Assessing the invasive status of *Cryptostegia grandiflora* and *C. madagascariensis* in southern Africa and predicting potential risk areas

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ABSTRACT

Biological invasions are a major threat to global biodiversity. The complexity and high cost associated with management of invasions emphasizes the need for a strategic approach that can predict and prioritise potential invasive species. Risk assessments are commonly used tools that evaluate a species potential to become invasive. While risk assessments can be based on a variety of species characteristics, accurate estimates of a species contemporary distribution and the species potential future range, provide key information to prioritise management decisions. Understanding the factors driving the distribution of invasive species at different spatial scales can provide insight into the full range of environmental variables that influence its distribution. At broad-scales climate variables are expected to be the dominant factors determining where a species occurs and at finer scales, biotic interactions, disturbance, soil type and microclimatic conditions are predicted to become more important. In consequence, coarser scales are usually more suitable for directing management strategies (i.e. where to focus monitoring or control efforts), while finer scales are better to examine environmental features that influence distribution patterns within a single habitat.

In this study, a multi-scale approached was used to assess the risk and predict the potential distribution of two *Cryptostegia* species identified as emerging invaders in southern Africa. Occurrence surveys were conducted across Botswana, Namibia and South Africa to determine the current extent and invasive status of *Cryptostegia grandiflora* and *Cryptostegia madagascariensis*. The potential broad-scale distribution of both species was predicted using species distribution models. By incorporating climate data and the current global distribution of both species habitat suitability maps were created using maximum entropy (MaxEnt; Chapter 2). At local scale, an invasive *C. grandiflora* population occurring along the Mogalakwena River in northern South Africa was used to determine the variables influencing fine-scale spatial variation in occurrence and cover (Chapter 3).

Occurrence surveys confirmed both species are present in southern Africa. *Cryptostegia grandiflora* is widespread occurring as cultivated, naturalised and invasive populations in many semi-arid regions of southern Africa. In contrast, few *C. madagascariensis* occurrences were observed and none found outside of cultivation. Habitat suitability maps predicted large areas beyond current distribution highly suitable for both species. The mean temperature during the coldest quarter is the key restricting factor and predicted areas with temperatures below 15 °C to be unsuitable. The results from fine-scale surveys revealed that the drivers influencing *C. grandiflora* occurrence differed from those most strongly correlated with the cover of the species. Erosion and bare soil had weaker influences on *C. grandiflora* cover than on species occurrence, suggesting that this species can occur in moist disturbed areas but possibly achieves optimal growth under conditions of high leaf litter, low non-woody plant cover and deep soils with high moisture to initially establish.

Given the widespread distribution, existing invasive populations and large uninvaded suitable range, *C. grandiflora* is a high risk species with the potential to severely impact riparian areas in semi-arid regions of southern Africa. *Cryptostegia grandiflora*'s current extent, high seed production and large dispersal range excludes eradication as a feasible management option. Monitoring and control efforts should instead focus on high priority areas already invaded or likely to be within the suitable ranges. In particular riparian areas in or adjacent to economically and ecological valuable areas (i.e. protected areas), should be targeted to prevent spread. In contrast, *C. madagascariensis*'s limited cultivated occurrences and restricted suitable range shows this species is not high risk and is not an imminent threat to southern Africa and is an ideal candidate for eradication.

CHAPTER 1

1.1. General introduction

Biological invasions are a major driver of global environmental change, impacting ecosystem services and decreasing native biodiversity (Pimentel et al., 2005; Simberloff et al., 2013; McGeoch et al., 2016). The on-going growth in the human population, rising global trade, and the increasing volume of travel and transport are promoting the distribution of species beyond their native ranges (Colautti and MacIsaac, 2004; Hulme et al., 2009; Wilson et al., 2009; Seebens et al., 2015). As a result, alien species are introduced into novel geographic regions through various pathways; intentional introductions for agricultural, forestry or horticulture (Faulkner et al., 2015) or accidental introductions as, for example, stowaways in transport (McCulloughet al., 2006; Hulme et al., 2009; Faulkner et al., 2015). Preventing the introduction of alien species, particularly when unintentional, can be difficult (Leung et al., 2002; Hulme et al., 2009). As a result, monitoring introduction pathways and mapping the potential distribution of alien species is essential in assessing species invasion risk and prioritising management actions accordingly (Kumschick et al. 2012; Latombe et al., 2016).

Identifying which species have the potential to successfully establish in given areas is crucial for prioritising management actions (Renteria et al., 2017). However not all introduced species are equally invasive (Vitousek et al., 1997; Mack et al., 2000; Pimentel et al., 2005; Randall et al., 2009; Larkin, 2012), and only an estimated fraction of a percent of all plant species that are introduced outside their native ranges by humans become invasive (Williamson and Fitter 1996). The invasive potential of a species (i.e. the species "invasiveness", *sensu* Richardson and Pyšek, 2006) is influenced by several factors. Species that successfully establish outside of their native range often share similar traits, broadly including long-distance seed dispersal, high seed production and fast growth rates (Pyšek et al., 1993; Rejmánek, 1996; Rejmánek and Richardson, 1996; Keller and Drake, 2009; Dukes and Mooney, 1999; Lockwood et al., 2005; Chytrý et al., 2008; Ibáñez et al., 2014). For example, vines with their climbing habit, fast growth rates and reliance on other plants to access resources (including moisture, light and nutrients) contribute to their successful establishment (Harris et al., 2007; Delgado et al., 2016).

Similar to differences in species invasive potential, habitats also vary considerably in their level of invasion (Chytrý et al., 2008), and certain habitats are more susceptible to invasion (i.e. an area's "invasibility", *sensu* Richardson and Pyšek, 2006). Habitats associated with frequent disturbance (e.g. human activity, flooding, erosion, and overgrazing) and high resource availability are particularly vulnerable to the establishment of invasives (Mack and D'Antonio, 1998; Davis et al., 2000; Richardson et al., 2000). Riparian areas are examples of habitats where the extent of invasion is especially apparent compared to other ecosystems (Stohlgren et al., 2002; Catford et al., 2012). Indeed, high nutrient and water availability typically associated with riparian areas are conducive to the successful establishment of native and invasive species (Catford and Jansson, 2014; Catford and Kyle, 2016). Moreover, flooding and human activities in riparian areas, cause levels of resource availability to fluctuate (Richardson et al., 2007) and create gaps in plant cover, providing opportunities for invasive species to establish (Bronette and Amoros, 1996; Davies et al., 2000). Additionally, riparian areas may act as dispersal corridors for invasive species that are already established in a region, enhancing species dispersal distance and probability of invasive plants establishing new populations (Tickner et al., 2001; Renofalt et al., 2005; Maskell et al., 2006; Miller and Matlack, 2010; Davis, 2011).

Understanding the mechanisms and conditions that facilitate plant invasions is a key step in the management of invasive species and the associated decision-making processes (Richardson and Pyšek, 2006; Nentwig, 2010; Wilson et al., 2007). Therefore, being able to accurately predict the risk of species becoming invasive and identify areas that are potentially vulnerable to invasion is valuable for invasive species management (Hulme, 2009; Van Kleunen et al., 2009). However, the factors that drive invasion patterns may different across spatial scales (Pearson and Dawson, 2003; Guisan and Thuiller, 2005). At broad spatial scales, climate (i.e. precipitation and temperature) is often the chief factor determining which areas will be suitable for a species, whereas at finer spatial resolutions other abiotic factors (i.e. soil type, soil moisture and disturbance) and biotic interactions (i.e. competition) are likely to be more influential (Pearson and Dawson, 2003; Swenson et al., 2007; Gomez et al., 2010). As a result, determining appropriate control approaches depends on the spatial extent of the invasion and the scale at which management will be implemented (Wiens, 1986; Stohlgren et al., 1998). Data from coarser scales are usually more appropriate for directing management strategies (i.e. where to focus monitoring or control efforts), while data from finer scales are better to examine environmental features that influence distribution patterns within a single habitat (Foxcroft et al., 2009).

Predicting a species' broad-scale contemporary distribution and potential future range provides key information to prioritise management decisions (Davidson et al., 2017). Indeed, the management of an invasive species may fail if its potential range is poorly estimated, with monitoring and/or control efforts being wasted in unsuitable habitats (Moore et al., 2011). Accurate delimitation of the distribution of a species is therefore a crucial component of assessing a species invasion risk and determining the feasibility of possible management strategies (i.e. eradication, containment or control; Kaplan et al., 2012). Predicting a species' potential distribution (i.e. comparing the species observed vs. possible range; Byers et al., 2002; Elith and Leathwick, 2009) has many applications for managing invasive species (Ferrier, 2002; Graham et al., 2008). For example, anticipating probabilities of introduction and predicting potential changes in the geographic distribution of invasive species can aid monitoring efforts by reducing the extent of survey ranges and prioritise areas to target (Peterson and Vieglais, 2001; Václavík and Meentemeyer, 2009; Gallien et al., 2010; Gormley et al., 2011; Barve, et al., 2011; Booth et al., 2014).

A number of statistical models can be used to predict the spatial distribution of invasive species (Peterson et al., 2003; Thuiller et al., 2005). Species distribution models (SDMs) are tools which make use of a species' occurrence data (i.e. presence data) and a selection of environmental predictor variables (e.g. climate) to estimate the potential distributions of the species (Byers et al., 2002; Guisan and Thuiller, 2005; Elith and Leathwick, 2009). One of these species distribution modelling methods that has been successfully applied to invasive plant management is the Maximum Entropy (MaxEnt) approach (Phillips et al., 2006). MaxEnt is a machine learning method that compares occurrences to environmental variables to generate predictions of suitable habitat in unsampled regions (Phillips et al., 2006). The advantage of MaxEnt for predicting the potential distribution of invasive species is, that it uses presence-only data (Phillips et al., 2006; Phillips and Dudík, 2008; Pearson et al., 2007). Compared to other SDMs, MaxEnt has good predictive performance and accuracy, particularly when dealing with sparse occurrence data that is often the case with invasive species during early stages of invasion (Elith et al., 2006; Phillips et al., 2006; Dudík et al., 2007; Pearson et al., 2007).

In contrast to broad-scale distribution modelling, quantifying the influence that environmental variables have on species local distributions requires detailed information at a fine spatial resolution (Guisan and Thuiller, 2005; Carboni, 2011). While such data are often not as widely available as, for example, coarse-scale remotely sensed data (Peterson et al., 2003) or interpolated climate data (WorldClim; Hijmans et al., 2005), fine-scale SDMs can more readily identify the direct (i.e. proximal *sensu* Austin 2002) drivers of species occurrence patterns (Thuiller et al., 2004). Moreover, changes in habitat conditions can occur over short distances, especially in heterogeneous environments (Carboni, 2011; le Roux et al., 2013). Thus, fine-scale data is needed to give insight into how biotic and abiotic interactions (e.g. light availability, soils moisture and competition) change across environmental space and how it influences the distribution of alien species (Wisz et al., 2012; Descombes et al., 2016).

Information collected at multiple spatial scales from the local (i.e. single habitat) to regional (i.e. country) can help analyse and predict the potential risk a species poses to an area (Rouget and Richardson, 2003; Richardson et al., 2004). These predictions or risk assessments are used by researchers, managers and policy makers to formulate effective management strategies (Pheloung et al., 1999; Kriticos et al., 2003). In addition to predicting the distribution of a species, risk assessments evaluate introduction pathways, introduction history, species traits, habitat invasibility and impacts in existing invaded ranges, to facilitate monitoring and prevention activities (Kulhanek et al., 2011; Faulkner et al., 2015).

Risk assessments are often use to optimize limited control and monitoring efforts. In South Africa the *Conservation of Agricultural Resources Act (1983)* (CARA) and the *National Environmental Management: Biodiversity Act (July 2016)* (NEM:BA; Table. 1) categorise alien plant species according to the potential risk they pose. Each category dictates the management action of the species (Kaplan et al., 2014). The South African National Biodiversity Institute launched a programme on incursion response in 2008 in accordance with draft regulations in NEM:BA to monitor and report on invasive species in South Africa. The role of the incursion response programme is to co-ordinate surveillance, rapid response and monitoring of emerging invasive plant species in order to assess the potential risk and prevent negative impacts on ecosystems and biodiversity (Wilson et al., 2013). This has been done through the listing of existing invasive and potential invaders, placing restrictions on how such species can be used, and landowners' responsibility to control populations (Kaplan et al., 2014).

Table 1: Summary of the invasive species categories according to the ecological and economic threats they pose as listed under the *National Environmental Management: Biodiversity Act (*2014 as revised 2016*)* (NEM:BA).

National Environmental Management: Biodiversity Act (July 2016)	
Category 1a	Invasive species which must be combatted and eradicated. Any form of trade or planting is strictly prohibited. This has been taken to mean that the goal of management is nation-wide eradication (Wilson et al., 2013).
Category 1b	Invasive species which must be controlled and where possible, removed and destroyed. Any form of trade or planting is strictly prohibited.
Category 2	Invasive species or species deemed to be potentially invasive, in which a permit is required to carry out a restricted activity. Category 2 species include commercially import species.
Category 3	Invasive species which may remain in prescribed areas or provinces. Further planting, propagation or trade is however prohibited.

1.2. *Cryptostegia* species

Cryptostegia (Apocynaceae) is perennial climbing shrub native to Madagascar that has naturalised in many tropical and sub-tropical regions of the world (Mahorasy and Forster, 1991; Klackenberg, 2001; Palmer and Vogler, 2012). The genus consists of two species namely *Cryptostegia grandiflora* Roxb. ex R. Br and *C. madagascariensis* Decne. Both species have been identified as potential emerging invaders in southern Africa. The two species are currently listed as 1b by NEM:BA. However, before this study, only a few occurrence records were available for either species in southern Africa. Their successful establishment in other climatically similar regions of the world (McFadyen and Harvey, 1990; Kriticos et al., 2003) highlights the potential risk these species pose to southern Africa and the need to determine their current and potential distribution.

