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Distribution of invasive alien *Tithonia* (Asteraceae) species in eastern and southern Africa and the socio-ecological impacts of *T. diversifolia* in Zambia

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Background: Many alien plant species, such as *Tithonia diversifolia*, *T. rotundifolia* and *T. tubaeformis*, have been introduced to areas outside of their natural distribution range to provide benefits, but have subsequently become invasive, threatening biodiversity and agricultural productivity.

Objectives: The aim of this study was to determine the current distribution and dates of introduction of invasive *Tithonia* species in eastern and southern Africa and to document the effects of *T. diversifolia* on rural livelihoods in Zambia.

Method: Roadside surveys, and other sources of information, were used to determine the distribution of invasive *Tithonia* species in eastern and southern Africa. Household interviews were conducted to gauge perceptions and understand the impacts of *T. diversifolia* on local livelihoods in Zambia's Copperbelt province.

Results: *Tithonia diversifolia* is widespread in Uganda, Kenya, Tanzania, South Africa, Malawi and parts of Zambia but less so in Zimbabwe. *Tithonia rotundifolia* was comparatively uncommon in eastern Africa but common in some southern African countries, while *T. tubaeformis* was invasive in Swaziland, South Africa, Zambia and possibly also Zimbabwe. According to the majority of respondents in Zambia, *T. diversifolia* has negative impacts on native vegetation, mobility or access, water availability, crop yields and animal health.

Conclusion: Invasive *Tithonia* species are widespread and spreading throughout much of Africa. Livelihood and biodiversity costs have not been considered by those actively promoting the use and further dissemination of *T. diversifolia*. We therefore recommend that detailed cost–benefit studies should be undertaken to support informed decisions on the future management of these species.

Introduction

Invasive alien species pose significant threats to biodiversity and human well-being, especially where rural communities are dependent on natural resources (Shackleton et al. 2007; Vaz et al. 2017; Vilá et al. 2010). Many invasive species were introduced intentionally as ornamentals, for restoration in degraded landscapes, as agro-forestry species or as crops (Rejmánek & Richardson 2013). Many of these species are beneficial, contributing to rural livelihoods by providing a wide range of products (Kull et al. 2011; Shackleton et al. 2007). Assessing people's perceptions of these invasive species can provide insights into their negative impacts, but also into attitudes and perceptions regarding their management (Mwangi & Swallow 2008; Rai et al. 2012). This information can inform decisions on whether or not to attempt control, especially where the target species has both benefits and costs ('conflict species') (see Novoa et al. 2016; Shackleton, Le Maitre & Richardson 2015; Van Wilgen & Richardson 2014).

Of the 11 species in the genus *Tithonia*, all native to North and Central America (Arias, Martin & Gimenez 1982), three (*T. diversifolia* [Hemsl.] A.Gray [Mexican sunflower]; *T. rotundifolia* [Mill.] S.F.Blake [red sunflower]; and *T. tubaeformis* [Jacq.] Cass [wild Mexican sunflower]) have become invasive in Africa and elsewhere. *Tithonia diversifolia*, a perennial shrub, producing seeds throughout the year, with the capacity to grow clonally, leading to the development of dense stands (Muoghalu & Chuba 2005), is invasive in more than 35 countries (> 20 in Africa, CABI 2017). Invasions are rapid, facilitated by the production of between 80 000 and 160 000 wind-dispersed seeds/m^2 annually (CABI 2017). It was probably intentionally introduced to many countries as an ornamental and hedge plant, but was later promoted for soil improvement, livestock fodder and as a 'green manure' (Jama et al. 2000), which has not only contributed to its spread, but has also led to conflicts regarding its benefits and costs. *Tithonia rotundifolia*, an annual producing fewer seeds, which are heavier and larger than those of *T. diversifolia*, contributing to rapid seedling growth and facilitating establishment in resource-poor environments (Muoghalu & Chuba 2005), has the widest natural range of all *Tithonia* species in Central America (Blake 1921), extending from southern Mexico to Panama, mainly in arid zones below 1000 m (Tovar-Sánchez et al. 2012). However, little is known about the distribution of *T. rotundifolia* outside of its natural range. *Tithonia tubaeformis* occurs naturally in temperate zones 1000 m above sea level (Tovar-Sánchez et al. 2012). It is invasive in southern Africa (Henderson 2007) and Argentina (Larenas-Parada et al. 2004).

Although much has been published about the positive attributes of *T. diversifolia* (Jama et al. 2000), there are very few studies, outside of Nigeria, that address its negative impacts. In addition, there have been no socio-ecological studies on how rural communities perceive and are affected by *Tithonia* species. Here we assessed (1) the current distribution of *T. diversifolia*, *T. rotundifolia* and *T. tubaeformis* in eastern and southern Africa and (2) the effects of *T. diversifolia* on local livelihoods in the Copperbelt province, Zambia.

