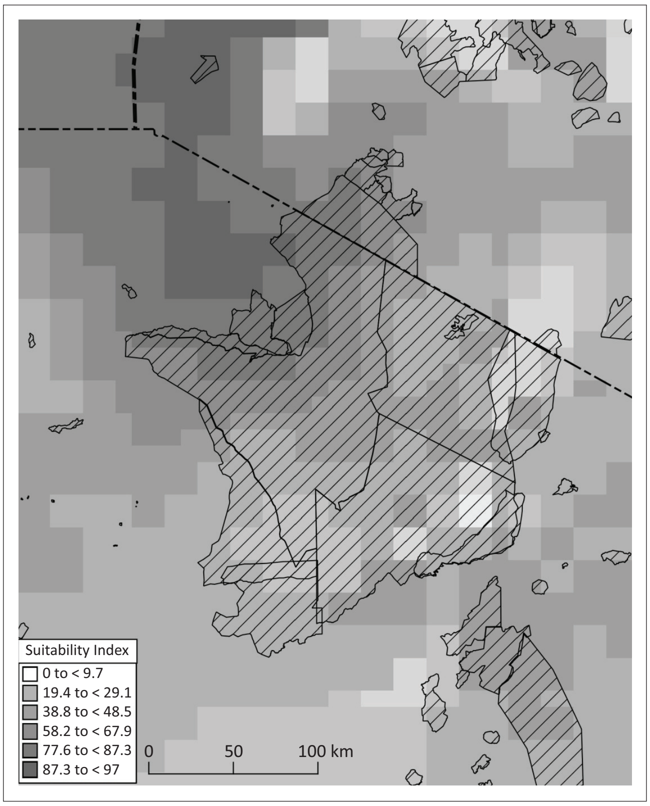



Grid cells are approximately 14 × 14 km. Surveyed cells where the species was not found are shaded light grey, while dark grey indicates presence and black indicates abundant and/or spreading invasions.

**FIGURE 4:** Distribution of six invasive alien plant species, (a) *Chromolaena odorata*, (b) *Lantana camara*, (c) *Opuntia stricta*, (d) *Parthenium hysterophorus*, (e) *Prosopis* species and (f) *Tithonia diversifolia*, in and around the Serengeti-Mara ecosystem, East Africa.

1500 animal deaths, reduced productivity, loss of pasture and higher control costs (Van Oosterhout 2004). In South Africa, lantana poisoning accounts for about 25% of all reported cases of livestock poisoning by plants (Wells & Stirton 1988). There have even been recorded fatalities in people, especially children, after consuming the green fruit (CABI 2016; Sharma 2007). *Lantana camara* can also alter fire regimes, allowing fires to penetrate into forests and woodlands that are normally resistant to fire (Berry, Wevill & Curran 2011; Day et al. 2003).

*Parthenium hysterophorus* is an annual herb native to tropical America, which has become a widespread invader of rangelands and cropping fields in at least 34 countries in Africa, Asia, Australia and the Middle East (Adkins & Shabbir 2014). The species is allelopathic, which enables it to suppress natural vegetation in a wide range of habitats (Aggarwal & Kohli 1992; Evans 1997; McFadyen 1992;




Grey shading depicts the Eco-climatic Indices (suitability of each location); the darker the shading, the more suitable the climate in that area is for *Parthenium hysterophorus* to establish and proliferate.

**FIGURE 5:** CLIMEX generated map of the relative climatic suitability of the Serengeti-Mara ecosystem and surrounding areas for *Parthenium hysterophorus* based on a model developed by McConnachie et al. 2011.

Van der Laan 2006), including native grasses in the Kruger National Park (Van der Laan 2006). The weed was estimated to reduce stocking rates in Queensland, Australia, by 25% for light to medium infestations, and by as much as 80% for heavy infestations (McFadyen 1992) and by as much as 90% in India (Jayachandra 1971). *Parthenium hysterophorus* also causes severe allergenic reactions (dermatitis, hay fever and asthma) in a large proportion of people who come into contact with it, as well as in livestock and wildlife (Patel 2011; Towers & Mitchell 1983). The weed is now considered, by 90% of the farmers in the lowlands of Ethiopia, to be the most serious weed of croplands and grazing areas (Tamado & Milberg 2004).