C*ryptostegia grandiflora* and *C. madagascariensis* have been introduced across many tropical and subtropical regions of the world. The majority of reported introductions are for horticultural purposes (Kriticos et al., 2003; Starr et al., 2003); however, in some areas the species were introduced as a potential source of vegetable rubber (Vishwanath et al., 1943; Polhamus et al., 1934 as seen in Klackenberg, 2001). In areas where C*ryptostegia* species have invaded, the ecological and economic impacts are severe. *Cryptostegia grandiflora* has become invasive in many regions worldwide (Harvey, 1987; Chippendale, 1991; Kriticos et al., 2003), and in Ethiopia, for example, has impacted local livelihoods by invading and replacing the native vegetation along rivers in the Afar region (Luizza et al., 2016). One of the areas worst affected by this species is northern Queensland (Australia), where *C. grandiflora* has invaded over 700 000 ha, with additional smaller populations in the southwest of the state (Kriticos et al., 2003; Palmer and Vogler, 2012). Indeed, in tropical Australia, *C. grandiflora* has been described as the single biggest threat to natural ecosystems (McFadyen and Harvey, 1990; Humphries et al., 1991; Tomley, 1995; Fensham, 1996). The destruction of habitats by *C. grandiflora* invasions is an important threat to native and endemic animals, with this species invasion reportedly leading to the loss of a number of rare bird species (Humphries et al., 1991). Furthermore, large mono-specific stands may directly decrease pasture carrying capacity and invasions along water courses obstruct access to water for stock (Chippendale, 1991; Tomley and Evans, 2004). The costs of managing invasions of *C. grandiflora* to the northern Queensland beef industry have been estimated at US$15 million per annum (Anon, 2001). Although toxic and generally unpalatable, during dry seasons significant stock losses have also been reported in Australia due to poisoning of animals that have fed on the plants (which contain cardiac glycosides: Cook et al., 1990; Parsons and Cuthbertson, 1992). Indeed, within its native range Malagasy people are cautious of *C. grandiflora* and discourage handling plant trimmings, as they apparently cause eye, ear and nose irritation (White, 1923; Oakes and Butcher, 1962). The presence of glycosides with toxic effects on cardiac systems in *C. grandiflora* (Mackey, 1996) can cause heart malfunction, stomach and intestinal disorders in humans and animals (Cook et al., 1990; Parsons and Cuthbertson, 1992). Interestingly, *C. grandiflora* possesses many biochemical properties and has been investigated for its anti-inflammatory (Castro et al., 2014), antioxidant (Abdelsalam and Bagdadi, 2009; Mukherjee et al., 1999) and antibacterial properties (Doskotch et al., 1972; Singh et al., 2011).

The other species in the genus, *C. madagascariensis*, also occurs in tropical and subtropical regions of the world. Based on the occurrence data available from *C. madagascariensis*' invaded ranges, introductions are not as frequent and/or well documented as for *C.*

grandiflora (Klackenberg, 2001). Invasive populations have been recorded in Brazil, Montserrat and Hawaii (Starr et al., 2005; Staples et al., 2006; da Silva et al., 2008). In the semi-arid regions of Ceara State, Brazil, *C. madagascariensis* invasions cover large areas, impacting native vegetation.

Due to their similar morphological characteristics it can be difficult to distinguish between the two *Cryptostegia* species, as seen in Hawaii and Brazil where plants were initially identified as C. *grandiflora*, but upon further inspection revealed to be *C. madagascariensis* (Staples et al., 2006; da Silva et al., 2008). However, identifications can be reliably made when flowers and/or seed pods are present on plants (Table 2; Fig. 1).

Table 2: Summary of the distinguishing features of *Cryptostegia grandiflora* and *C. madagascariensis* (Mahorasy and Forster, 1991; Klackenberg, 2001; Palmer and Vogler, 2012).

	C. grandiflora	*C. madagascariensis*
	Flowers	
Length	48 - 70 mm	42 - 64 mm
Width	15 - 30 mm	14 - 26 mm
Colour	Pale lilac (nearly white)	Deep purple
	Leaves	
Length	60 - 90 mm	20 - 110 mm
Width	30 - 50 mm	15 - 55 mm
Petioles	Purple	Yellow green
	Seed pods	
Length	80 - 130 mm	50 - 70 mm

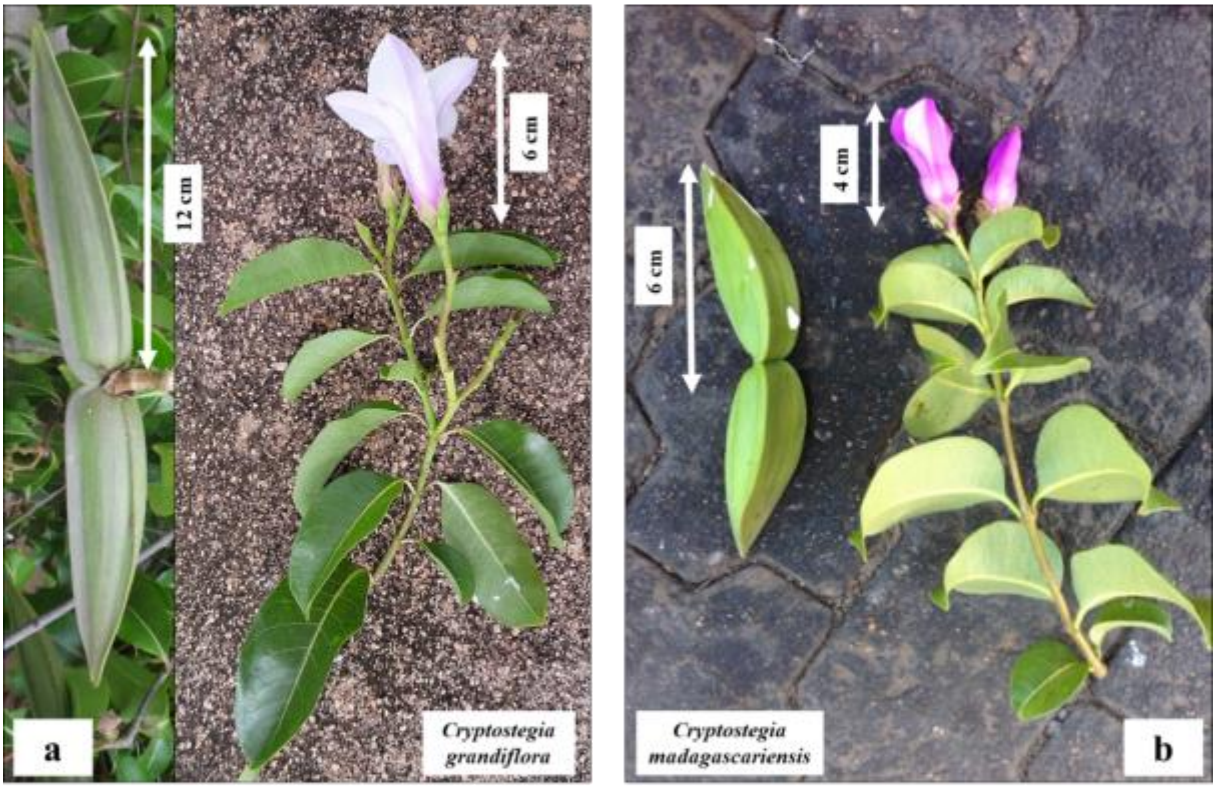

Figure 1: The pods and flowers of a) *Cryptostegia grandiflora* from an invasive population along the Mogalakwena River in South Africa and; b) cultivated *C. madagascariensis* from Lethlakane in Botswana.

Several factors appear to contribute to *Cryptostegia* species' successful establishment outside of their native ranges. A large *C. grandiflora* individual can produce more than 8000 wind- or water-dispersed seeds in a single reproductive episode (Tomley, 1995; Bebawi and Campbell, 2002) and can set seed at least twice per year (Grice, 1996; Brown et al., 1998). The species can flower opportunistically with rainfall, producing more pods and flowering more often in wetter years (Grice, 1996). Both species grow on a wide variety of soil types, including saline soils, and across savannah, riparian and coastal habitats with rainfall between 400 and 1400 mm per year (Palmer and Vogler, 2012). *Cryptostegia grandiflora* has two growth habits, one as free-standing shrubs where water is scarce, while in areas in close proximity to water sources (i.e. along riparian areas) plants forms whip-like vines which allow the species to climb and smother other plants (ARMCANZ 2001; Head et al., 2015). This contributes to *Cryptostegia* species' success as they are able to adapt their growth form to available resources. For example, in the absence of supporting structure (i.e. vegetation or human-made structures), *Cryptostegia* can still continue to grow and spread.

1.3. Dissertation structure

This dissertation aims to assess the potential risk posed by *C. grandiflora* and *C. madagascariensis* by determining the drivers of the species distributions, and to suggest possible management options. The first research chapter (Chapter 2) uses occurrence data from surveys (conducted in Botswana, Namibia and South Africa), global occurrence records from online resources (GBIF and CABI) and published literature – along with climate data – to predict areas suitable for, and at risk of, invasion by the two *Cryptostegia* species. Chapter 3 focuses on a finer spatial scale, examining the abiotic and biotic factors that influence the fine-scale variation in the density and distribution of *C. grandiflora* along an invaded river. The final chapter (Chapter 4) synthesizes results from the two research chapters, integrating the results from the fine-scale and broad-scale analyses to assess the invasive status of *C. grandiflora* and *C. madagascariensis* in southern Africa, and to suggest possible management options to assist prioritising management actions.

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CHAPTER 2

Predicting the potential distribution and invasion risk of *Cryptostegia grandiflora* and *Cryptostegia madagascariensis* in southern Africa

2.1. Introduction

Invasive species are a serious and growing threat that is causing severe ecological and economic damage around the world (Hobbs and Humphries 1995; Mack et al., 2000; Pimentel et al., 2005). Indeed, biological invasions have been identified as one of the biggest contributors to biodiversity loss (Simberloff, 2005; Pyšek et al., 2012), through altering ecosystem functionality, structure and composition (D'Antonio and Vitousek 1992). South Africa is one of the countries worst affected by invasive species (Richardson and van Wilgen, 2004). Given the complexity associated with the management of invasive species once established, the most cost-effective approach is often to try to prevent introductions into uninvaded areas (Leung et al., 2002; Wittenberg, 2005; Simberloff et al., 2005). However, despite stricter prevention efforts, the increasing movement of goods and people around the globe has led to new introductions of species outside of their native ranges (Davies and Sheley, 2007). The detection of newly invaded habitats is difficult at a local scale and even more challenging over larger areas (Wilson et al., 2013). As a result, a key challenge for managers and policy makers is predicting possible future invaders and prioritizing areas susceptible to invasion for monitoring (Wittenberg and Cock, 2005).

Effective management of new biological invasions requires a proactive approach that can rapidly detect invasive species and anticipate areas at risk of future invasion, facilitating efficient monitoring and control (Václavík and Meentemeyer 2009; Robinson et al., 2010; Gallien et al., 2012). Indeed, the most efficient time to manage introduced invasive species is during the early stages of invasion (Gormley et al., 2011; Jiménez-Valverde et al., 2011; Booth et al., 2014), although this can be difficult as often little is known about a species at the earliest stages of invasion (Moody and Mack 1988; Mack et al., 2000; Davies and Sheley, 2007). Therefore, assessment techniques that can objectively rank alien species by invasion risk without onerous data requirements are needed to prioritize alien species management resources (Leung and Delaney, 2006).

Species distribution models (SMDs) have been successfully applied to proactive invasive species risk assessment (Phillips et al., 2006; Dudík et al., 2007). SDMs are correlative models that use available environmental and species occurrence data to predict where a species is likely to occur based on the environmental conditions where it is currently present (Guisan and Thuiller, 2005; Elith and Leathwick, 2009; Jiménez-Valverde et al., 2011). SDMs have many applications for conservation (see e.g. Anderson et al., 2002; Raxworthy et al., 2003; Guisan and Thuiller, 2005) and their predictions are increasingly being used to manage rare or endangered species and to predict species' responses to climate change and habitat transformation (Elith and Burgman, 2002: Elith and Leathwick, 2009).

SDMs have also been successfully utilised in invasive species management for assessing the risk of invasion by alien species and identifying areas vulnerable to invasion (Mooney and Hobbs 2000; Hoffman et al. 2008; Jarnevich and Reynolds 2011). As a result, these models have aided the development of management strategies by providing insight into the spatial variation in suitability of habitats and identifying potential invasion risk across areas of interest (Beaumont et al., 2009; Dukes, 2010). Therefore, the ability of SDMs to predict the potential range of invasive species in novel geographic regions, especially when few occurrence data are available from the species' native or invaded ranges, has important implications for improving the accuracy of risk assessment and guiding management strategies (Funk and Richardson, 2002; Guisan and Thuiller, 2005; Miller et al., 2010). Furthermore, these models can help to identify factors that promote invasion and prioritize sites for monitoring and control efforts (Hobbs and Humphries 1995; Pyšek and Richardson 2010).

Despite recent progress in the application of SDMs to forecasting species distributions (Hattab et al., 2017), predicting invasive species ranges can be challenging as these models make assumptions that are not necessarily true for all species (both indigenous and alien species distributions; Gallien et al., 2012; Guisan and Thuiller, 2005; Welk 2004; Wilson et al., 2007). First, SDMs assume that species are in equilibrium with the environment, having dispersed to all areas with suitable conditions (Gallien et al., 2012; Václavík and Meentemeyer, 2009). However, most invasive species may still be spreading and are therefore not in equilibrium with the environment, particularly during their early stages of invasion when insufficient time has passed to allow colonisation of all suitable areas (Rouget and Richardson, 2003; Crooks, 2005; Guisan and Thullier, 2005; Broennimann and Guisan, 2008; Peterson et al., 2008; Jimenez et al., 2011). A second assumption of SDMs is that sampling effort is equally distributed over the across the entire area modelled (Welk, 2004; Soberon and Peterson 2005; Elith et al., 2006). However, occurrence data for modelled species, especially invasives, may often be particularly sparse, and generally consists of presence-only records that are irregularly sampled and spatially biased towards more accessible areas (Phillips et al., 2008; Welk 2004; Soberon and Peterson 2005; Elith et al., 2006). Additionally, presence-only data can limit the performance of some SDMs (Fielding and Bell 1997; Welk 2004; Hernandez et al., 2006; Phillips et al., 2006), and models based on occurrence data solely from a species' native range may not accurately define that species potential invasive range (Wisz et al., 2008). This may occur when the native range of an invasive species is restricted by barriers (geographic or biotic exclusion) that limit its ability to express its full range of environmental tolerances (Welk 2004). As a result, models created from occurrence data from both the native and invasive ranges can produce a more complete picture of an invading species' potential distribution (Mau-Crimmins et al., 2006; Gallien et al., 2012; Mainali 2014). Finally, alien species might experience evolutionary niche shifts (or niche expansion) or biotic release during invasions (Broennimann et al., 2007; Rödder and Lötters, 2009; Petitpierre et al., 2012). Both of these processes alter the relationships observed between species occurrence and environmental conditions within the native range and, as a result, may degrade predictions for the species distribution within its invaded range (Broennimann et al., 2007; Merow et al., 2017).

Notwithstanding these challenges, SDMs are still useful tools to examine the risk of invasive species establishment and forecast future distributions (Thuiller et al., 2005; Franklin, 2010; Guisan et al., 2013). Predicting the current and potential distribution of alien species is essential for biological invasion management (Rejmánek, 2000; Guisan and Thuiller, 2005). For instance, potential distribution predictions from SDMs can assist in identifying uninvaded priority areas where monitoring to detect occurrences can be implemented and invaded areas where containment, eradication and control efforts should be focussed (Leung et al., 2002; Lodge et al., 2006; Robinson et al., 2010; McGeoch et al., 2016).