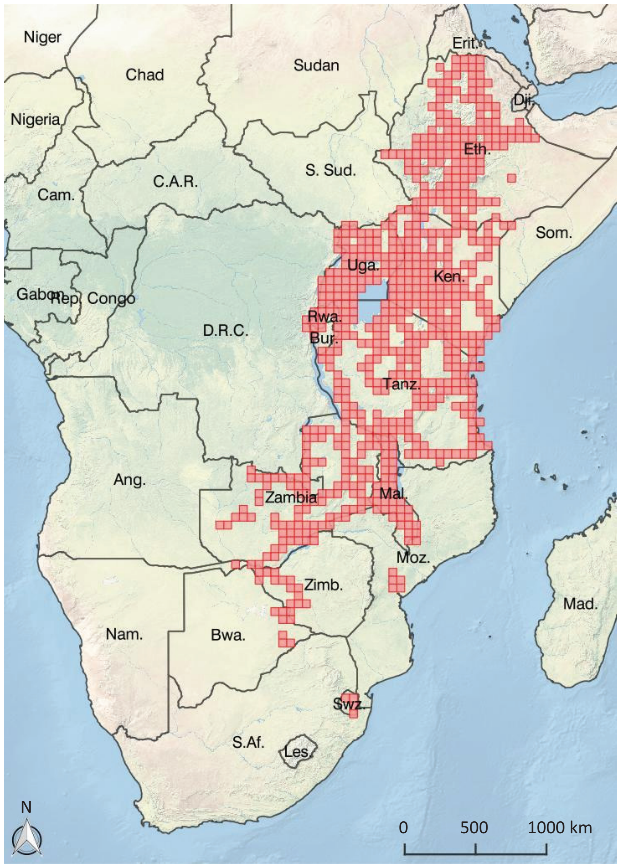
Methods

Study site

Zambia's Copperbelt province was selected as a suitable region to undertake the socio-economic surveys because *T. diversifolia* is abundant, and there were previous reports that farmers had abandoned their lands in Zambia as a result of invasions. The province lies on the eastern Central African Plateau, consisting of gently undulating terrain ranging in elevations from 900 m to 1500 m. The province has a mild climate with an average annual temperature of 20°C and receives approximately 1288 mm of rainfall per year. In 2010, the Copperbelt province had a population of 2 million people, about 15% of the total Zambian population (Central Statistical Office 2012). In that year, the average household size was 5.3 with a literacy rate of 83%, which was higher than the national average of 70% (Central Statistical Office 2012). The majority of people in the province are employed in the mining and energy sectors, with < 20% of the provincial population being small-scale farmers. The total area planted to crops, mainly maize, tobacco, groundnuts and potatoes was ~120 000 ha in 2014 (6.5% of the total area cultivated in Zambia).

History of first introductions and current distribution of invasive *Tithonia* species in eastern and southern Africa

The date of first introduction of *Tithonia* species was estimated from literature surveys, herbarium specimens and personal communication with local botanists. The current presence and status of *T. diversifolia*, *T. rotundifolia* and *T. tubaeformis* invasions was recorded in eastern and southern Africa (Ethiopia, Kenya, Malawi, Rwanda, Swaziland, Tanzania, Uganda and Zambia) in roadside surveys between 2008 and 2017 (Figure 1), using similar methods to those of Henderson (2007), Rejmánek et al. (2016), Shackleton et al. (2017b, 2017c, 2017d), Witt and Luke (2017) and Witt et al. (2017). During this time, we drove considerable distances, covering tens of thousands of kilometres (Figure 1). The location of *Tithonia* species was recorded using a handheld GPS device and categorised as present, naturalised or invasive (as defined by Pyšek et al. 2004). 'Present' indicated individuals being grown as ornamentals, but not spreading; 'naturalised' denoted self-perpetuating populations; and 'invasive' denoted widespread occurrence within a defined area or local abundance with small, but very dense stands. Additional information on distribution was obtained from the *Southern African Plant Invaders Atlas* (Henderson 1998); the websites *Flora of Mozambique* (2017), *Flora of Zambia* (2017) and *Flora of Zimbabwe* (2017); herbarium records from Botswana, Kenya, Mozambique, Uganda and Zimbabwe; personal observations by national and local botanists; and the general literature (Rejmánek et al. 2016). The large-scale distribution of the three *Tithonia* species was then mapped at the resolution of half degree grid cells (~55 km × 55 km) (Figure 2), providing a large-scale approximation of the presence of *Tithonia* species across the region.



S.Af., South Africa; Les, Lesotho; Swz, Swaziland; Bwa., Botswana; Mad., Madagascar; Nam., Namibia; Zimb., Zimbabwe; Moz., Mozambique; Mal., Malawi; Ang., Angola; Rwa., Rwanda; Bur., Burundi; Cam., Cameroon; Tanz., Tanzania; Uga., Uganda; Ken., Kenya; Eth., Ethiopia; Som., Somalia; S.Sud., South Sudan; Erit., Eritrea; D.R.C., Democratic Republic of Congo; C.A.R., Central Africa Republic; km, kilometres.

FIGURE 1: Map showing in red (~55 km × 55 km/half degree grid cells) the areas surveyed between 2008 and 2017 for *Tithonia* species in eastern and southern Africa. Areas surveyed by others in southern Africa are not included.

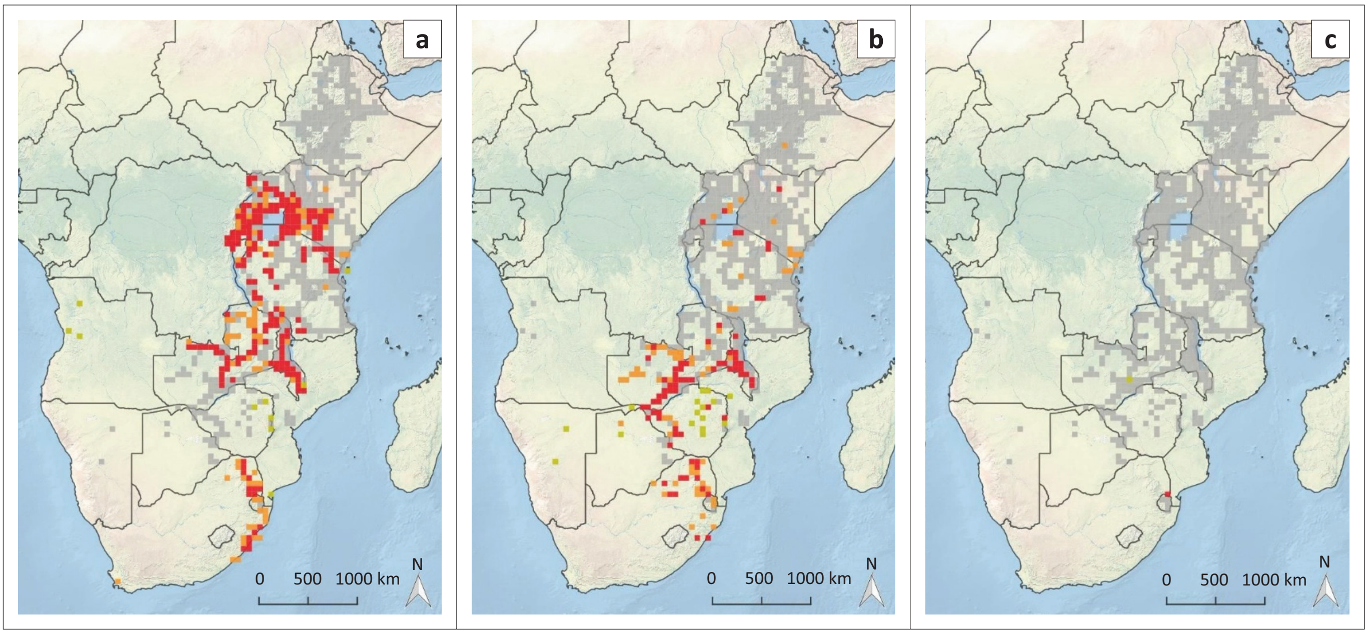
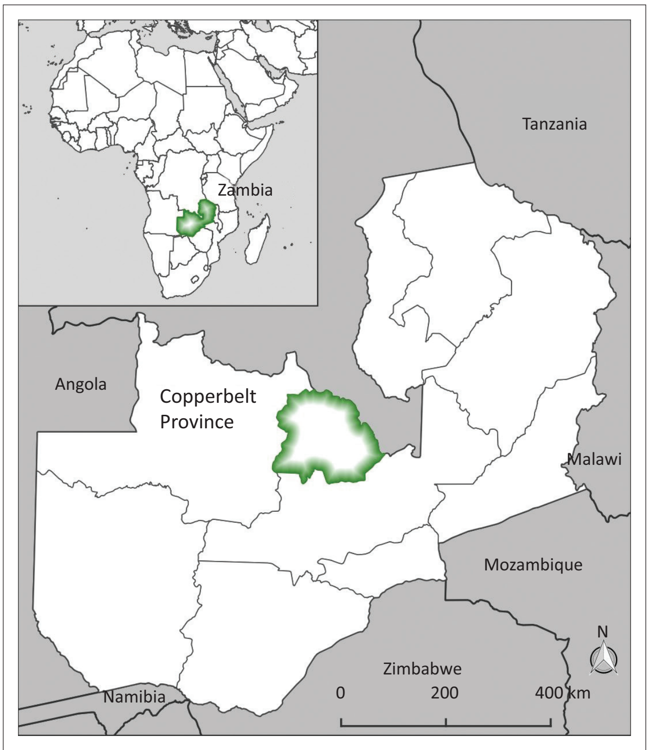