Shrubs/trees in the genus *Prosopis* were introduced into East Africa in the 1980s, with some species and hybrids having already invaded over 1 million ha in Kenya, where they have the potential to invade nearly half of Kenya's surface area (Maundu et al. 2009; Witt 2010). The species, including *P. juliflora*, were originally introduced to Kenya, and have recently invaded Tanzania. Invasive *Prosopis* spp. are associated with many negative impacts, thereby reducing grazing capacity (Ndhlovu, Milton-Dean & Esler 2011), eliminating many species from invaded ecosystems (Dean et al. 2002; Schachtschneider & February 2013; Shackleton et al. 2015; Steenkamp & Chown 1996) and reducing water resources (Dzikiti et al. 2013). Thus, despite some benefits in the form of fuelwood and edible pods (livestock fodder), their overall net economic contribution is negative, and set to worsen further as the species continues to spread (Wise, Van Wilgen & Le Maitre 2012). In Ethiopia, *P. juliflora* has reduced understorey cover for perennial grasses from 68% to 2%, and has reduced the number of grass species from seven to two (Kebede & Coppock 2015); in South Africa, a relatively light *Prosopis* spp. invasion (15% cover) led to a 34% reduction in the grazing capacity (Ndhlovu et al. 2011). By transforming habitats and eliminating pasture species, *P. juliflora* is threatening the survival of Grévy's zebra (*Equus grevyi*) in invaded areas (Kebede & Coppock 2015). Dense stands reduce access and impede the movement of people and animals, while the thorns frequently cause injury. Local communities in Kenya, Sudan, Eritrea, Malawi, South Africa and Pakistan have all reported negative consequences of these invasions (Brown, Boudjelas & De Poorter 2004; Pasiecznik et al. 2001). In semi-arid parts of Africa, *Prosopis* trees have depleted the natural resources on which many thousands of people depend, spawning conflict between communities over the diminishing resources.

*Chromolaena odorata* is a scrambling shrub introduced from Central America. It is an aggressive invader of savanna ecosystems, where it has the potential to transform the vegetation (Henderson 2001). One mature plant can produce roughly 1 million seeds per year, which enables rapid spread and the establishment of large populations over a relatively short period (Witkowski & Wilson 2001). Its ability to form dense, impenetrable thickets leads to the displacement of native plant species (Te Beest, Esler & Richardson 2015a), while the dry stems and leaves, which are rich in oils, also increase fire intensities (McFadyen 2004), contributing to additional biodiversity loss. In South Africa, infestations are impacting negatively on the breeding biology of the Nile crocodile (Leslie & Spotila 2001), while in Cameroon it is displacing native species in the family Zingiberaceae, a major food source for the endangered western lowland gorilla (Van der Hoeven & Prins 2007). In Southeast Asia, it is a serious weed affecting oil palm, rubber, coffee, cashew, fruit and forestry (Waterhouse 1993). Some agricultural areas in Southeast Asia 'have been abandoned because Siam weed [*i.e. C. odorata*] has taken over pasture and crops' (CRC for Weed Management 2003:1). It also causes serious health problems in livestock and people (Aterrado & Talatala-Sanico 1988; Sajise, Palis & Lales 1972; Soerohaldoko 1971), while significantly reducing the livestock-carrying capacities of pastures.

*Tithonia diversifolia* is an annual or perennial shrub introduced from Central America, which invades savannas and grasslands (Henderson 2001). The species forms dense stands which can displace native plants and the animals associated with them. Its production of numerous small, light seeds, coupled with its ability to spread vegetatively, allows it to invade and to establish readily and rapidly in new locations (Muoghalu & Chuba 2005). In Nigeria, it was shown to reduce species diversity in invaded plots by 25% (Oludare & Muoghalu 2014), displacing native vegetation in wetlands (Borokini 2011), and contributing to the local extinction of valued native species, including some important medicinal plants (Oludare & Muoghalu 2014). It is even reported to be out-competing the formidable invasive shrub *C. odorata* (Olubode, Awodoyin & Ogunyemi 2011). As such it is now considered to be one of the most damaging of all invasive plant species in Nigeria (Borokini 2011). *Tithonia diversifolia* also competes with agricultural crops (Illori et al. 2010) and invasions have reportedly led to the abandonment of some farms in the Copperbelt region of Zambia (A.B.R. Witt pers. observ., 2010).