One of the commonly used approaches that has been applied successfully to model the distribution of invasive species is maximum entropy modelling (MaxEnt; Phillips et al., 2006; Phillips and Dudík, 2008). MaxEnt is a machine learning algorithm that uses presence-only data to estimate the occurrence probability for a species based on environmental variables (Phillips et al., 2006; Pearson et al., 2007). Compared to other presence-only SDMs, MaxEnt has good predictive performance and accuracy, particularly when dealing with sparse occurrence data (Elith et al., 2006; Phillips et al., 2006; Dudík et al., 2007; Pearson et al., 2007).

Two species that are currently of concern in southern Africa, but for which very little is known about the current or potential distribution, are C*ryptostegia grandiflora* Roxb. ex R. Br and *C. madagascariensis* Decne. (Asclepiadaceae). In South Africa *C. grandiflora* and *C. madagascariensis* are listed as category 1b species (i.e. they require compulsory control) under the regulations of the *National Environmental Management: Biodiversity Act* (NEM:BA 2014). Both *Cryptostegia* species have been recorded in continental southern Africa; however, distribution data of the species are limited with only few records from the northern regions of South Africa and Namibia (Appendix A). *Cryptostegia grandiflora* and *C. madagascariensis* are widely cultivated in tropical and subtropical regions of the world (DNRM 2001), and both species have relatively broad climatic niches (Kriticos, et al., 2003) that include conditions similar to southern Africa. *Cryptostegia* species have significant economic and ecological impacts in invaded areas elsewhere, including the loss of pasture, impeding access to water and threatening native biodiversity (Tomley, 1995; Souza et al., 2016). Indeed, the magnitude and extent of the impacts associated with *Cryptostegia* invasions elsewhere suggest that the species could potentially pose a serious risk in southern Africa.

Therefore, the aims of this chapter were to a) collect occurrence data for *C. grandiflora* and *C. madagascariensis* species by searching published literature and national databases and through targeted field surveys, and b) predict the potential global and southern African distribution of *C. grandiflora* and *C. madagascariensis* based on climatic conditions. This research will inform risk assessment for both *Cryptostegia* species by providing data on the species' current distributions and predictions for their potential ranges.

2.2. Data and methods

Study species

Cryptostegia grandiflora and *C. madagascariensis* are native to Madagascar, where the two species possess partially overlapping distributions (McFadyen and Harvey, 1991). Within its native range, *C. grandiflora* typically grows in dry tropical areas (McFadyen and Harvey, 1990; Marohasy and McFadyen, unpublished data), occurring in the south-west of Madagascar's western coastal plain, below 500 m a.s.l., in areas receiving 350-800 mm rainfall annually (Fig. 1) (McFadyen and Harvey, 1991). In contrast, *C. madagascariensis* occurs over a larger area in Madagascar, from the south-west to the extreme north (Fig 1), in areas receiving rainfall of 400-2400 mm annually (McFadyen and Harvey, 1991).

Cryptostegia grandiflora and *C. madagascariensis* have successfully established in a number of climatically suitable areas across the globe (Kriticos et al., 2003). *Cryptostegia madagascariensis* is grown as an ornamental plant in Kenya, Florida, the West Indies, and Western Australia, and is invading riverine forests of the semi-arid north-eastern region of Brazil (Da Silva et al., 2008). Naturalised *C. madagascariensis* populations have also been recorded on several of the main Hawaiian Islands, including Moloka‘i and O‘ahu (Black et al., 2010). The global distribution of *C. grandiflora* is primarily tropical and sub-tropical, but extends into some semi-arid climatic regions (Jenkins 1944; Tomley 1995; Kriticos et al., 2003; Souza et al., 2016; Luizza et al., 2016). Areas where *C. grandiflora* is grown as an ornamental species include Egypt, Morocco, the southern states of the USA, India, some Indian Ocean Islands and northern South America (GBIF, 2016). Invasive populations of *C. grandiflora* are found in Mexico, the drier West Indian islands, New Caledonia, Australia and Ethiopia (McFadyen and Harvey, 1990; Tomley 1995; Rodriguez-Estrella et al., 2010; Luizza et al., 2016).

Study area and occurrence data

Global occurrence records from both the native and introduced ranges of *C. grandiflora* and *C. madagascariensis* were collected from published literature (Jenkins, 1944; McFadyen and Mackey, 1990; Tomley 1995; Kriticos, 1996; Kriticos et al., 2003; Grice, 2006; Luizza et al., 2016), the Global Biodiversity Information Facility (GBIF, 2016), and the Commonwealth Agricultural Bureau International (CAB International, 2000). Additionally, distribution records for *C. grandiflora* and *C. madagascariensis* in southern Africa were compiled from the South African Plant Invaders Atlas (SAPIA; Henderson, 2016; http://www.agis.agric.za/ October, 2016) and the South African National Biodiversity Institute Invasive Species Programme (Wilson et al., 2013; pers. comm. P. Shisani, 2014). These records were supplemented by observations reported to myself by private individuals, and by field surveys (Table 1; see also Appendix A). A total of 118 *C. grandiflora* records were available from southern Africa prior to this study, with the majority (97 records) located in the northern regions of the South Africa, with 17 records from Namibia and four from Botswana. Only three *C. madagascariensis* occurrence records were available in databases for southern Africa before this study’s surveys were conducted (Henderson, 2016).

Most southern African occurrence records for *C. grandiflora* and *C. madagascariensis* lacked adequate information regarding their invasive status (i.e. whether the plant was ornamental or occurred outside cultivation). Knowing the invasive status of each record is crucial for predicting the potential distribution of *Cryptostegia* species. To ensure that the occurrences used in the predictive modelling only reflect environmental suitability in the absence of human interference, records from cultivated specimens should be omitted from modelling, because conditions in cultivated areas may provide favourable environments for establishment and growth otherwise not present in natural areas (Merow et al., 2013). Additionally, although quite distinct from other species in the drier regions of southern Africa, the two *Cryptostegia* species may be difficult to distinguish from each other and could be incorrectly identified, especially when plants are not reproductive: *C. madagascariensis* is distinguished from *C. grandiflora* by its shorter pods and darker purple flowers (Marohasy and Forster, 1991; Klackenberg 2001; see Table 1 in Chapter 1). Indeed, it has been noted that distinguishing between *C. grandiflora* and *C. madagascariensis* can be challenging (Department of Natural Resources, 2000), as seen in Brazil where *C. madagascariensis* was originally identified as *C. grandiflora* (Da Silva et al., 2008).

For these reasons, the species identity and invasion status of southern African records for the two *Cryptostegia* species required confirmation where these data were missing or where identification was uncertain. Thus, field surveys were conducted across southern Africa to confirm identifications of existing records of the two species (*C. grandiflora* or *C. madagascariensis),* to define the invasive status for records lacking such data, and to search for any previously undocumented occurrences of the species.

The field surveys were conducted in the three southern Africa countries where *Cryptostegia* spp have been reported (pers. observation January 2014; pers. comm. L. Henderson 2015; pers. comm. P. Shisani, 2014): Botswana, Namibia and South Africa. Guided by the existing occurrence records, survey routes were planned to verify occurrences and to search for new occurrences of *Cryptostegia* spp in regions where the species had previously been reported. Three separate routes were surveyed, two in the Limpopo Province of South Africa and one in northern Botswana and Namibia. The surveys were conducted by vehicle, with two observers in one vehicle driving along predetermined routes and recording the identity and invasion status of each *Cryptostegia* population found. Only one record per invasive population was included in the subsequent modelling of *Cryptostegia* distributions.

The invasive status of all occurrences was classified according to Richardson et al., (2000) as either: 1) cultivated plants; 2) non-naturalised plants outside of cultivation; 3) naturalised plants or; 4) invasive plants. Cultivated plants were planted as ornamental plants in gardens or grown in managed areas (e.g. in mining areas and sewage treatment plants). Non-naturalised plants outside of cultivation included all individuals found outside gardens that did not appear to form self-sustaining populations and were observed in close proximity to human influence. Naturalised populations were characterized by multiple plants that occurred outside of cultivation and appeared to be reproducing consistently (i.e. where self-sustaining) without direct human intervention (Richardson et al., 2000). Invasive populations were identified by large numbers of individuals that appeared to produce reproductive offspring at considerable distances from parent plants and had spread over large areas (Richardson et al., 2000; Pyšek et al., 2004; Henderson, 2007).

Table 1. A summary of available global occurrence records (extracted by 31 December 2016) for *C. grandiflora* and *C. madagascariensis*. These records include occurrences in- and outside of cultivation, naturalised and, invasive populations. The records are listed per database and some duplicates exist (i.e. were listed in more than one database). See Appendix A for detailed occurrence records and sources.

Source	**Number of records obtained**	
	Cryptostegia grandiflora	*Cryptostegia madagascariensis*
Public data sources		
CAB International	46	29
Global Biodiversity Information Facility (GBIF)	325	315
South African Plant Invaders Atlas (SAPIA)	35	2
SANBI	110	0
Published literature	15	4
Field surveys		
Ludi Kern southern Africa surveys	151	10
Other communicated observations	21	2
Total	**752**	**433**

Climate data

Bioclimatic variables were extracted from the WorldClim (Version 1.4) dataset (Hijmans et al., 2005; www.worldclim.org) at a spatial resolution of 2.5-arc minutes. Six bioclimatic variables that are thought to represent ecologically relevant factors for *Cryptostegia* distributions were selected based on the published literature. Mean annual temperature (BIO1) and mean temperature of the warmest (BIO10) and coldest quarters (BIO11) were chosen to determine how temperature affects the species distribution and, specifically, *C. grandiflora*’s sensitivity to frost (as suggested by Chippendale, 1991). Annual precipitation (BIO12) and mean precipitation of the wettest (BIO16) and driest (BIO17) quarters were also included. These precipitation variables were selected based on previous research that suggested that rainfall may limit the distribution of *C. grandiflora* (Curtis 1946; although see also Kriticos et al., 2003).

Model training and evaluation

Species distribution modelling of *C. grandiflora* and *C. madagascariensis* was conducted for all global terrestrial areas using a maximum entropy approach in MaxEnt (v 3.2.19; available from http://www.cs.princeton.edu/~schapire/maxent/) based on the six climate variables extracted from WorldClim (Hijmans et al., 2005) and the global occurrence data from the native and invaded ranges of both species. Using both native and global invasive occurrence records allows for a further exploration of the potential climate range not represented in Madagascar (Broennimann et al., 2007; Mau-Crimmins et al., 2006). The original dataset of the global and native occurrences (752 and 433 for *C. grandiflora* and *C. madagascariensis* respectively) was subsequently refined to subsets of 155 occurrences for *C. grandiflora* and 102 for *C. madagascariensis* to include only the data with invasive status information available. This subset included the native occurrences and invasive populations obtained from publications (Jenkins, 1944; Tomley, 1995; McFadyen and Harvey, 1990; Kriticos et al., 2003; Da Silva et al., 2008; Black et al., 2010; Rodriguez-Estrella et al., 2010; Luizza et al., 2016), and verified identifications from southern African surveys. Records from online resources (i.e. GBIF and CABI) with information available about the invasive status of the species were also included in the subsets. All the occurrence records that did not indicate the invasive status (i.e. cultivated, naturalised or invasive) were excluded. The subsets were created to reduce the possibility of over-estimation of the species potential distributions by excluding cultivated occurrences. Indeed, the occurrences selected to train distribution models should reflect the climate suitability of the modelled species in the absence of human interference, since cultivated areas may provide artificially favourable conditions (i.e. water) for the species that are otherwise absent outside of cultivation.

The MaxEnt models were run with default settings (following Phillips and Dudík, 2008). The number of background points used was 10,000, number of iterations 500, convergence threshold 0.00001, and regularization multiplier 1. The 'auto features' option in MaxEnt software was selected that allows MaxEnt to automatically select the optimal set of features for a model based on the size of the training data set (Phillips and Dudík, 2008; Merow et al., 2013). To provide a robust assessment of model performance, four replicated runs for each species were executed by employing cross-validation (Pearson et al., 2007; Phillips et al., 2006). In cross-validation, occurrence data is randomly split into a number of subsets ("folds"). Models are generated leaving out each fold in turn (i.e. during model training), and the excluded folds are used for intrinsic evaluation (i.e. during model testing; Hernandez et al., 2006). Model performance was assessed using the Area under curve (AUC) measure from the receiver operating characteristic (ROC) plots (Fielding and Bell, 1997; Lobo et al., 2007; Peterson et al., 2008). AUC measures the ability of the model to correctly classify a species as present or absent. Previous authors have considered AUC values of 0.50 – 0.60 to represent an insufficient model, 0.60 – 0.70 a poor model, 0.70 – 0.80 an average model, and values of 0.80 – 0.90 and > 0.9 to indicate good and excellent models respectively (Hanley and McNeil 1982; Pearce and Ferrier 2000; Elith et al. 2006). Continuous probability of occurrence values were transformed into binary presence-absence predictions (predicted occurrence = 1; predicted absence = 0) using the "equal training specificity and sensitivity" threshold (Liu et al., 2005).

2.3. Results

Global and southern Africa occurrence of *C. grandiflora* and *C. madagascariensis*

Cryptostegia grandiflora and *C. madagascariensis* currently occur in many tropical and subtropical areas (Fig. 1).