FIGURE 2: Maps showing the current known distribution of *Tithonia diversifolia* (a); *T. rotundifolia* (b); and *T. tubaeformis* (c) in eastern and southern Africa (55 km × 55 km/half degree grid cells) using data collected in this study and other sources of information. Grey grid cells show areas surveyed; red grid cells indicate areas where the *Tithonia* species were found to be invasive (widespread and/or abundant); orange cells where they were present and/or naturalised; and yellow cells where they were recorded with no other information.



km, kilometres.

FIGURE 3: Map showing the location of Zambia in Africa (inset) and the Copperbelt province in Zambia where the socio-economic surveys were undertaken.

Livelihoods survey

The socio-economic effects and perceptions of *T. diversifolia* invasions were assessed by interviewing 166 individuals, in their own language, at randomly selected households using semi-structured questionnaires, in villages and towns in Copperbelt province, Zambia, where *T. diversifolia* occurs (Figure 3). *Tithonia diversifolia* was selected as a case study because it is the most widespread and abundant *Tithonia* species in Africa, is widely promoted as a green manure and as such is considered to be a 'conflict' species. Questionnaires are increasingly used to provide quantitative data on the perceptions and effects of invasive alien species on society (see Mwangi & Swallow 2008; Shackleton et al. 2015, 2017b, 2017c, 2017d).

The questionnaires collected information on (1) the demographic characteristics of the respondent, (2) his or her knowledge and perceptions of the introduction and spread of *T. diversifolia*, (3) his or her perceptions and knowledge of the benefits and negative impacts of *T. diversifolia* and (4) local practices, wants and needs pertaining to the management of *T. diversifolia*.

Results

History of first introductions and current distribution of *Tithonia* species in eastern and southern Africa

The first known record of *T. diversifolia* in eastern Africa is from a herbarium specimen collected in Uganda in 1917. In southern Africa *T. diversifolia* was first recorded in South Africa in 1927 (L. Henderson [ARC-PPRI], pers. comm., 14 March 2017). The first herbarium specimens in Zimbabwe were collected in 1944 (C. Chapano [National Herbarium of Zimbabwe], pers. comm., 24 March 2017), with three specimens collected in Mozambique in 1967, 1974 and 1979 (T. Chiconela [Edoardo Mondlane University], pers. comm., 28 March 2017). *Tithonia diversifolia* and *T. rotundifolia* were already present in disturbed areas in Malawi, Mozambique, Zambia and Zimbabwe in the 1960s (Wild 1968). In West Africa, *T. diversifolia* was thought to have been brought into Nigeria, from Israel, as a maize contaminant in the 1970s

(Lordbanjou 1991; Olubode, Awodoyin & Ogunyemi 2011). Other than Nigeria it has also been recorded as being invasive in Cameroon, Chad and the Central African Republic (CABI 2017).

Tithonia diversifolia has spread rapidly since its introduction into eastern and southern Africa, and it is now widespread in Kenya, Rwanda, Tanzania and Uganda, with significant invasions in Malawi, South Africa (Henderson 2007) and parts of Zambia (Figure 2). Although recorded in Angola (Rejmánek et al. 2016), Mozambique and Zimbabwe (Flora of Zimbabwe 2017; M. Hyde pers. comm., 16 March 2017) the full extent of these invasions is unknown (Figure 2). In areas surveyed in Ethiopia, *T. diversifolia* was rare (Tadesse 2004), and there are no records from either Namibia (C. Mannheimer [Consultant Botanist], pers. comm., 20 March 2017) or Botswana (K. Keotshepile [Peter Smith University of Botswana University], pers. comm., 22 March 2017).

Tithonia rotundifolia has been present in South Africa since at least 1946 (L. Henderson [ARC-PPRI], pers. comm., 14 March 2017), with the first herbarium specimen collected in Zimbabwe, near Bulawayo, in 1944 (Bolnick 1995). It was first seen in Zambia in the 1950s (Bolnick 1995; Duvigneaud 1958), with the first record for eastern Africa from Zanzibar in 1949 (Williams 1949). *Tithonia rotundifolia* is also regarded as being invasive in Nigeria (Otusanya & Ilori 2014). In southern Africa *T. rotundifolia* is now widespread in Malawi, Zambia and Zimbabwe (Flora of Zimbabwe 2017; M. Hyde pers. comm., 16 March 2017) and increasing rapidly in South Africa (Henderson 2007) (Figure 1). It has not been recorded in Angola (Rejmánek et al. 2016) or Rwanda; is rare in Botswana (K. Keotshepile [Peter Smith University of Botswana Herbarium], pers. comm., 22 March 2017), Mozambique (T. Chiconela [Edoardo Montlane University], pers. comm., 28 March 2017) and Namibia (C. Mannheimer [Consultant Botanist], pers. comm., 20 March 2017); and uncommon in Kenya, Swaziland, Tanzania and Uganda (with one record for Ethiopia).