# Discussion

## Potential impacts on the Serengeti-Mara ecosystem

Many exotic species, that have the potential to become invasive, do not always spread rapidly when first introduced to a new environment, but the rate of spread often increases once the species has naturalised and becomes invasive. Many of the species we recorded have not been found in the Serengeti-Mara area until relatively recently, so we can reasonably expect the rate of spread into currently uninvaded areas to increase in the near future. Although it is sometimes assumed that relatively unmodified ecosystems (such as the protected areas of the Masai-Mara and Serengeti) will be resistant to invasions, there is also evidence to the contrary. For example, the establishment of *C. odorata* can be facilitated in savannas and grasslands by small-scale disturbances that create micro-sites for establishment, ultimately aiding their long-term persistence in grass-dominated areas (Te Beest, Mpandza & Olff 2015b). This is borne out by the fact that *C. odorata* has aggressively invaded savanna vegetation in the Hluhluwe-Imfolozi Park in South Africa (Dumalisile 2009; Howison 2009). It cannot be assumed that these protected ecosystems will remain uninvaded. *Parthenium hysterophorus* is also invasive in many other protected areas in Africa, and we have observed that this species, which is often regarded as only being able to invade disturbed or over-grazed areas, establishes readily on termite mounds that are scattered across the Serengeti-Mara landscape, providing widespread foci from which further invasions can commence.

Although invasive alien plants pose substantial threats to the integrity of the Serengeti-Mara ecosystem, this has not yet been widely recognised. For example, in a recent comprehensive treatment of the ecology and conservation of the Serengeti (Sinclair et al. 2015), invasive alien plants are only mentioned once, where it is stated that:

> although the exact extent of these invasions is not known, these species have taken over grasslands in other ecosystems and could exclude wildebeest from accessing critical areas in the future. (p. 168)

Given that the large numbers of grazing mammals are dependent on good-quality forage, and given further that invasions by the alien plant species currently establishing in the area can reduce carrying capacities by up to 90% (Jayachandra 1971; McFadyen 1992; Ndlovu et al. 2011; Yapi 2014), large impacts can be expected. For example, Ogutu et al. (2009) found that the abundance of six large grazing mammal species declined markedly and persistently throughout the Masai-Mara National Reserve between 1989 and 2003, and that the declines were contemporaneous with progressive habitat deterioration because of a range of factors, although invasion by alien plants was not considered. The Serengeti wildebeest population is regulated by food supply, and the main cause of mortality (75% of cases) was found to be under-nutrition (Mduma, Sinclair & Hilborn 1999). Rampant invasion would almost certainly result in large losses of rangeland fodder, leading to drastic declines in populations of wildebeest and other large grazing mammals. A drastic decline in wildebeest numbers would trigger many changes, as wildebeest are currently remarkably abundant, and influence virtually every dynamic of the ecosystem (Grant et al. 2015). Thus, plant invasion could potentially have big effects not only on ecosystem integrity and productivity but also on tourism, which is a very important contributor to the economies of both Kenya and Tanzania.

## Appropriate management responses

Given that alien plant invasions pose large threats to the Serengeti-Mara ecosystem, it would seem prudent to develop and implement control programmes to reduce the severity of these threats. We propose that three key interventions should be implemented as a matter of urgency. Firstly, all alien plant species, especially those that are known to be naturalised, invasive or potentially invasive, should be removed from the grounds of tourist facilities. Secondly, control programmes aimed at eliminating outlier populations should be implemented to slow spread. Finally, biological control solutions should be implemented wherever possible. We discuss each of these in the following sections.