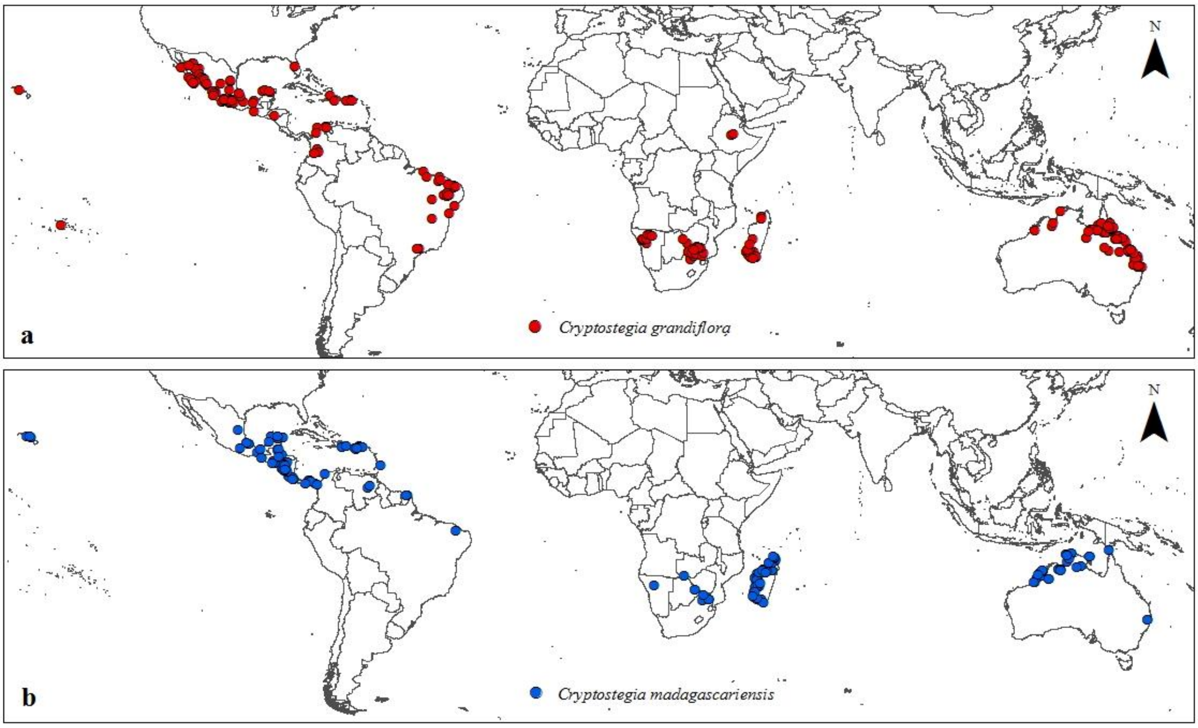

Figure 1: Global locality records of a) *Cryptostegia grandiflora* and b) *Cryptostegia madagascariensis* (data summarized in Table 1).

From the original 163 reported occurrences of *Cryptostegia* species across southern Africa, identifications and localities of 138 *C. grandiflora* and ten *C. madagascariensis* occurrences respectively (Appendix A) were confirmed across the surveyed areas in southern Africa (Fig. 2a).

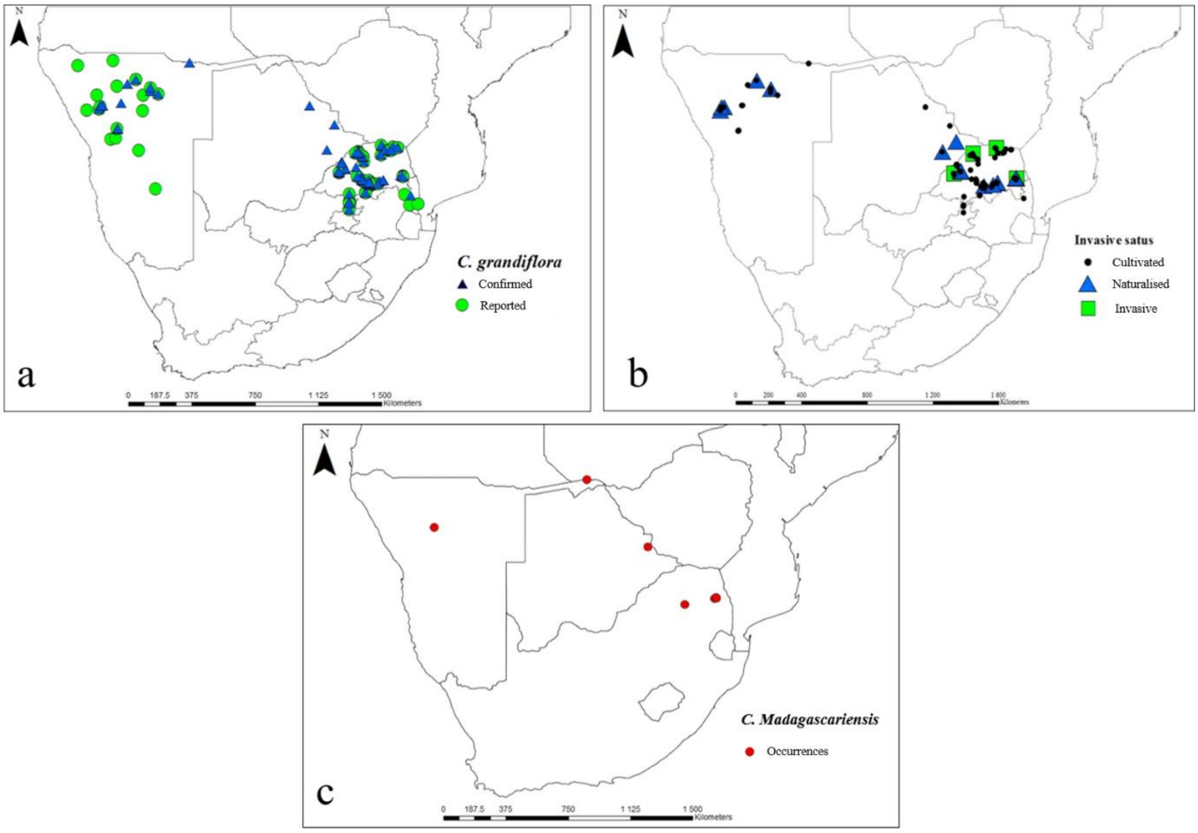

Figure 2: Occurrence records for a) *C. grandiflora* in southern Africa. Green symbols represent occurrences reported prior to the onset of this study. The blue triangles represent all the occurrences confirmed, b) invasive status of recorded *C. grandiflora* occurrences, and c) confirmed *C. madagascariensis* occurrences.

The field surveys conducted across the three countries revealed the majority of occurrences to be cultivated plants (e.g. growing as hedges on fences or self-supporting shrubs; Fig. 3a) and non-naturalised plants outside of cultivation (Fig. 3b and 3d) in rural settlements in the more arid regions. The majority of the occurrences outside of cultivation (i.e. naturalised and invasive occurrences) were present in areas where some form of disturbance was visible (e.g. erosion and flooding). Sixteen naturalised populations were recorded in Botswana, Namibia and South Africa (Fig. 2c). Five invasive populations were confirmed in Lephalale, Mogalakwena (Fig. 3b), Musina and Phalaborwa, all in the Limpopo Province in South Africa.

Figure 3: Occurrences of *C. grandiflora* and *C. madagascariensis* observed during field surveys in 2015. a) Self-supporting cultivated *C. madagascariensis* plant, b) invasive *C. grandiflora* population invading a river, c) Non-naturalised *C. grandiflora* growing on abandoned mining infrastructure, and d) an example of naturalised *C. grandiflora* population growing in drainage lines.

Predicted global and southern Africa suitability of *C. grandiflora* and *C. madagascariensis*

The potential global suitability models based on native and invasive occurrence data for *C. grandiflora* and *C. madagascariensis* showed good predictive ability with mean cross-validated AUC values of 0.976 ± 0.01 (mean ± SD) and 0.983 ± 0.003 respectively. MaxEnt models trained using the native and invasive occurrences predicted that both species' predicted distributions extend beyond their current distribution (Fig. 4). Regions climatically suitable for both *Cryptostegia* species included large portions of north and eastern Australia, Brazil, Bolivia, Florida and Mexico and the east coast of Africa (from Mozambique to Ethiopia).

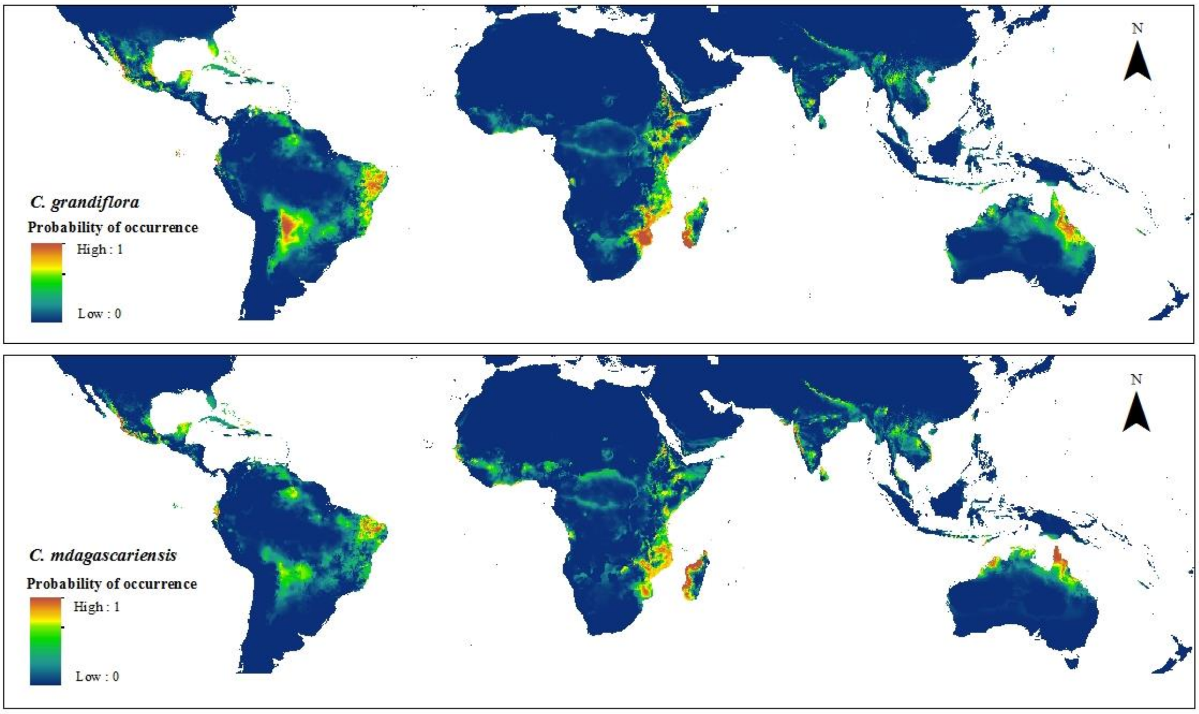

Figure 4: Habitat suitability maps showing the potential distribution of a) *Cryptostegia grandiflora* and b) *Cryptostegia madagascariensis* based on existing native and invasive occurrence records.

While the potential distributions of the two species largely overlapped, *C. madagascariensis* was predicted to be absent from several areas suitable for *C. grandiflora* (e.g. the northern provinces of South Africa and southern U.S.A. and Mexico), while other areas suitable for *C. madagascariensis* were not suitable for *C. grandiflora* (e.g. northern Queensland in Australia and west coast of Madagascar).

Within southern Africa, MaxEnt predicted areas of suitable climatic conditions for *C. grandiflora* across a considerable proportion of the northern regions of South Africa bordering Botswana, Zimbabwe and Mozambique (Fig. 5). In particular, models predicted almost the entire Mozambique to be suitable for both species. Additionally, the southern region of Zimbabwe and areas around the Kariba Dam were predicted to be highly suitable for *C. grandiflora*. The predicted suitable range for *C. madagascariensis* in southern Africa is largely restricted to Mozambique with only a small area in the north-eastern border of South Africa.

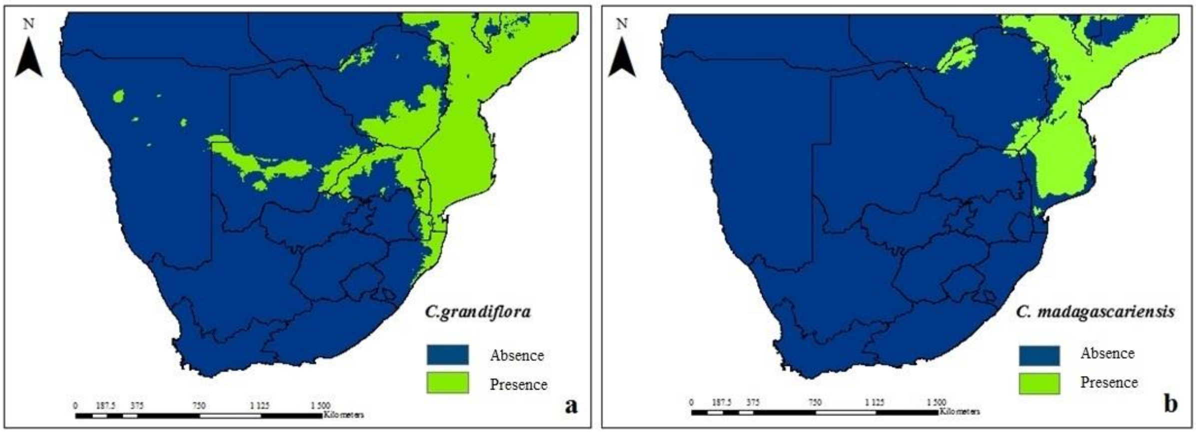

Figure 5: Presence-absence maps for southern Africa showing the predicted distribution of a) *C. grandiflora* and b) *C. madagascariensis* in southern Africa using the native and global invasive occurrence records. Green areas represent predicted presences, and blue areas predicted absences.

Variable importance

MaxEnt models indicated that *C. grandiflora* and *C. madagascariensis* responded similarly to the six bioclimatic variables. Temperature of the coldest quarter showed the highest percentage importance for both species (Table 2), with optimal temperatures for the coldest quarter ranging between 15° and 25°C for both species (Fig. 7).

Table 2: Model performance of MaxEnt models (AUC values) and % contribution of climatic variables to MaxEnt models based on native and invasive occurrences of *Cryptostegia grandiflora* and *Cryptostegia madagascariensis*. Values in bold show the highest variable contribution. AUC = Area Under Curve. SD = standard deviation.