There are no formal records of *T. tubaeformis* in Africa, but it is known to occur in Zambia (G. Howard [IUCN], pers. comm., 16 March 2016), with unconfirmed records from Zimbabwe and Mozambique (M. Hyde pers. comm., 16 March 2017; D. Simelane [ARC-PPRI], pers. comm., 19 March 2017). It is localised, but abundant where it occurs in Swaziland (D. Simelane [ARC-PPRI], pers. comm., 19 March 2017) and South Africa (L. Henderson [ARC-PPRI], pers. comm., 14 March 2017). It was not recorded in any of the remaining countries surveyed. The absence of records may be because of recent introduction or misidentifications. According to Tovar-Sánchez et al. (2012) *T. rotundifolia* and *T. tubaeformis* readily hybridise in Mexico, and hybrids have been found in Argentina, where both species have been introduced (Larenas-Parada et al. 2004).

Socio-demographic characteristics of the surveyed households

We reached both men and women in our surveys (63% and 37%, respectively). The mean (± standard deviation [SD]) age of respondents was 53 ± 14 years. Almost all (99%) were involved in farming with the exception of only two respondents (1%). Most respondents had some level of schooling, with 48% having only primary schooling and 37% having secondary schooling. Some had either no schooling (6%) or a tertiary education (9%). Household size averaged (± SD) 6 ± 3 people.

Most respondents (77%) owned livestock. In total 57% of households had goats, with a mean (± SD) of 7 ± 12 goats per household. Cattle were the next most commonly owned livestock species, and 44% of households owned a mean (± SD) of 5 ± 14 cattle per household. Only 7% of households owned sheep, with a mean (± SD) of 1 ± 5 sheep per household. Most (79%) households grazed their livestock within 5 km of their homesteads, with the remainder grazing them up to 20 km away. A scarcity of grazing (43%) followed by insufficient water (22%), disease (19%) and weeds (4%) were the biggest issues that livestock owners faced.

Almost all households (99%) also grew crops. The majority of households grew maize (41%) followed by ground nuts (14%) and cassava (11%), with beans, vegetables and sweet potatoes being grown by between 5% and 10% of households. Bananas, sorghum, soybeans, millet, sunflowers and tomatoes were grown by fewer than 5% of households. Most households (51%) had 1 ha to 1.6 ha of land, while 18% owned more than 2 ha and 21% had 1 ha or less.

Local knowledge on *Tithonia diversifolia* introduction and presence in Zambia

Over half of respondents (55%) did not know when *T. diversifolia* arrived in their area. Of those who did have an idea, 24% thought that *T. diversifolia* arrived before 2008 and 19% thought it had arrived later. Two-thirds (67%) of respondents said that *T. diversifolia* was currently present in rangelands where they grazed their livestock. The majority of respondents (79%) did not know the reason for introduction, but some believed it to have been introduced as an ornamental (hedge) plant, for medicinal purposes and as livestock feed (5% for each of these purposes, respectively). Most respondents were unsure about how it spreads (58%). Of those who did have an idea about its spread, 30% said it spreads naturally (wind and water), 7% said that people were responsible for moving it around and 4% said that it was spread by livestock. The parts of the landscape that were prone to invasion (as highlighted by respondents in order of importance) were croplands, areas around homesteads, along roadsides, on hills and rangelands, and near rivers and dams. Most respondents (49%) said that there was minimal cover of *T. diversifolia* (< 25%) in rangelands, with 31% saying there was almost no cover. Eighteen per cent of respondents said that *T. diversifolia* covered between 25% and 50% of the rangelands where they grazed their livestock. The majority of respondents (80%) viewed *T. diversifolia* to be increasing in abundance in their area.

Benefits and costs of *Tithonia diversifolia* invasions

Respondents identified a variety of benefits and costs associated with *T. diversifolia* invasions (Table 1). On average, most respondents (62%) could not say whether a particular aspect was positively or negatively affected, or unaffected, by *T. diversifolia*, but for the 38% who did express an opinion, there were more who considered that the net outcome was negative (29%) than positive (9%). In general, the costs were mentioned more frequently and by a higher proportion of respondents (Table 1). Key negative aspects raised by respondents included impacts on grass and tree cover, mobility or access, water availability, crop yield and animal health (Table 2). To a lesser extent *T. diversifolia* was also said to reduce the abundance of medicinal and other valuable plant species. More than 40% of respondents said that *T. diversifolia* was the most problematic weed in croplands (followed by several other alien species; Table 2). Of the respondents who mentioned impacts on crop yields, 23% said that it can reduce crop yields by 75%, and around 10% mentioned losses of 25% – 50% if not managed in fields. *Tithonia diversifolia* was also considered the most problematic weed in pastures, followed by *Argemone mexicana* L. (Papaveraceae), *Datura stramonium* L. (Solanaceae), and *Lantana camara* L. (Verbenaceae) (Table 3). Most of the problematic weed species identified by respondents in rangelands and croplands are invasive alien species as opposed to native weed species (Table 3).

Over a quarter (29%) of respondents had seen goats eating *T. diversifolia*, followed by cattle and sheep, with 45% saying that it had no negative impacts on the health of goats whereas only 25% felt this was not the case for cattle. A third of respondents (34%) said that if animals eat too much *T. diversifolia* they get sick, with less than 5% of respondents mentioning that livestock deaths can be attributed to consumption of *T. diversifolia*.

Numerous benefits arising from *T. diversifolia* invasion were also identified by respondents (Table 1). A number of respondents thought that *T. diversifolia* increased grass (23%) and tree (21%) abundance. Some respondents (15%) felt that *T. diversifolia* presence in croplands increased crop yields (15%). Other benefits mentioned included use as a medicinal plant (33%) to treat abscesses, snakebite and dysentery. Furthermore, *T. diversifolia* was sometimes seen as a beneficial ornamental or hedge plant, as livestock feed and as green manure (Table 1).