**Removal of alien plants around tourist facilities:** All alien plants, whether invasive or not, should ideally be removed from the grounds of any developed parts of the protected areas. Tourist and staff facilities can be a major source of invasive species, and this would be best addressed by removing all alien plants while populations are still small. In the Kruger National Park, South Africa, Foxcroft and Freitag-Ronaldson (2007) found that the park staff played a major role in facilitating alien plant invasions. Staff members unwittingly introduced alien species into the gardens of tourist camps as well as into their own gardens, for ornamental and other uses. Many species subsequently escaped and became invasive. Attempts to remove these species began in the mid-1980s, but there was significant resistance from the residents towards the alien plant control team for many years (Foxcroft et al. 2008). This was overcome as an understanding of the problem grew, and strategies employed by the Kruger National Park team included an initial focus on high-risk species (leaving lower-risk species in place in the meantime), and clearing gardens whenever there was staff turnover that resulted in temporary vacating of houses. Similar problems can be expected in the Serengeti-Mara ecosystem. However, there is legislative and other support for invasive species interventions in and outside of protected areas in Africa, and specifically in Kenya, which would provide strong justification for the removal of alien species in the face of resistance (Table 2).

**Implementation of control programmes:** Control programmes should be initiated as soon as possible, with priority being given to lightly invaded areas, isolated populations or the edges of invading populations. Higgins, Richardson and Cowling (2000) demonstrated that clearing strategies that prioritised low-density sites dominated by juvenile alien plants proved to be significantly more cost-effective than strategies that targeted densely invaded areas. These authors also found that delaying the initiation of clearing operations considerably increased the eventual costs of control and the risks to native biodiversity. Such early interventions can be very effective, as shown by the results of clearing of *P. hysterophorus* in the 'Mara Triangle' (Figure 3).

**Implementation of biological control:** We strongly advocate the fullest possible use of biological control, which should be integrated with other control practices, wherever possible. Biological control is a safe, inexpensive and sustainable

**TABLE 2:** Some national, regional and African legislation, policies, conventions and treaties that make reference to invasive alien plants.

| Legislative instruments | Relevant provisions and authorities |
|---|---|
| *The Suppression of Noxious Weeds Act*, Cap 325 (Kenya) | A number of invasive plants including *Eichhornia crassipes*, *Datura stramonium*, *Prosopis juliflora* and *Parthenium hysterophorus* are listed under the Act which empowers an 'inspector' to instruct landowners to remove listed plants, failing which they may be prosecuted (National Council for Law Reporting 2012). |
| *Environmental Management and Coordination Act* of 1999 (Kenya) | Section 51 (e) provides guidelines prohibiting and controlling the introduction of alien species into natural habitats. In fact, an Environmental Impact Assessment (EIA) needs to be undertaken before alien species of flora and fauna can be introduced into ecosystems (National Environment Management Authority 2016). |
| *Forest Act*, 2005 (Kenya) | Section 54 (8) (a) states that any person introducing any exotic genetic material or invasive plants without authority from the Forestry Service commits an offence (Kenya Forest Service 2016). |
| National Strategy and Action Plan for the Management of Invasive Species in Kenyan Protected Areas | Various objectives and actions including awareness creation, prevention, capacity development and control including the 'sensitization of law enforcers to enhance and enforce existing legislations that bar introduction of exotic species into protected areas as per the various acts' (Kanga et al. 2013). |
| *Wildlife Conservation and Management Act*, 2013 (Kenya) | Section 93 states that anyone knowingly introducing an invasive alien species into a wildlife conservation area, or failing to comply with the measures prescribed by the Cabinet Secretary, as set out under the Act, will be committing an offence (Kenya Wildlife Service 2016). |
| African Convention on the Conservation of Nature and Natural Resources (1968) | Requires all parties to prohibit the entry of zoological or biological species, whether indigenous or imported, wild or domesticated, that may cause harm to protected areas (African Union 2016). |
| Protocol concerning Protected Areas and Wild Fauna and Flora in the East African Region (Nairobi, 1985) | Calls for the adoption of appropriate measures to prohibit the intentional or accidental introduction of alien or new species which may cause significant or harmful changes to the sub-region. Calls for contracting parties to take measures to regulate the introduction of non-indigenous animal or plant species into protected areas (Environmental Treaties and Resource Indicators 2016). |