	Cryptostegia grandiflora	***Cryptostegia madagascariensis***
Number of records (native and invasive)	155	102
Average training AUC (± SD)	0.98	0.99
Average test AUC (± SD)	0.98	0.98
	% Variable importance	
Annual mean temperature	7.2	9.3
Mean temperature warmest quarter	19.2	6.9
Mean temperature coldest quarter	**40.5**	**38.0**
Annual mean precipitation	13.8	5.4
Mean precipitation wettest quarter	9.5	24.4
Mean precipitation driest quarter	9.9	16.0

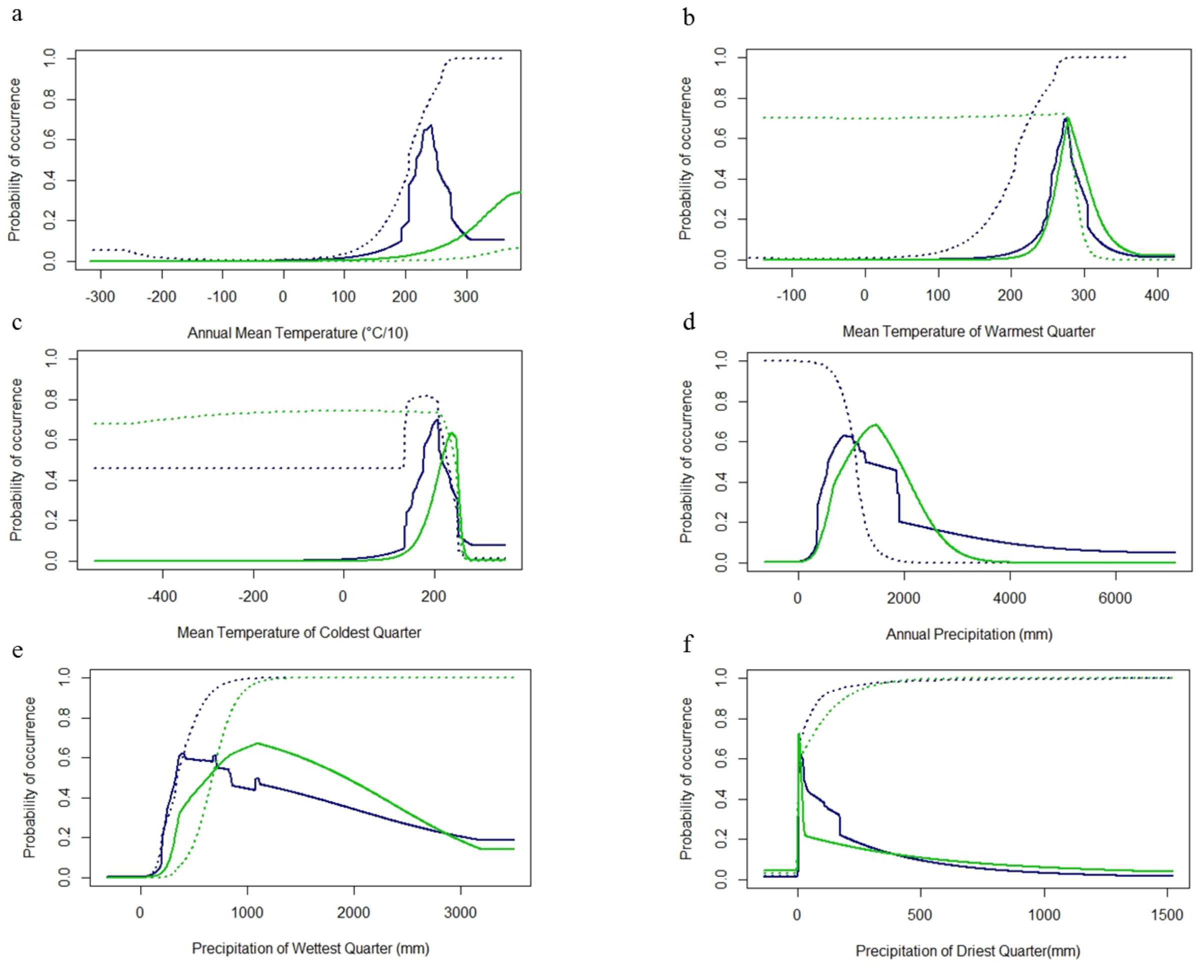

Figure 7: Response curves of the six climatic predictor variables used in the global distribution models for *Cryptostegia grandiflora* (in blue) and *C. madagascariensis* (in green). a) Mean annual temperature, b) mean temperature of the warmest quarter, c) mean temperature of the coldest quarter, d) annual precipitation, e) precipitation of the wettest quarter and, f) precipitation of the driest quarter. Solid lines represent probability of species occurrence when the variable is considered independently from the other predictor variables. The dotted lines consider each variable’s effect on the species occurrence whilst accounting for the effects of all other predictor variables. Temperature values shown on the graphs are ° C/10.

2.4. Discussion

Cryptostegia grandiflora and *C. madagascariensis* have similar global distributions, occurring chiefly in tropical and subtropical regions, but also extending into some semi-arid areas (e.g. portions of Ethiopia, South Africa, Namibia and Botswana). The observed occurrences demonstrate that both species have relatively broad climatic niches and can successfully establish in regions differing from their native conditions (Klackenberg, 2001; Kriticos et al., 2003; da Silva et al., 2008; Rodriguez-Estrella et al., 2010; Luizza et al., 2016). This suggests that Madagascar's conditions may possibly not express the full range of climatic tolerance of *Cryptostegia* spp (in agreement with Kriticos et al., 1996), or that within Madagascar other factors like geographical barriers (i.e. dispersal limitations) or biotic interactions may be restricting the species distributions (McFadyen and Harvey 1990; Kriticos et al., 2003; Gallagher et al., 2010).

The temperature during the coldest quarter was the climatic variable that most strongly influenced the distribution of both *Cryptostegia* species, in agreement with findings that low temperatures are a biologically limiting factor for these species, influencing their growth and successful establishment (Symontowne, 1943; Curtis, 1946; Kriticos et al., 1996). However, despite this sensitivity to cold temperatures, *C. grandiflora* may occur in areas prone to frost (e.g. colder regions in sub-tropical north-eastern Australia; Chippendale, 1991), where landforms (e.g. gullies and creeks) create microclimatic conditions protecting *C. grandiflora* from extreme low temperatures (Chippendale, 1991; Kriticos et al., 1996). Similarly, despite studies suggesting that *Cryptostegia* can be intolerant of low rainfall (McFadyen and Harvey, 1990; Chippendale, 1991; Curtis, 1946), both naturalised and invasive *C. grandiflora* populations have been recorded in semi-arid and arid regions of Ethiopia, Mexico, Brazil and southern Africa (Kriticos et al., 2003; da Silva et al., 2008; Rodriguez-Estrella et al., 2010; Luizza et al., 2016) in riparian areas (or alternative water sources e.g. oases in Mexico; Rodríguez-Estrella et al., 2010). This highlights that within broadly unsuitable regions, local micro-climates can provide suitable conditions that cannot be predicted from macro-climate data solely.

Acquiring detailed occurrence data for invasive species can often be impractical and costly (Mau-Crimmins et al., 2006). However, direct field observations can greatly increase the knowledge of a species' invasive status and characteristics (McConnachie et al., 2011). Indeed, the data provided by the surveys in southern Africa have provided important insights into the current and potential distribution of *C. grandiflora* and *C. madagascariensis* in this region. For example, the surveys revealed that *C. grandiflora* is the dominant species in the region, with no naturalised or invasive populations of *C. madagascariensis* recorded in southern Africa. This is similar to observations from Kenya, where, despite having abundant fruits and seemingly viable seeds, all of the *C. madagascariensis* plants observed in that country were cultivated and showed no evidence of naturalisation or seedling establishment (McFadyen, 1985).

The surveys also showed that the majority of occurrences for both species occurred in rural settlements in the drier regions of southern Africa, with both species grown as ornamental plants. It can be assumed that these cultivated plants are the initial source of propagules, which, in suitable conditions, may spread away from human settlements (particularly in drainage lines) to establish naturalised populations. Similar to the species' other invaded ranges, the successful establishment of *Cryptostegia* species beyond cultivated areas coincided with some form of disturbance associated with development, grazing, erosion, artificial water sources or flooding (McFadyen unpublished report 1985; Viera et al., 2004; Stow, 2008; see also Chapter 3). Nonetheless, in both the native and other invaded ranges, *Cryptostegia* species are predominantly restricted to riparian areas or other artificial water sources (McFadyen unpublished report, 1985; Chippendale, 1991; Mahorasy and Forster, 1991; Kriticos et al., 2003; da Silva et al., 2008; Rodriguez-Estrella et al., 2010; Luizza et al., 2016). In this study, *C. grandiflora* populations showed similar distribution patterns, with all of the observed naturalised and invasive populations occurring in close proximity to a water source. For example, the invasive population recorded in Musina (northern South Africa) had high densities of *C. grandiflora* occurring around a sewage treatment plant and had spread into adjacent drainage lines.

Consistent with observations from this study's surveys, the predicted range for *C. grandiflora* was considerably larger than that for *C. madagascariensis* in southern Africa. This suggests, based on current occurrence records and climatic suitability, that *C. grandiflora* poses a higher invasion risk to southern Africa than *C. madagascariensis*. However, *C. madagascariensis*' invasion success in other regions (e.g. Brazil) with similar climates to southern Africa, suggests that *C. madagascariensis* could potentially become invasive in the future. The few observed occurrences may not necessarily be due to unsuitable conditions, but could be because *C. madagascariensis* has not yet had sufficient time to spread (i.e. the species is currently in a lag phase) or that fewer individuals than *C. grandiflora* have been introduced (Crooks, 2005; Jiménez-Valverde et al., 2011).

2.5. Conclusion and management implications

Data collated from global occurrences, southern African surveys and MaxEnt model predictions increased our understanding of *Cryptostegia*'s current and potential distribution. At the regional scale, knowledge of the occurrences and potentially suitable areas for invasive species can guide future management strategies (Peterson and Vieglais 2001; Leung et al., 2002; Richardson et al., 2010). The data from this study specifically show that in southern Africa *C. madagascariensis* is an ideal candidate for eradication. Given the small number of known occurrences and the limited extent of suitable areas for *C. madagascariensis*, individual *C. madagascariensis* plants should be targeted for control.

The widespread occurrence of existing invasive populations of *C. grandiflora* highlights the risk this species already poses to southern Africa. In addition, SDM predictions illustrates that expansion beyond the current known distribution is possible. Using this information, priority areas can be identified where monitoring and control efforts should be focussed. For example, invasive populations occurring close to protected areas, like the Kruger National Park, should be considered for immediate control to prevent spread into conservation areas. However, *C. grandiflora*‘s large dispersal range (Grice, 1996) and tendency to occur in riparian areas (Luizza et al., 2016; Rodrıguez-Estrella et al., 2010) that serve as dispersal corridors (Renöfält et al., 2005; Pyšek and Prach, 1993) suggests that this species may be capable of spreading over large distances during seed dispersal. In particular, in areas where flooding occurs seeds can be dispersed large distances from the original populations. Control options like containment lines and large-scale herbicide application may therefore not be feasible options to manage *C. grandiflora*. Alternative options, including biological control (which has shown some success in Australia; Tomley and Evans, 2004), should be investigated.

Species distribution modelling techniques, including MaxEnt, are useful for assessing the potential risk of alien species and can, therefore, help identify areas for active surveillance (Elith and Leathwick, 2006; Phillips et al., 2006; Pearson et al., 2007; McGeoch et al., 2016). However, these models are constrained by the amount, and characteristics, of available data. For example, across large extents (e.g. southern Africa) environmental data are typically only available at relatively coarse scales (e.g. WorldClim; Hijmans et al., 2005). However, habitat conditions within some habitat types, including riparian areas, can change considerably over short distances (Descombes et al., 2016). As a result, SDMs may provide only coarse estimates of some species' potential distributions and may be insufficient to describe spatial variation in occurrence patterns at local scales where majority of management decisions are made (Hulme 2003; Thuiller et al., 2005; Descombes et al., 2016 Koop et al., 2012). Therefore, in addition to the implementation of coarse-scale SDMs that predict broadly suitable habitats, our understanding of spatial variation in the distribution and density of alien species within individual habitats would benefit from the additional exploration of finer scale data (Rouget and Richardson, 2003; Richardson et al., 2004).

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2.7. Appendix A

Table A1: Detailed records of surveys conducted in Botswana, Namibia and South Africa (June and July 2015), records from the South African Plant Invaders Atlas (SAPIA) database and records reported by the South African Biodiversity Institute (Wilson et al., 2013). These records include all *C. grandiflora* and *C. madagascariensis* populations and individual plants observed, their GPS coordinates and their invasive status. RSA = South Africa, NAM = Namibia and BOT = Botswana.

Source	**Date**	**Country**	**Lat**	**Long**	**Species**	**Invasive Status**
Southern Africa surveys	01/04/2015	RSA	-23.49	28.66	*C. grandiflora*	Cultivated
Southern Africa surveys	29/04/2015	RSA	-23.96	28.96	*C. grandiflora*	Cultivated
Southern Africa surveys	29/04/2015	RSA	-24.08	28.97	*C. grandiflora*	Cultivated
Southern Africa surveys	29/04/2015	RSA	-24.09	28.97	*C. grandiflora*	Cultivated
Southern Africa surveys	29/04/2015	RSA	-24.32	29.36	*C. grandiflora*	Naturalised
Southern Africa surveys	29/04/2015	RSA	-24.21	29.92	*C. grandiflora*	Outside cultivation
Southern Africa surveys	29/04/2015	RSA	-24.19	30.07	*C. grandiflora*	Cultivated
Southern Africa surveys	29/04/2015	RSA	-24.18	30.10	*C. grandiflora*	Outside cultivation
Southern Africa surveys	29/04/2015	RSA	-24.17	30.11	*C. grandiflora*	Outside cultivation
Southern Africa surveys	29/04/2015	RSA	-24.16	30.10	*C. grandiflora*	Naturalised
Southern Africa surveys	29/04/2015	RSA	-24.26	29.86	*C. grandiflora*	Naturalised
Southern Africa surveys	30/04/2015	RSA	-23.95	31.15	*C. grandiflora*	Invasive
Southern Africa surveys	30/04/2015	RSA	-23.93	31.15	*C. grandiflora*	Outside cultivation
Southern Africa surveys	30/04/2015	RSA	-23.94	31.14	*C. grandiflora*	Invasive
Southern Africa surveys	30/04/2015	RSA	-23.95	31.15	*C. grandiflora*	Invasive
Southern Africa surveys	30/04/2015	RSA	-23.96	31.15	*C. grandiflora*	Naturalised
Southern Africa surveys	30/04/2015	RSA	-23.96	31.14	*C. grandiflora*	Cultivated
Southern Africa surveys	30/04/2015	RSA	-23.95	31.13	*C. grandiflora*	Outside cultivation
Southern Africa surveys	30/04/2015	RSA	-23.92	31.13	*C. grandiflora*	Naturalised
Southern Africa surveys	30/04/2015	RSA	-23.92	31.05	*C. grandiflora*	Naturalised
Southern Africa surveys	30/04/2015	RSA	-23.92	31.05	*C. grandiflora*	Outside cultivation
Southern Africa surveys	30/04/2015	RSA	-23.92	31.04	*C. grandiflora*	Outside cultivation
Southern Africa surveys	30/04/2015	RSA	-23.58	28.11	*C. grandiflora*	Outside cultivation
Southern Africa surveys	30/06/2015	RSA	-23.58	28.10	*C. grandiflora*	Naturalised
Southern Africa surveys	30/06/2015	RSA	-23.57	28.09	*C. grandiflora*	Outside cultivation
Southern Africa surveys	30/06/2015	RSA	-23.57	28.09	*C. grandiflora*	Outside cultivation
Southern Africa surveys	30/06/2015	RSA	-23.57	28.10	*C. grandiflora*	Outside cultivation
Southern Africa surveys	30/06/2015	RSA	-23.56	28.10	*C. grandiflora*	Outside cultivation
Southern Africa surveys	30/06/2015	RSA	-23.56	28.10	*C. grandiflora*	Cultivated
Southern Africa surveys	30/06/2015	RSA	-23.56	28.10	*C. grandiflora*	Naturalised
Southern Africa surveys	30/06/2015	RSA	-23.56	28.10	*C. grandiflora*	Outside cultivation
Southern Africa surveys	30/06/2015	RSA	-23.56	28.10	*C. grandiflora*	Cultivated
Southern Africa surveys	30/06/2015	RSA	-23.68	27.74	*C. grandiflora*	Naturalised
Southern Africa surveys	30/06/2015	RSA	-23.69	27.74	*C. grandiflora*	Invasive
Southern Africa surveys	30/06/2015	RSA	-23.68	27.73	*C. grandiflora*	Invasive
Southern Africa surveys	30/06/2015	RSA	-23.68	27.74	*C. grandiflora*	Cultivated
Southern Africa surveys	30/06/2015	RSA	-23.21	27.89	*C. grandiflora*	Cultivated
Southern Africa surveys	01/07/2015	RSA	-23.21	27.90	*C. grandiflora*	Cultivated
Southern Africa surveys	01/07/2015	RSA	-23.21	27.91	*C. grandiflora*	Cultivated
Southern Africa surveys	01/07/2015	RSA	-23.28	27.91	*C. grandiflora*	Outside cultivation
Southern Africa surveys	01/07/2015	RSA	-23.22	27.90	*C. grandiflora*	Outside cultivation