TABLE 1: The percentage of respondents (n = 166) who regarded the effect of *Tithonia diversifolia* on a particular issue as either positive or negative, or who had no opinion on the issue, in the Copperbelt province, Zambia.

Issue	Percentage who regarded the effect as a benefit (%)	Percentage who regarded the effect as a cost (%)	Percentage who thought it had no effect, or who did not know (%)
Movement and access	-	65	35
Grass cover	23	63	14
Water availability	-	38	62
Crop yield	15	38	47
Livestock health	-	29	71
Tree cover	21	27	52
Shrub cover	67	15	19
NTFP availability	-	7	93
Wildlife abundance	-	1	99
Medicinal plant	33	-	67
Hedge (ornamental)	18	-	82
Livestock feed	10	-	90
'Green manure'	8	-	92

NTFP, non-timber forest products.

TABLE 2: Percentage of respondents (n = 166) who selected a particular weed species as having the largest negative impact on either rangelands or crops in the Copperbelt province, Zambia.

Species	Family	Rangelands (%)	Croplands (%)
Ageratum conyzoides	Asteraceae	-	10.0
Bidens pilosa	Asteraceae	4.2	6.2
Tithonia diversifolia	Asteraceae	23.0	41.0
Tithonia rotundifolia	Asteraceae	3.6	-
Hyptis suaveolens	Lamiaceae	-	3.9
Argemone spp.	Papaveraceae	21.0	4.9
Cyperus rotundus	Poaceae	3.1	6.2
Cynodon dactylon	Poaceae	2.4	6.2
Pennisetum purpureum	Poaceae	2.1	-
Axonopus compressus	Poaceae	2.1	4.9
Datura stramonium	Solanaceae	19.0	10.0
Lantana camara	Verbenaceae	15.0	6.2

Management of *Tithonia diversifolia* by local communities

Despite divergent views on the benefits and costs of *T. diversifolia*, the majority of respondents actively managed *T. diversifolia* to reduce its impacts. In pasturelands, 89% of the respondents attempted to control *T. diversifolia* primarily though slashing (Table 4). The majority of respondents (79%) also removed it from their croplands to reduce its potential negative impacts on crops (Table 4). Most (61%) respondents spent 1 day per year clearing *T. diversifolia*, while 18% reported spending around 5 days per year on this activity. Of those who actively cleared *T. diversifolia*, 58% paid for help at a cost of $12 – $24 per ha. Of those respondents using

TABLE 3: The percentage of respondents (n = 166) who used particular management practices to control *Tithonia diversifolia* in rangelands and croplands in the Copperbelt Region, Zambia.

Management practice	Rangelands (%)	Croplands (%)
Slashing or cutting	45	43
Ploughing	23	1
Nothing	11	21
Chemical control	11	10
Burning	10	0
Hoeing	0	12
Hand pulling	0	13

TABLE 4: The percentage of respondents (n = 166) who regarded the effect of control measures against *Tithonia diversifolia* on a particular issue as either bringing about improvements or reductions in their well-being, or who had no opinion on the issue, in the Copperbelt Region, Zambia.

Issue	Improve well-being (%)	Reduce well-being (%)	Not much difference to well-being (%)
Grazing lands	19	3	78
Livestock health	18	3	79
Crop yield	41	7	52
General well-being	14	2	84

herbicides, 34% spent \$10 – \$50 per year and 16% paid more than \$50. Many of those interviewed (35%) said that crop losses would be higher if *T. diversifolia* was not controlled.

Most respondents (84%) thought that management of *T. diversifolia* would not make much difference to their livelihoods at current rates of invasion (Table 4). However, 41% said that control would benefit crop yields. Very few mentioned that increased control of *T. diversifolia* would have a negative effect on their livelihoods, suggesting that the overall benefits of the plant are low.

Discussion

History of introductions and current distribution of *Tithonia* in Africa

Tithonia diversifolia has been present in eastern (Uganda) and southern Africa (South Africa) for over 100 and 90 years, respectively. It has subsequently been recorded in all southern Africa countries with the exception of Lesotho, Botswana and Namibia (Figure 2). In eastern Africa, *T. diversifolia* is widespread and abundant in countries around Lake Victoria but apparently rare in Ethiopia (Tadesse 2004).

In South Africa, *T. diversifolia* invades temperate subtropical areas, while in eastern Africa it invades the tropical savannas (Peel, Finlayson & McMahon 2007). Although no bioclimatic models are available for *T. diversifolia*, it almost certainly has the potential to spread further. According to Rejmánek et al. (2016) it appears to be spreading rapidly in Angola where it was recorded in 7 of 14 vegetation types surveyed. *Tithonia diversifolia* has expanded its broad distribution in South Africa by almost 40% between 2000 and 2016 (from 49 to 68 quarter-degree grid cells; Henderson & Wilson 2017). That said, *T. diversifolia* is probably unlikely to invade large areas in arid and semi-arid countries such as Botswana and Namibia, and low temperatures may inhibit invasions in Lesotho.

Tithonia rotundifolia is not nearly as widespread and abundant as *T. diversifolia* in eastern Africa, northern Zambia and Malawi. The former has not been recorded in Angola (Rejmánek et al. 2016), although it is present in Botswana and Namibia. The low invasion levels by *T. rotundifolia* in eastern Africa could be because it was first introduced to the region 30 years later than *T. diversifolia* (the longer a plant species is present, the larger the propagule bank and the greater the probability of dispersal and establishment; Rejmánek et al. 2005). *Tithonia rotundifolia* may therefore still increase in range in both eastern and southern Africa. It has, for example, expanded from 19 to 47 quarter-degree grid cells between 2000 and 2016 in South Africa (Henderson & Wilson 2017), a more rapid rate of expansion than *T. diversifolia*.