option for gaining control of many invasive alien plant species. The main benefits of biological control are that the agents establish self-perpetuating populations and often establish throughout the range of the target weed, including areas that are not accessible for chemical or mechanical control; control of the weed is permanent; there are no negative impacts on the environment; the cost of biological control programmes is low relative to other approaches, and in most cases only requires a once-off investment; and benefits can be reaped by many stakeholders independent of their financial status and irrespective of whether they contributed to the initial research (Greathead 1995). Studies in South Africa have demonstrated phenomenal returns on investment in economic terms from biological control projects, where estimated benefit:cost ratios ranged from 8:1 up to 3726:1 (Van Wilgen & De Lange 2011). Biological control is arguably an indispensable element of any integrated programme to control invasive alien plants, as most other interventions will fail in the long term if used in isolation. Despite this, concerns over the safety of the practice often prevent its implementation in many countries. Much of the resistance to the use of biological control arises from ignorance, but the track record of the practice suggests that this should not be the case. It was estimated that by the end of 2012, there were 1555 separate and intentional releases of 469 species of weed biological control agents against 175 species of non-native target weeds (when related taxa of unidentified plant species, such as some *Opuntia* species, are counted as single target weeds) (Winston et al. 2014). These so-called 'classical' biological control projects have been conducted in a total of 90 countries (Winston et al. 2014), with an excellent record of safety and success (Van Wilgen, Moran & Hoffmann 2013).

There are already several agents that would be available for use against major weed species that currently threaten the Serengeti-Mara ecosystem. For example, infestations of *O. stricta* have been brought under control in the Kruger National Park, South Africa, by the introduction and establishment of a sap-sucking bug, *Dactylopius opuntiae* (Cockerell) (Dactylopiidae) (Foxcroft & Hoffmann 2000; Hoffmann, Moran & Zeller 1998). This classical biological control agent was recently released on *O. stricta* in Laikipia County, Kenya, where it has established and is reducing the density and spread of this invasive cactus. In Australia, the ability of *P. hysterophorous* to form tall and dense invasive stands has been considerably reduced through the release of multiple biological control agents, thus substantially increasing the effectiveness of other control interventions (Dhileepan & McFadyen 2012). Work on developing suitable biological control for *P. hysterophorus* has been initiated in South Africa, building on the work in Australia (Strathie, McConnachie & Retief 2011), with a number of agents already having been released in the field. A chrysomelid beetle, *Zygogramma bicolorata* Pallister (Chrysomelidae) has also been released in Ethiopia and around Arusha, Tanzania, although establishment in the field is yet to be confirmed. Biological control research in South Africa has also addressed *L. camara* (Urban et al. 2011), with a number of these agents already present in East Africa. However, some newly released and established agents in South Africa could complement those agents already present in Kenya and Tanzania, such as the flowerbud-galling mite *Aceria lantanae* (Cook) (Eriophyidae) and the root-feeding flea beetle *Longitarsus bethae* (Chrysomelidae) (Urban et al. 2011). Attempts have been made to establish the gall-forming fly, *Cecidochares connexa* (Macquart) (Tephritidae), on *C. odorata* in northwestern Tanzania, but we will only be able to confirm establishment at the end of 2017. A number of other agents for the control of *C. odorata* have also been released and have subsequently been established in South Africa (Zachariades et al. 2011b). A number of seed-feeding beetles have been released in South Africa and elsewhere for the control of invasive *Prosopis* species (Zachariades et al. 2011a), and research is currently underway to develop agents that feed on the vegetative parts of this invasive tree. Research has also been initiated in South Africa to develop agents for the control of *T. diversifolia* (Simelane, Mawela & Fourie 2011). It is imperative that the Kenyan and Tanzanian authorities work together to facilitate the introduction, mass rearing and release of additional classical biological control agents to complement any current and future invasive plant management strategies in the Serengeti-Mara ecosystem. Failure to do so would result in the possible demise of one of the natural wonders of the world, the annual wildebeest migration.

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## Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

## Authors' contributions

A.B.R.W. was responsible for initiating the field surveys, which he conducted with the assistance of S.K. T.B. undertook spatial analyses and compiled the maps. The interpretation of results and writing of the article was shared between B.W.v.W. and A.B.R.W.

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