Southern Africa surveys	01/07/2015	RSA	-23.22	27.90	*C. grandiflora*	Outside cultivation
Southern Africa surveys	01/07/2015	RSA	-23.22	27.90	*C. grandiflora*	Outside cultivation
Southern Africa surveys	01/07/2015	RSA	-23.22	27.89	*C. grandiflora*	Cultivated
Southern Africa surveys	01/07/2015	RSA	-22.64	28.78	*C. grandiflora*	Outside cultivation
Southern Africa surveys	01/07/2015	RSA	-21.42	15.97	*C. grandiflora*	Invasive
Southern Africa surveys	07/07/2015	NAM	-21.42	15.96	*C. grandiflora*	Outside cultivation
Southern Africa surveys	07/07/2015	NAM	-21.43	15.96	*C. grandiflora*	Cultivated
Southern Africa surveys	07/07/2015	NAM	-21.44	15.95	*C. grandiflora*	Cultivated
Southern Africa surveys	07/07/2015	NAM	-20.38	14.96	*C. grandiflora*	Outside cultivation
Southern Africa surveys	07/07/2015	NAM	-20.37	14.96	*C. grandiflora*	Cultivated
Southern Africa surveys	07/07/2015	NAM	-20.37	14.96	*C. grandiflora*	Cultivated
Southern Africa surveys	07/07/2015	NAM	-20.37	14.97	*C. grandiflora*	Outside cultivation
Southern Africa surveys	07/07/2015	NAM	-20.21	15.02	*C. grandiflora*	Cultivated
Southern Africa surveys	07/07/2015	NAM	-20.21	15.13	*C. grandiflora*	Outside cultivation
Southern Africa surveys	07/07/2015	NAM	-20.21	15.02	*C. grandiflora*	Outside cultivation
Southern Africa surveys	07/07/2015	NAM	-20.21	15.16	*C. grandiflora*	Invasive
Southern Africa surveys	07/07/2015	NAM	-20.11	16.15	*C. grandiflora*	Naturalised
Southern Africa surveys	08/07/2015	NAM	-20.11	16.16	*C. grandiflora*	Cultivated
Southern Africa surveys	08/07/2015	NAM	-20.10	16.16	*C. grandiflora*	Outside cultivation
Southern Africa surveys	08/07/2015	NAM	-20.11	16.17	*C. grandiflora*	Cultivated
Southern Africa surveys	08/07/2015	NAM	-20.12	16.17	*C. grandiflora*	Cultivated
Southern Africa surveys	08/07/2015	NAM	-19.04	16.47	*C. grandiflora*	Cultivated
Southern Africa surveys	09/07/2015	NAM	-19.03	16.47	*C. grandiflora*	Outside cultivation
Southern Africa surveys	09/07/2015	NAM	-18.81	16.94	*C. grandiflora*	cultivated
Southern Africa surveys	09/07/2015	NAM	-19.23	17.70	*C. grandiflora*	Naturalised
Southern Africa surveys	09/07/2015	NAM	-19.25	17.71	*C. grandiflora*	Naturalised
Southern Africa surveys	10/07/2015	NAM	-19.25	17.71	*C. grandiflora*	Outside cultivation
Southern Africa surveys	10/07/2015	NAM	-19.43	17.71	*C. grandiflora*	Cultivated
Southern Africa surveys	10/07/2015	NAM	-19.24	17.70	*C. grandiflora*	Cultivated
Southern Africa surveys	10/07/2015	NAM	-19.24	17.70	*C. grandiflora*	Cultivated
Southern Africa surveys	10/07/2015	NAM	-19.25	17.70	*C. grandiflora*	Cultivated
Southern Africa surveys	10/07/2015	NAM	-19.57	18.11	*C. grandiflora*	Cultivated
Southern Africa surveys	10/07/2015	NAM	-19.57	18.11	*C. grandiflora*	Outside cultivation
Southern Africa surveys	10/07/2015	NAM	-19.57	18.11	*C. grandiflora*	Cultivated
Southern Africa surveys	10/07/2015	NAM	-17.90	19.79	*C. grandiflora*	Cultivated
Southern Africa surveys	10/07/2015	NAM	-17.91	19.79	*C. grandiflora*	Cultivated
Southern Africa surveys	10/07/2015	NAM	-22.0	27.8	*C. grandiflora*	Cultivated
Southern Africa surveys	11/07/2015	NAM	-22.55	27.1	*C. grandiflora*	Cultivated
Southern Africa surveys	13/07/2015	BOT	-20.21	26.2	*C. grandiflora*	Naturalised
Southern Africa surveys	13/07/2015	BOT	-21.17	27.5	*C. grandiflora*	Naturalised
Southern Africa surveys	13/07/2015	BOT	-24.37	29.33	*C. grandiflora*	Cultivated
Southern Africa surveys	13/07/2015	BOT	-24.37	29.33	*C. grandiflora*	Cultivated
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.38	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.38	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.38	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.38	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.38	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.38	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.39	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.40	29.34	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.40	29.34	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.41	29.35	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.44	29.38	*C. grandiflora*	Outside cultivation

SANBI	01/06/2015	RSA	-24.45	29.40	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.45	29.41	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.46	29.41	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.30	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.30	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.29	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.28	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.28	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.28	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.27	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.27	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.27	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.27	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.26	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.25	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.24	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.23	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.18	28.99	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.18	28.99	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.18	28.98	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.18	28.98	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.16	28.98	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.89	28.30	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.89	28.30	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.89	28.30	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-25.33	28.28	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-25.34	28.28	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-25.34	28.28	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-25.38	28.28	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-25.38	28.28	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-25.41	28.28	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-25.74	28.28	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.44	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.81	29.17	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.84	29.17	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.84	29.17	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.85	29.17	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-22.72	28.61	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.35	29.29	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.31	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.32	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.32	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.32	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.32	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.32	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.32	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation

SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.37	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.18	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.18	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.34	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.35	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.38	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.42	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.42	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.42	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.42	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.42	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.34	29.42	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.34	29.43	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.33	29.43	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.32	29.43	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.32	29.43	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.31	29.48	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.32	29.40	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.32	29.40	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.32	29.39	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.32	29.38	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.32	29.37	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-24.36	29.33	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-23.77	27.75	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-23.75	27.75	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-23.97	28.70	*C. grandiflora*	Outside cultivation
SANBI	01/06/2015	RSA	-23.99	31.16	*C. grandiflora*	Outside cultivation
SAPIA Database	30/12/2013	RSA	-23.95	31.15	*C. grandiflora*	Outside cultivation
SAPIA Database	30/12/2011	RSA	-24.38	29.82	*C. grandiflora*	Outside cultivation
SAPIA Database	30/12/2013	RSA	-18.80	16.93	*C. grandiflora*	Outside cultivation
SAPIA Database	30/12/2000	RSA	-22.74	28.79	*C. grandiflora*	Outside cultivation
SAPIA Database	30/12/1996	RSA	-22.64	28.78	*C. grandiflora*	Outside cultivation
SAPIA Database	30/12/1996	RSA	-22.71	28.77	*C. grandiflora*	Outside cultivation
SAPIA Database	01/12/2005	RSA	-22.74	28.78	*C. grandiflora*	Outside cultivation
SAPIA Database	01/08/2013	RSA	-22.72	28.77	*C. grandiflora*	Outside cultivation
SAPIA Database	01/07/2013	RSA	-22.74	28.79	*C. grandiflora*	Invasive
SAPIA Database	01/02/2014	RSA	-22.86	28.91	*C. grandiflora*	Naturalised

SAPIA Database	01/07/2013	RSA	-22.76	28.84	*C. grandiflora*	Invasive
SAPIA Database	01/07/2013	RSA	-22.92	29.04	*C. grandiflora*	Invasive
SAPIA Database	01/02/2014	RSA	-22.90	29.02	*C. grandiflora*	Invasive
SAPIA Database	01/02/2014	RSA	-22.33	30.00	*C. grandiflora*	Invasive
SAPIA Database	01/02/2014	RSA	-22.40	30.60	*C. grandiflora*	Invasive
SAPIA Database	01/02/2014	RSA	-22.42	30.89	*C. grandiflora*	Invasive
SAPIA Database	01/02/2014	RSA	-22.42	30.86	*C. grandiflora*	Outside cultivation
SAPIA Database	01/02/2014	RSA	-22.42	30.87	*C. grandiflora*	Naturalised
SAPIA Database	01/02/2014	RSA	-22.62	30.14	*C. grandiflora*	Outside cultivation
SAPIA Database	01/02/2015	RSA	-22.61	30.16	*C. grandiflora*	Cultivated
SAPIA Database	01/02/2015	RSA	-22.59	30.43	*C. grandiflora*	Cultivated
SAPIA Database	01/02/2015	RSA	-22.83	30.00	*C. grandiflora*	Cultivated
SAPIA Database	01/02/2015	RSA	-22.57	30.51	*C. grandiflora*	Outside cultivation
SAPIA Database	01/02/2015	RSA	-23.77	27.75	*C. grandiflora*	Naturalised
SAPIA Database	01/02/2015	RSA	-23.97	28.70	*C. grandiflora*	Naturalised
SAPIA Database	01/02/2015	RSA	-23.17	29.08	*C. grandiflora*	Outside cultivation
SAPIA Database	01/02/2015	RSA	-23.95	31.15	*C. grandiflora*	Outside cultivation
SAPIA Database	01/02/2015	RSA	-23.95	31.15	*C. grandiflora*	Cultivated
SAPIA Database	01/02/2013	RSA	-23.99	31.16	*C. grandiflora*	Cultivated
SAPIA Database	01/11/2011	RSA	-24.38	29.82	*C. grandiflora*	Naturalised
SAPIA Database	01/02/2013	RSA	-24.92	31.25	*C. grandiflora*	Outside cultivation
SAPIA Database	01/02/2014	RSA	-25.49	31.51	*C. grandiflora*	Outside cultivation
SAPIA Database	01/11/1996	RSA	-25.45	31.96	*C. grandiflora*	Outside cultivation
SAPIA Database	01/02/2015	RSA	-25.43	31.94	*C. grandiflora*	Outside cultivation
SAPIA Database	01/02/2015	RSA	-24.31	29.47	*C. grandiflora*	Naturalised
SAPIA Database	01/11/1996	RSA	-23.96	31.14	*C. grandiflora*	Outside cultivation
SAPIA Database	01/10/2000	RSA	-23.94	31.13	*C. grandiflora*	Outside cultivation
SAPIA Database	01/06/2005	RSA	-23.94	31.13	*C. grandiflora*	Outside cultivation
SAPIA Database	01/02/2016	RSA	-23.93	31.13	*C. grandiflora*	Outside cultivation
SAPIA Database	01/07/2013	RSA	-20.11	16.17	*C. grandiflora*	Outside cultivation
SAPIA Database	01/07/2013	RSA	-17.51	24.27	*C. grandiflora*	Cultivated
SAPIA Database	01/07/2013	RSA	-22.81	29.89	*C. grandiflora*	Outside cultivation
Southern Africa surveys	29/04/2015	RSA	-23.95	31.15	*C. madagascariensis*	Cultivated
Southern Africa surveys	30/04/2015	RSA	-24.31	29.47	*C. madagascariensis*	Cultivated
Southern Africa surveys	30/04/2015	RSA	-23.96	31.15	*C. madagascariensis*	Cultivated
Southern Africa surveys	30/04/2015	RSA	-23.96	31.14	*C. madagascariensis*	Cultivated
Southern Africa surveys	30/04/2015	RSA	-23.95	31.13	*C. madagascariensis*	Cultivated
Southern Africa surveys	30/04/2015	RSA	-23.94	31.13	*C. madagascariensis*	Cultivated
Southern Africa surveys	30/04/2015	RSA	-23.94	31.13	*C. madagascariensis*	Cultivated
Southern Africa surveys	08/07/2015	NAM	-23.93	31.13	*C. madagascariensis*	Cultivated
Southern Africa surveys	13/07/2015	NAM	-20.11	16.17	*C. madagascariensis*	Cultivated
Southern Africa surveys	14/07/2015	BOT	-17.51	24.27	*C. madagascariensis*	Cultivated
SAPIA Database	01/02/2015	RSA	-21.17	27.51	*C. madagascariensis*	Cultivated
SAPIA Database	01/02/2015	RSA	-23.95	31.15	*C. madagascariensis*	Cultivated

CHAPTER 3

Biotic and abiotic factors influencing fine-scale variation in the density, occurrence and cover of *Cryptostegia grandiflora*

3.1. Introduction

Invasive alien plant species pose a serious risk to biodiversity and have caused severe economic and ecological damage globally (Mack et al., 2000; Pyšek and Richardson, 2010). As a result, biological invasions are considered the second-largest global threat, after habitat destruction, to biodiversity (Walker and Steffen 1997; Wilcove et al., 1998). With the increased breaching of geographic boundaries by widespread human transport of species, introductions of alien species are a continuous, and growing, threat (Clout and Veitch 1992; Hulme, 2009; Richardson and Rejmánek, 2011). Once introduced, the control of invasive plants is most effective during the early stages of invasion (Hulme 2006; Keller et al., 2007). However, early detection involves extensive monitoring that can be costly and time consuming (Mack et al., 2000; Leung et al., 2002). To this end, assessing the potential risk of an invasive species and anticipating areas vulnerable to invasion is a crucial first step towards the management and control of invasive species (Rouget et al., 2016).