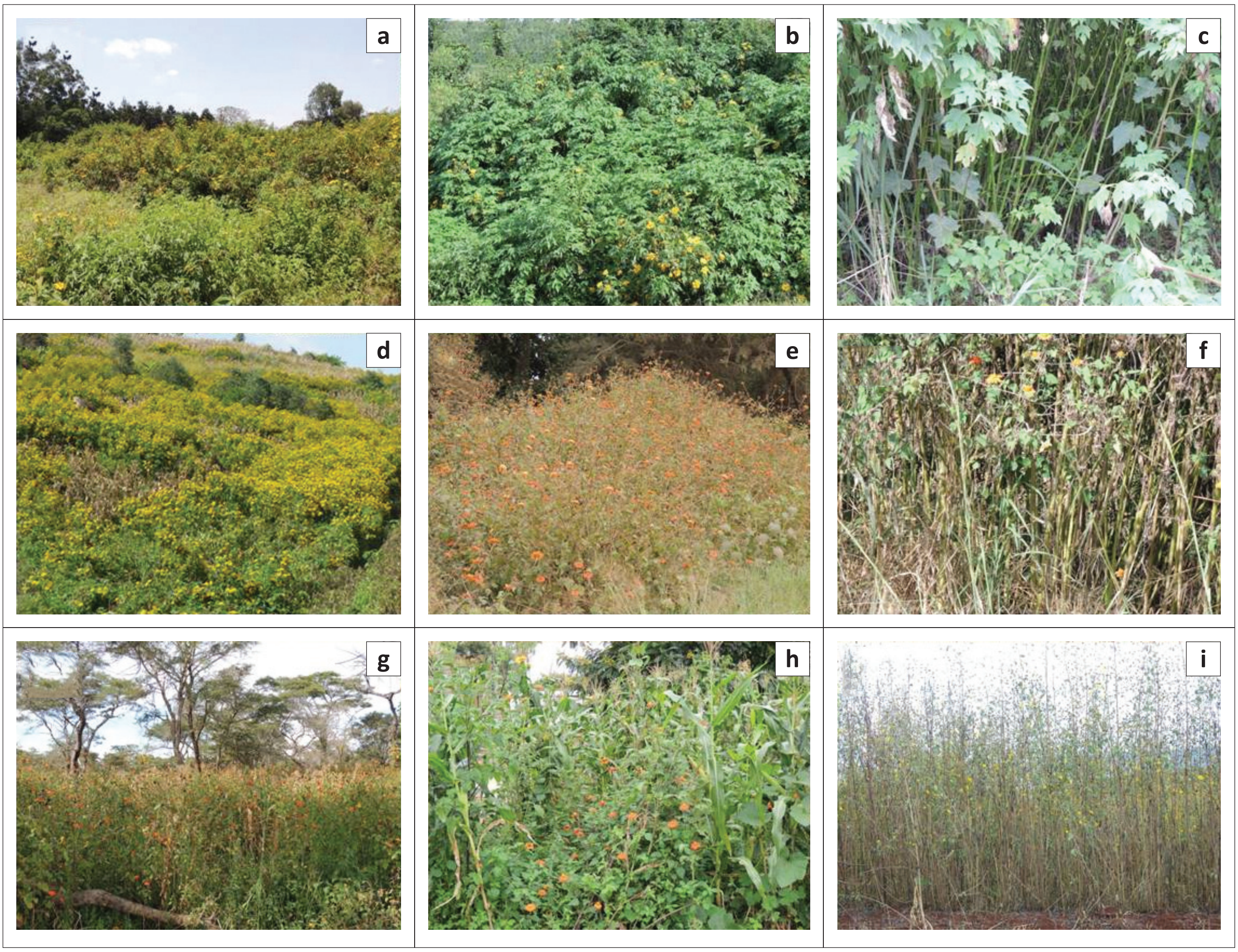
Besides propagule pressure, the characteristics of invaded ecosystems, recipient communities and invading species are important factors to consider (Catford, Jansson & Nilsson 2009). For example, *T. diversifolia* rarely co-occurs with *T. rotundifolia* in southern Africa. *Tithonia rotundifolia* is most invasive in parts of South Africa that have a climatic classification of temperate – dry winter, warm summer (Peel et al. 2007) and where *T. diversifolia* is largely absent. Areas where *T. rotundifolia* is common often experience cold winters, with frequent frost. Soil nutrient levels may also influence distribution patterns. For example, *T. rotundifolia* produces heavier and larger seeds than *T. diversifolia* and is better adapted to nutrient poor soils (Muoghalu & Chuba 2005), which may explain its dominance in large parts of Zambia, Malawi and Zimbabwe that are nutrient poor (Malmer 2007). We therefore postulate that *T. rotundifolia* could become established more widely in semi-arid countries such as Botswana and Namibia.

It is still too early to predict the potential distribution of *T. tubaeformis*, but its presence in South Africa, Zambia and Zimbabwe is an indication that it is adapted to local conditions and has the potential to expand its range. Hybridisation between this species and *T. rotundifolia* (which happens in South America; Tovar-Sánchez et al. 2012) may also influence future spread.

Negative impacts of *Tithonia diversifolia*

Tithonia diversifolia has some benefits in Zambia, although the costs outweighed the benefits for the majority of those interviewed. In particular, costs associated with movement, access and reduced grass cover were regarded as high, with additional negative impacts on water availability, crop yields, livestock health and tree cover (Tables 1 and 4). Many invasive plants form dense monospecific stands, inhibiting access to water resources or grazing lands (Mwangi & Swallow 2008; Shackleton et al. 2017b, 2017c, 2017d). Dense stands of *T. diversifolia* are also known to reduce species richness (Borokini 2011; Sun, Chen & Wang 2007), contributing to the local extinction of valued native species, including medicinal plants (Oludare & Muoghalu 2014). In Nigeria, *T. diversifolia* invasions have reduced plant diversity at one site by 25.4%, from 59 to 44 species; impacts that are considerably higher than those recorded for the highly aggressive invasive plant *Chromolaena odorata* (Agboola & Muoghalu 2015), which *T. diversifolia* can displace (Olubode, Awodoyin & Ogunyemi 2011; A. Witt [CABI] pers. obs., 24 February, 2016). The invasions in Nigeria reduced the mean number of flowers, fruits, seeds per fruit and mean weight of seeds and stunted the growth of some native plant species (Agboola & Muoghalu 2015). The impacts of *T. diversifolia* invasions on biodiversity and human well-being could therefore be worse than those recorded for *C. odorata* (Shackleton et al. 2017c; Van der Hoeven & Prins 2007).

Tithonia diversifolia invades and competes with agricultural crops and reduces yields (Ilori et al. 2010, Figure 4), as highlighted by respondents in this study (Tables 1 and 4). This is in agreement with Akobundu (1987) and Imeokpara and Okusanya (1994), who found *T. diversifolia* to be one of the most 'underestimated' problems in Nigerian agriculture, especially in rice and maize fields. According to Chukwuka, Ogunyemi and Fawole (2007), most farmers in invaded areas



Source: Photos courtesy of a–c and e–h (A.B.R.W.); d (G. Howard); and i (D. Simelane)

FIGURE 4: (a and b) *Tithonia diversifolia* invasions in Kenya, (c) *T. diversifolia* undergrowth in Zomba, Malawi, (d) *T. diversifolia* invasion in maize field in Malawi, (e) *T. rotundifolia* invasion in Zambia, (f) *T. rotundifolia* undergrowth in Zambia, (g and h) *T. rotundifolia* invasions in maize fields in Zambia and (i) *T. tubaeformis* invasion in Swaziland.

in Nigeria have abandoned their farmlands because of invasions by *T. diversifolia*. Because *T. diversifolia* is a prolific seeder, it can rapidly colonise crop fields and increase labour costs (Jama et al. 2000). In western Kenya, landholders cut back Mexican sunflower hedges to reduce competition with crops in neighbouring fields (Jama et al. 2000).

The ability of *T. diversifolia* to displace other plant species can also be attributed to allelopathy. It contains allelochemicals (Miranda et al. 2015; Otusanya & Ilori 2012), which may inhibit germination and growth of some plant species (Otusanya, Ilori & Adelusi 2007), posing phytotoxic threats to agricultural crops (Ilori, Otusanya & Adelusi 2007; Otusanya et al. 2007; Otusanya & Ilori 2012; Otusanya, Ogunwole & Tijani 2015; Tongma, Kobayashi & Usui 1997). The yields of selected crops have also been significantly inhibited by *T. rotundifolia* extracts (Otusanya & Ilori 2014), but *Tithonia* species may also have stimulatory attributes (Oyerinde, Otusanya & Akpor 2009). For example, aqueous leaf extracts of *T. diversifolia* did not affect the germination of maize seeds, and the extracts enhanced shoot height, fresh weight, dry weight and leaf area in older plants (Oyerinde et al. 2009).

Many respondents in this survey were also unsure about the relative benefits and costs of *T. diversifolia* (Table 1). This is quite different to the findings of other socio-economic surveys, where the costs were significantly higher than the benefits for most issues and respondents were more certain of different impacts. For example, *C. odorata* in Tanzania (Shackleton et al. 2017c), *L. camara* in Uganda (Shackleton et al. 2017b) and *Opuntia stricta* in Kenya (Shackleton et al. 2017d) all had very few or no benefits and high livelihood costs.

Benefits of *Tithonia diversifolia*

Respondents identified medicinal properties as benefits of *T. diversifolia*, which is used to treat abscesses, hepatitis, infections, snakebites, amoebic dysentery and diabetes (Jama et al. 2000; Passoni et al. 2013). *Tithonia diversifolia* is also widely used by traditional healers in its native range in Mexico (Heinrich et al. 1998). Most of the pharmacological action in *T. diversifolia* is because of the presence of sesquiterpene lactones (STLs) and some chlorogenic acid derivatives (CAs) in the leaves of

T. diversifolia (Passoni et al. 2013). Although short-term use may be beneficial, prolonged ingestion of STLs and CAs can be toxic (Passoni et al. 2013).

Some respondents also said that they used *T. diversifolia* as a hedge plant, as seen elsewhere (Nginja et al. 1998). The use of *T. diversifolia* for fuelwood (Nginja et al. 1998), compost (Nginja et al. 1998), soil erosion control (Nginja et al. 1998), building materials (Otuma et al. 1998), shelter for poultry (Otuma et al. 1998) and for pest and weed control (Adoyo, Mukalama & Enyola 1997; Akanbi & Ojeniyi 2007; Baruah et al. 1994; Dutta, Chaudhuri & Sharma 1993; Tongma, Kobayashi & Usui 1997) was not confirmed by any respondents in our study.

Some respondents also mentioned that *T. diversifolia* is occasionally used as livestock feed and as a green manure (Table 1), as noted elsewhere (Anette 1996; Farinu et al. 1999; Odunsi, Farinu & Akinola 1996; Olayeni et al. 2006; Roothaert & Patterson 1997; Roothaert, Arimi & Kamau 1997). *Tithonia diversifolia* is widely promoted throughout Africa as a green manure, as its leaves have high concentrations of nitrogen, phosphorous and potassium, and they decompose rapidly in the soil (Palm, Myers & Nandwa 1997). Its use has been reported to improve soil fertility in Kenya (Jama et al. 2000), Malawi (Ganunga, Yerokun & Kumwenda 1998), Nigeria (Ayeni, Lordbanjou & Majek 1997), Rwanda (Drechsel & Reck 1998) and Zimbabwe (Jiri & Waddington 1998). The application of 1.5 tonnes of leaves per hectare increased maize yields by between 39% and 162% when compared to unfertilised fields (Ganunga et al. 1998) and in some instances resulted in higher crop yields than when inorganic fertilisers were used (Jama et al. 2000).

The practicality of using *T. diversifolia* as a green manure to increase crop yields (as opposed to chemical fertilisers) over large areas is seldom considered. In many cases, the effort required may well outweigh the benefits gained, or alternative approaches may be less costly. A lack of awareness of the merits of using leaves to improve soil fertility, as well as labour and transport costs, may explain this (Jama et al. 2000).

Kendall and Van Houten (1997) recommend applications of 5 tonnes of *T. diversifolia* leafy dry matter per hectare. According to Kendall and Van Houten it takes one person about 4 min to collect 1 kg of fresh *T. diversifolia* biomass, which means that collecting 5 tonnes would take about 42 days based on an 8-hour working day. Assuming labour costs of ~ $2.69/day (the minimum wage for unskilled workers in Kenya; *Kenya Gazette Supplement No 107* 2017), costs for harvesting 1 tonne to 5 tonnes could range from approximately $22 to $113 (not including transport, and labour costs associated with chopping the leaves into small sections and working them into the soil). Undertaking this activity may be further constrained because *T. diversifolia* is sticky and exudes a pungent smell (Jiri & Waddington 1998).