Effective management of invasive species relies on forecasting the potential threat of a species (Simberloff 2003; Richardson and Thuiller, 2009). Assessing the risk of an alien species becoming invasive requires an understanding of the mechanisms that facilitate successful establishment and subsequent spread (Levin, 1992; Richardson and Pyšek, 2006; Wilson et al., 2007). The potential drivers of the distribution of invasive species broadly include the abiotic environment, biotic interactions, disturbances, the biological traits of the invader, dispersal vectors, and introduction history (Richardson et al., 2004; Pyšek and Hulme, 2005). All of these variables are known to influence invasive species distribution patterns, although their effect on the occurrence of a species varies across different spatial scales (Stohlgren et al., 2006). At a broad scale, climate is expected to be the main factor determining where species occur, whereas at finer scales land use, disturbance, competition and resource availability are thought to be more important predictors (Thuiller et al., 2005; Koop et al., 2012). Therefore, it is only by assessing occurrence patterns of an invasive species at different spatial scales that the full range of environmental variables that influence its distribution can be identified (Rouget and Richardson, 2003; Richardson et al., 2004; Gallien et al., 2012; Descombes et al., 2016).

Climatic suitability models are a common method used to predict areas at risk of invasion (see Chapter 2; Elith et al., 2006; Peterson 2006; Franklin et al., 2013). However, these models are generally applied at coarse scales and are suited to identify broad regions with similar climatic and edaphic conditions to where a species is currently known to occur (Pearson et al., 2002; Franklin et al., 2013). Indeed, models based on macroclimatic variables alone do not always perform well in predicting species fine-scale distributions (Pearson and Dawson, 2003; Hampe, 2004; see Chapter 2 for an implementation of this approach for *C. grandiflora* and *C. madagascariensis*). As a result, climate modelling can be an effective method when the aim is to predict the potential global or national distribution of a species (Descombes et al., 2016). In contrast, however, management and conservation efforts are typically applied at local spatial scales and therefore require an understanding of the factors underpinning the fine-scale distribution of invasive species (Descombes et al., 2016).

Fine-scale surveys can be an efficient method to identify non-climatic environmental conditions influencing the distribution of invasive species, because macroclimatic variation is minimal across relatively small sampling extents (Descombes et al., 2016). Indeed, to accurately predict the spatial variability of invasion risk within a single habitat type, predictor variables that vary strongly over fine-scales are likely more relevant (Pearson and Dawson, 2003; Milbau et al., 2009). Such variables associated with the fine-scale distribution patterns of species include dispersal mechanisms, availability of water and light, topography, disturbance, soil conditions and competition (Milbau et al., 2009; Austin, 2011; Coutts et al., 2011; Aslan et al., 2012; Kaplan et al., 2014). Examining these fine-scale variables can provide valuable insight into a species occurrence patterns and the factors driving successful establishment.

Cryptostegia grandiflora is a successful invader with naturalised populations in South America, USA, the Caribbean, Hawaii, Australia and Africa (McFayden and Harvey, 1990; Grice, 1996; Kriticos et al., 2003; Rodrıguez-Estrella et al., 2010; Luizza et al., 2016; see also Chapter 2). Within its invaded range, *C. grandiflora* spreads rapidly forming impenetrable monospecific stands, particularly in riparian habitats and other mesic areas (Kriticos et al., 2003). Within South Africa five invasive *C. grandiflora* populations are known, all of which are located in riparian areas or in proximity to water sources in the northern regions of Limpopo Province (Chapter 2).

To determine the biotic and abiotic factors influencing local variation in the density, occurrence and cover of *Cryptostegia grandiflora*, fine-scale surveys were conducted in an invasive population along the Mogalakwena River, South Africa. The aims of this chapter were therefore to 1) document spatial variation in the density of *Cryptostegia grandiflora* along an invaded river, and 2) identify the fine-scale environmental factors correlated with the occurrence and cover of *C. grandiflora* and use this to predict where the species is likely to occur.

3.2. Materials and methods

Study species

In its native Madagascar, *C. grandiflora* (Fig. 1) is restricted to areas below 500 m a.s.l. with 350 – 800 mm annual rainfall (McFayden and Harvey, 1991). Outside of its indigenous range, invasions generally initially occur along waterways (Grice et al., 2000), where the species smothers riparian vegetation by forming dense, impenetrable thickets (Fig. 1d; McFadyen and Harvey, 1991). *Cryptostegia grandiflora* thickets threaten riparian areas by displacing indigenous vegetation, negatively affecting water quality, and increasing soil erosion by reducing grass cover (Harvey, 1987; Chippendale, 1991; Palmer and Vogler, 2004; Australian Weeds Committee, 2012). Where conditions are suitable, the species can subsequently spread out of riparian habitats to adjacent areas where it may outcompete native vegetation, and can disturb grazing pasture and limit access to water and food resources for stock and wildlife (Grice et al., 2000).

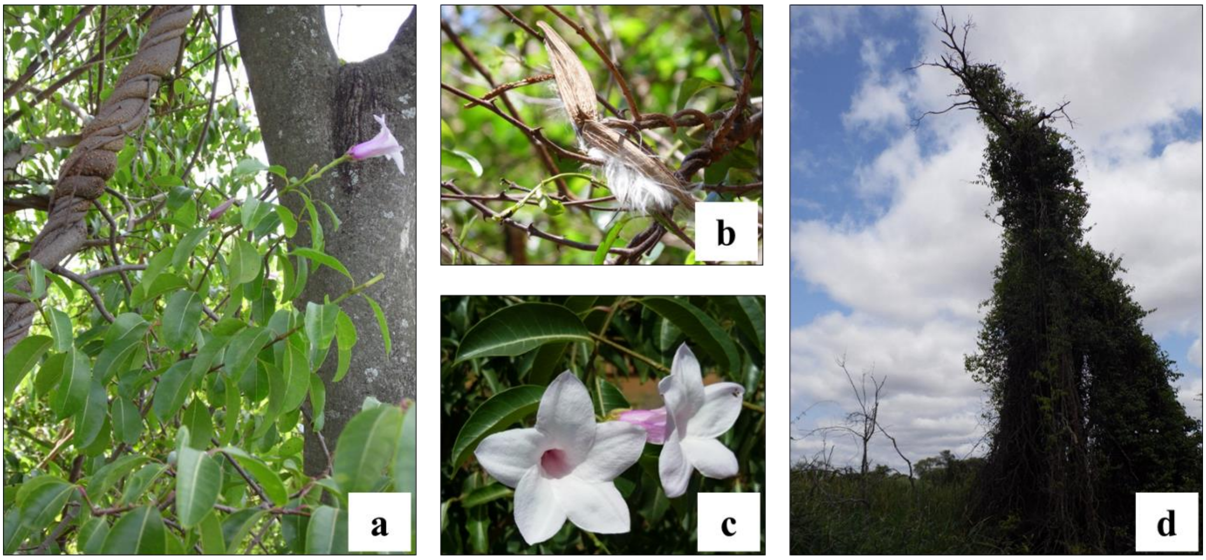

Figure 1. *Cryptostegia grandiflora* invasion along the Mogalakwena River. (a) *C. grandiflora* climbing an indigenous tree. (b) Mature *C. grandiflora* pods splitting open to release plumed seeds. (c) *Cryptostegia grandiflora* flowers. (d) *Cryptostegia grandiflora* vine smothering an indigenous tree.

Study site

In southern Africa little is known about the current distribution of *C. grandiflora* or the environmental factors that drive its fine-scale distribution patterns (see e.g. Chapter 2). In this study an invasive population of *C. grandiflora* occurring along the Mogalakwena River in the Limpopo province of South Africa (Fig. 2) was examined to determine the influence of several biotic and abiotic factors that could potentially drive the distribution of *C. grandiflora* at a fine scale.

Fine-scale *C. grandiflora* density, occurrence and cover surveys were focussed on a 7.2 km portion of the Mogalakwena River within the Mogalakwena Private Game Farm. *Cryptostegia grandiflora*'s presence along this portion of the Mogalakwena River was first noted in 2005, and by 2013 the population was well established along most of the study area (pers. comm. Caroline Kruger, 2013). The Mogalakwena River is a summer seasonal intermittent tributary of the Limpopo River. Forming part of the Limpopo Water Management Area, the Mogalakwena River receives three water releases during the dry winter months from the Glen Alpine Dam. The main land use in the area is agriculture but the study area is surrounded by natural savannah vegetation (within the arid sweet bushveld vegetation type; Acocks, 1988). Rainfall at the site ranges from 200 to 600 mm per annum and usually falls during the summer months between October and March (see Appendix A for monthly rainfall from 2012 to 2015) (Robinson, 1996; Kleynhans et al., 2005). Winters are mild and summer temperatures can rise to 45 °C (Weather Bureau, 1986; Robinson, 1996).

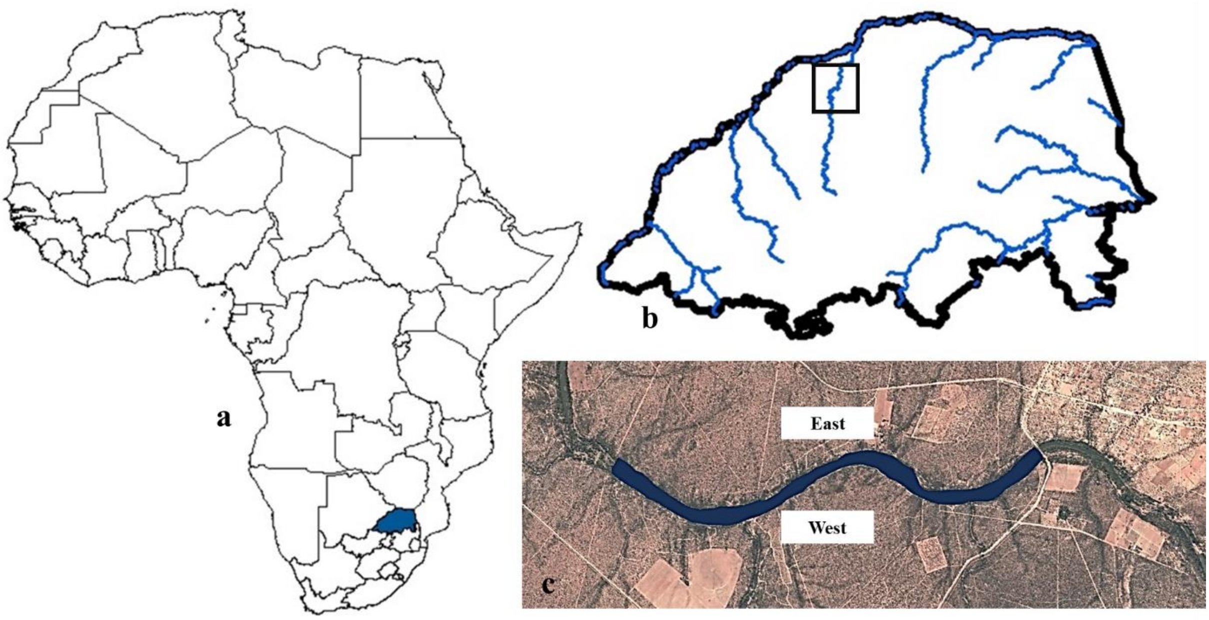

Figure 2. Study site located in South Africa in the north-western Limpopo Province (a and b) along a 4.5 km section of the eastern bank and 2.7 km section of the western bank of the Mogalakwena River (Map data: Google, DigitalGlobe, 2013).

Data collection: density survey

To determine the density of *C. grandiflora* along the Mogalakwena River, the length of the river within the study area was divided into 36 sections of 200 m (Fig. 3). Within each 200 m section, one 30 x 30 m survey quadrat, consisting of four 15 x 15 m sub-quadrats, bordering on the river was located using randomly generated GPS waypoints. Within each sub-quadrat *C. grandiflora* plants were counted based on individual stems or multiple stems originating from the same point (counting stopped at 100 plants), and average stem diameter and plant height visually estimated. Plants observed opportunistically further than 30 m from the river were additionally recorded. Two soil variables were quantified in each sub-quadrat (following Dale, 1978; Grice et al., 2000): soil erosion was classified in four categories, ranging from no erosion (= 0) to highly eroded (= 3), and soil texture was classified broadly as sand, loam or clay. The distance from each quadrat to the nearest perennial water source on the river (irrigation and natural dams) was measured using aerial imagery (Google, DigitalGlobe, 2013).

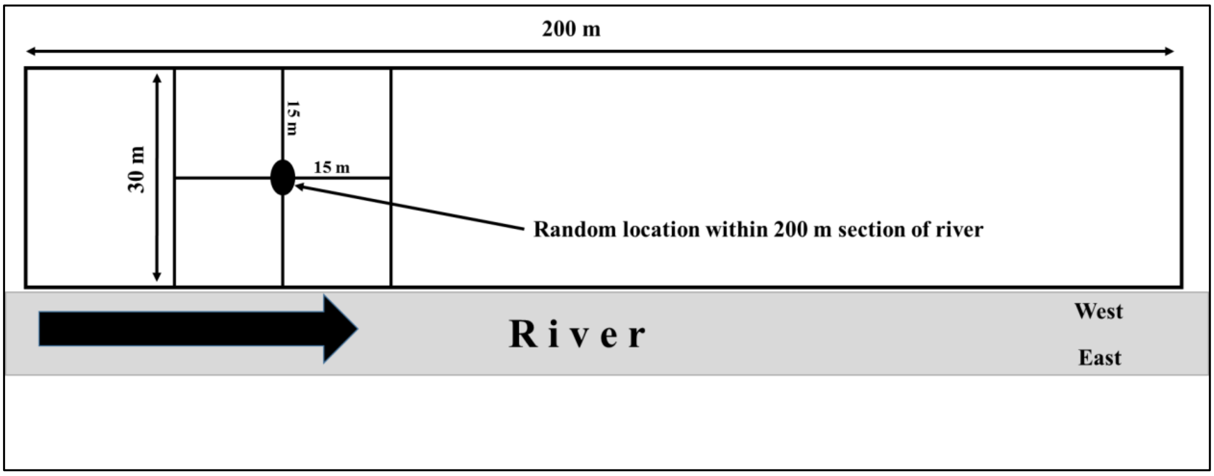

Figure 3. Schematic representing the layout of each 200 m section of the river with a randomly selected GPS location used as the centre point for the four contiguous 15 x 15 m sub-quadrats.