Harvesting and transport costs could be reduced by growing *T. diversifolia* as a hedge around croplands, but this would reduce available land for crop production. Farm boundaries are also used for crops and trees of higher value than *T. diversifolia*, but these are now being replaced in parts of Kenya (Jama et al. 2000). According to Jama et al. (2000) small landholdings cannot produce sufficient biomass to meet the nutrient requirements for crop production. This is supported by Palm et al. (1997), who also found that organic materials cannot reverse soil fertility declines because they are usually not available in sufficient quantities, are often low in nutrients and their processing and application are labour-intensive (Palm et al. 1997).

We are therefore of the opinion that it would be cheaper, in most cases, to apply inorganic fertilisers, considering that commercial fertilisers were available from the Kenyan government, in 2014, at costs ranging from $15 to $20 for 50 kg of fertiliser (PSCU 2014). As farmers' income levels rise, fertilisers may become a more attractive option.

Options for the control of *Tithonia* species

The majority of respondents were of the opinion that the costs of *T. diversifolia* outweigh any benefits, which suggests that the species should be managed (Tables 1 and 4). Management will have almost no negative impacts on livelihoods and could have substantial social and environmental benefits (Table 4). There has been very little effort, outside of South Africa, to control *T. diversifolia*, because of limited information about its negative impacts, or because active promotion avoids information about negative impacts (Sanchez 1999). For example, we identified many more publications on the benefits of *T. diversifolia* in Africa (Adoyo et al. 1997; Anette 1996; Jiri & Waddington 1998; Nginja et al. 1998; Otuma et al. 1998; Roothaert & Patterson 1997; Tongma, Kobayashi & Usui 1997, 1998) than on negative impacts (Agboola & Muoghalu 2015; Oludare & Muoghalu 2014). However, based on people's responses in Zambia, *T. diversifolia* does have negative impacts (Table 1) and is considered to be the weed with the biggest negative impacts by most respondents in the region (Table 4). As *Tithonia* species spread and densify, management costs will increase steeply, leading to the possible abandonment of productive cropland when the cost of control becomes prohibitive.

Widespread and abundant invasive alien plants are best controlled by integrated management strategies (Kaplan et al. 2017; Shackleton et al. 2017a; Van Wilgen et al. 2011), which involve a combination of manual, chemical and biological control best suited for the prevailing conditions, followed by restoration. Of these, biological control is arguably the most cost-effective and sustainable option. Research in South Africa has led to the identification of the tortoise beetle, *Physonota maculiventris* (Coleoptera: Chrysomelidae), which is sufficiently host-specific to be released for the control of *T. diversifolia* (D.O. Simelane [ARC-PPRI], pers. comm., 13 April 2017). Should the beetle be released in South Africa, it could spread to the rest of Africa, with implications for the use of *T. diversifolia*.

Unlike *T. diversifolia*, *T. rotundifolia* is not regarded as a 'conflict species'. As such the release of the damaging and host-specific biocontrol agents *Zygogramma signatipennis* Stål and *Z. piceicollis* Stål (Chrysomelidae: Chrysomelinae) in South Africa should be supported throughout the continent (Simelane, Mawela & Fourie 2011). Assuming that the negative impacts of *T. rotundifolia* are similar to those of *T. diversifolia*, the establishment of these agents should contribute to biodiversity conservation and improve crop yields. *Tithonia tubaeformis* is not considered as a target for biological control at this stage (D.O. Simelane [ARC-PPRI], pers. comm., 13 April 2017).

Control through utilisation is sometimes proposed as a means of inhibiting the spread of *T. diversifolia*, but is unlikely to have any impact as a management strategy and is problematic for a number of reasons (Nuñez et al. 2012; Van Wilgen et al. 2011). Widespread utilisation of problematic invasive alien species could create dependency on a resource that is targeted for reduction to very low levels. Utilisation may only be economically feasible in certain areas but not in remote or inaccessible sites or in cases where there are small scattered populations at the invasion front that should receive priority as targets for clearing. Finally, utilisation projects can, and often have, generated unintended consequences, including spreading of the target invasive species by people who want to benefit from utilisation projects where the species does not yet occur (Nuñez et al. 2012).

The need for economic studies

The use of *T. diversifolia* biomass as a green manure has contributed to increased crop yields, but overcoming food insecurity by introducing species that have negative impacts will not contribute to human welfare in the long term (Witt 2017). Individuals may benefit from the presence of *T. diversifolia*, while livelihood options for others may be considerably reduced. This anomaly can only be resolved by 'developing holistic solutions that consider the potential implications of all interventions, in all sectors, and in subsequent years' (Witt 2017). An analysis of whether the benefits from the use of *T. diversifolia* outweigh the costs would be needed to inform a decision on the most appropriate management approach. This has been done for *Acacia mearnsii* De Wild. (Fabaceae) in South Africa, where it is an important commercial tree but also an aggressive invader (De Wit, Crookes & Van Wilgen 2001). The results of the analysis indicated that a 'do nothing' scenario (with no attempts made to control spread) is not sustainable and that the most attractive option would be to combine physical clearing with biological control. A similar cost–benefit study on *Prosopis* in South Africa (Wise et al. 2012) has been useful for policy development. The net value of introduced alien plant species is typically not considered when introductions are made, and the decision to promote a particular species for its putative benefits, without considering the costs, has led to many problematic outcomes in the past. When the holistic picture is considered, it often becomes apparent that the harm done by invasive species exceeds any benefits and that a focus on aggressive control would deliver the best outcomes (De Wit et al. 2001; Nordblum et al. 2001; Wise et al. 2012).

Conclusion

Surveys have revealed that *Tithonia diversifolia, T. rotundifolia and T. tubaeformis* are already well established in many parts of Africa and have the potential to significantly increase their distribution, exacerbating biodiversity loss. Further promotion of these species, especially *T. diversifolia*, by various development agencies, should be discouraged as the costs of invasions to livelihoods will rapidly outweigh any benefits that accrue from their use, considering their potential for further spread and densification.

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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. conducted the surveys and contributed to writing up the article. R.T.S. conducted the socio-economic analyses and contributed to writing up the article. T.B. was responsible for map development. W.N. conducted the surveys and was responsible for data entry. B.W.v.W. contributed to writing up the article.

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