Data collection: occurrence and cover

Sixteen of the 36 surveyed quadrats were selected for more detailed surveying, following a random stratified sampling approach where four quadrats of high (> 2000 individuals/ha), medium (1001 – 2000 individuals/ha), low (1 – 1000 individuals/ha) and zero *C. grandiflora* density were selected. At each of these quadrats, a transect was established comprising six 1 m^2 plots placed at 10 m intervals perpendicular to the river. The first plot in each transect was located as close to the river as possible and the last placed 50 m inland, thus expanding outside the original 30 m area previously surveyed. In some transects not all six plots could be surveyed due to physical barriers (e.g. fences). Due to the low number of plots containing *C. grandiflora* in these transects, 16 additional transects were added 10 m downstream from the high density quadrats (i.e. four additional transects were surveyed 10, 20, 30 and 40 m downstream from each high density quadrat), resulting in a total of 32 transects.

Within each 1 m^2 plot the occurrence and percentage cover of *C. grandiflora* were recorded, as well as several biotic and abiotic variables. The variables selected were based on the initial density survey and similar studies conducted elsewhere on *C. grandiflora* (Dale, 1978; Grice et al., 2000; Rodrıguez-Estrella et al., 2010; Luizza et al., 2016). First, five environmental variables that were correlated with *C. grandiflora* occurrence in Australia were recorded in each plot: soil texture, bare soil cover, woody ground cover (i.e. aerial cover of all woody species < 4 m), erosion and distance to river (Dale, 1978; McFadyen and Harvey, 1991). An additional eight variables were recorded to quantify other environmental factors that could influence the occurrence and cover of *C. grandiflora*: soil moisture, soil depth, slope, topography, cover of rock, leaf litter and non-woody ground cover, and canopy cover (cover of all non-*C. grandiflora* species > 4 m). These variables were selected to broadly represent the main categories of factors that may influence fine-scale variation in plant occurrence patterns (temperature, water, soil nutrients, light, disturbances, and biotic interactions; Austin et al., 2011).

Soil texture observations were reduced to two categories prior to analysis by lumping clay and loam soils together since clay soils were only recorded in three plots. Three soil moisture measurements were taken in each plot using a FieldScout TDR 300 soil moisture reader (3.8 cm probe length; Spectrum Technologies, Illinois, USA), with the average of the three readings used in analyses. Soil moisture readings were repeated on four occasions (July and October 2014, March and August 2015), but since readings were strongly and significantly correlated (all $p < 0.05$) only data from July 2014 were used in analyses (details in Appendix B). One soil depth reading was taken per plot, using a thin pointed metal probe inserted into the soil. The remaining variables were visually estimated using a 20 % increment rank scale. Slope and topography showed little variation (the slope of > 90 % of plots was less than 10° and > 80 % of plots showed a flat topography) and were therefore not included in subsequent analyses. Collinearity among the remaining predictor variables was generally low, with bare soil and erosion showing the strongest correlation ($r = 0.78$; Appendix C).

Data analysis

Cryptostegia grandiflora density data from the initial survey were analysed using linear mixed effects models, testing if *C. grandiflora* density was related to soil texture and erosion. To account for spatial clustering of sub-quadrats, “Quadrat” was added as a random effect.

Using the data collected from the transects, the environmental predictors of *C. grandiflora* occurrence and cover were analysed using generalized linear mixed effect models, assuming a binomial distribution for both occurrence and cover data. To account for the nestedness of plots within transects, “Transect” was included as a random effect (Pinheiro and Bates, 2000; Bolker, 2008). A best subsets modelling approach was implemented where all combinations of predictor variables were tested, with the best performing models identified based on AIC values (Murtaugh, 2009). Hurdle models (Zuur et al., 2009) were implemented due to the large number of zeros in the dataset (as is often the case with alien occurrence surveys; Carboni et al., 2011), and because of the possibility that the mechanisms that determine the species presence can be different to those that determine its cover (Cragg, 1971; Ridout et al., 1998). In the hurdle models the occurrence of *C. grandiflora* was first modelled across all plots, while as a second step variation in *C. grandiflora* cover was analysed only in the plots where the species was present. Soil moisture could not be measured in 56 of the 129 plots due to the soil being too compact or because of physical barriers. Due to the potential importance of soil moisture for the establishment of *C. grandiflora* (Dale, 1978), analyses were repeated on the subset of the plots for which soil moisture data were available (hereafter "full dataset" refers to data from all plots and "soil moisture dataset" refers to subset of the dataset from which soil moisture was available). All statistical analyses were performed using R v 3.1.2 (R Core Development Team, 2015).

3.3. Results

Density

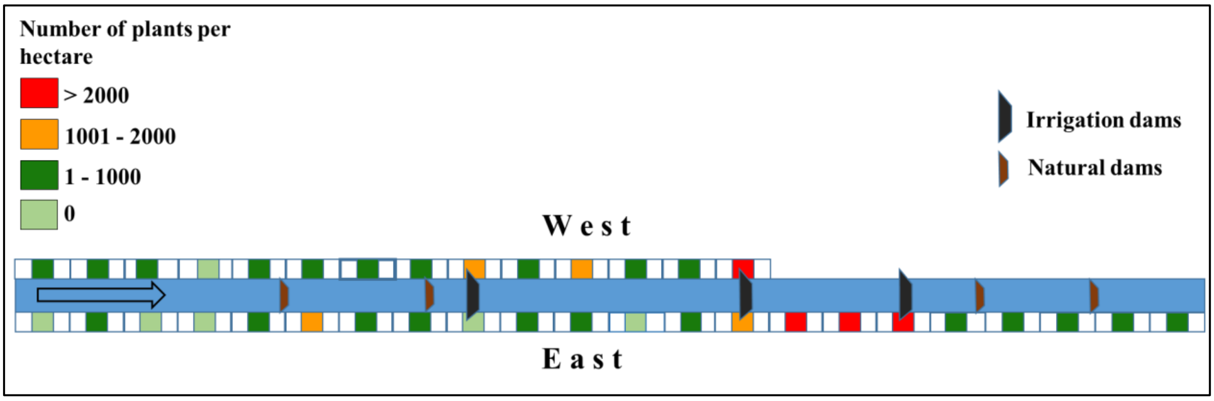

Figure 4. Schematic illustrating the 36 (200 x 30 m) survey areas (each containing one 30 x 30 m quadrat) along the Mogalakwena River, *C. grandiflora* densities and their proximity to water sources. See Fig. 5 for the relationship between *C. grandiflora* density and distance from permanent water sources.

A total of 2070 *C. grandiflora* plants were counted during the density survey. *Cryptostegia grandiflora* was absent from only six of the 36 quadrats (i.e. > 80 % prevalence; Fig. 4). This suggests that c. 18 ha of riparian vegetation along the studied section of the Mogalakwena River was invaded by *C. grandiflora* at the time of the survey (comprising an estimated c. 23'000 individuals). Plant density exceeded 2000 plants per hectare in over 20 % of quadrats, with a maximum density exceeding 4444 individuals/ha. *Cryptostegia grandiflora* density was significantly higher closer to water sources (three irrigation dams and four natural dams) (Poisson regression: $Chi^2 = 2498.1$, $p < 0.001$; Fig. 5). The majority of plants (99.4 %) occurred within the 30 m from the river with only 11 observations beyond 30 m. The maximum distance from the river where *C. grandiflora* was recorded was approximately 60 m, in a dry streambed that feeds into the river during the wet season. In the majority of sub-quadrats *C. grandiflora* plants had a mean stem diameter of < 1 cm and a mean height below 1 m (Fig. 6), with plants in only < 8% of sub-quadrats reaching an average height ≥ 3 m. Erosion and the soil texture were both significantly related to the density of *C. grandiflora*, with lower densities of the species in sites with sandy soils and no erosion (details in Appendix D).

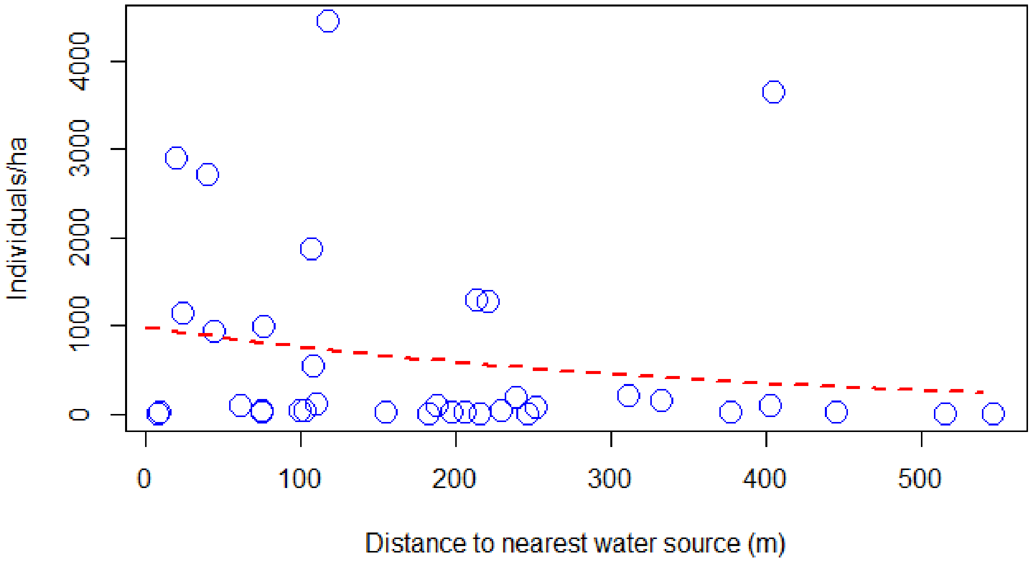

Figure 5. Significant negative relationship between *Cryptostegia grandiflora* density and distance to the nearest perennial water source (irrigation dams and natural dams). Dashed line indicates the best fit to the data as indicated by Poisson regression.

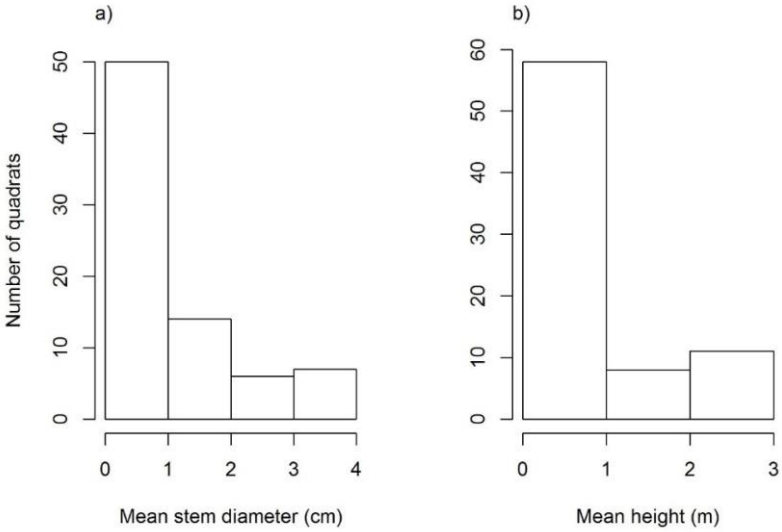

Figure 6. Mean estimated *Cryptostegia grandiflora* a) stem diameter and b) height per sub-quadrat. Mean stem diameter and height per sub-quadrat were estimated at 1 cm and 1 m intervals respectively.

Occurrence and cover

A total of 32 transects and 129 plots were surveyed for the occurrence and cover of *C. grandiflora*. Similar to the results from the density study, the occurrence of *C. grandiflora* was mostly restricted to the riparian area, with only 50 (3.4%) individuals recorded beyond 30 m from the river and *C. grandiflora* cover decreasing strongly with increasing distance from the river (Fig. 7).

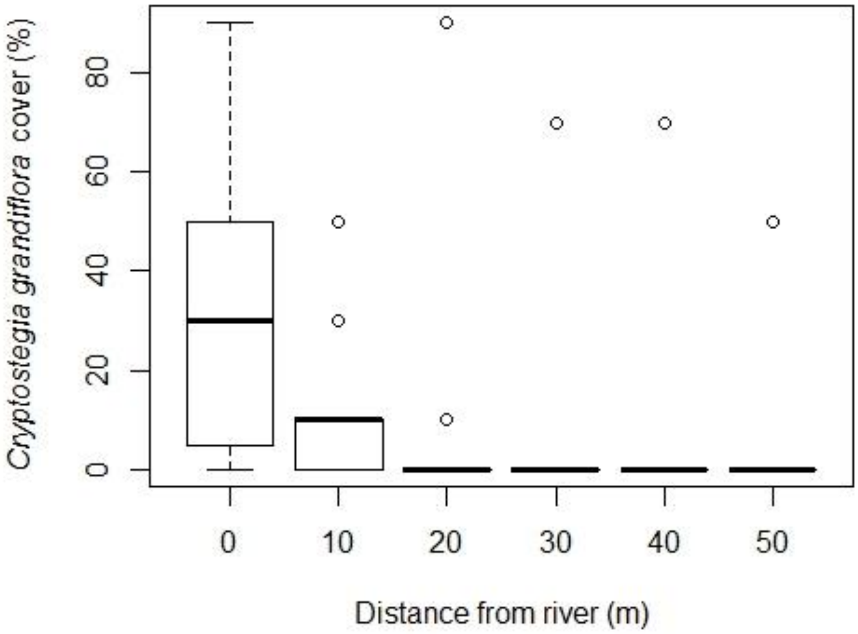

Figure 7: The relationship between the distance from the Mogalakwena River and *Cryptostegia grandiflora* cover (see Appendix E for plots of the relationships between the distance from the river and other variables, including the cover of *C. grandiflora* in only plots where the species was present). Boxplots indicate median (thick line), inter-quartile range (box), range (whiskers), and outliers (empty circles).

Results from the best subsets modelling showed that the occurrence of *C. grandiflora* was negatively related to distance from the river and positively correlated with the degree of soil erosion, in both the full dataset and soil moisture dataset (Table 1; see also Appendix F). In the best model based on the full dataset, the probability of occurrence of *C. grandiflora* was also lower in sandy soils than in clay or loam substrates. In contrast, in the best model based on the soil moisture dataset, soil moisture and cover of bare soil were both also negatively related to the occurrence of *C. grandiflora*. The model based on the full dataset explained c. 40% of the variation in the occurrence data, while the model based on the dataset including soil moisture explained less (c. 20%).

The predictor variables included in the *C. grandiflora* cover models were similar for the full dataset and soil moisture dataset. *Cryptostegia grandiflora* cover was positively related to soil depth and leaf litter cover and negatively related to non-woody ground cover for both datasets (Table 1). Additionally, *C. grandiflora* cover showed a positive relationship to distance from the river and soil moisture in the model based on the soil moisture dataset. Both models performed well, with 56 and 65% of the variation in cover explained by the models based on the full dataset and the soil moisture dataset respectively (Table 1).

Several variables were not included in the best models were included in other models with $\Delta AIC < 2$ (Appendix F). Soil depth, leaf litter cover, woody plant cover, canopy cover, rock cover and tree height were all positively related *C. grandiflora* occurrence (based on the full dataset), while non-woody plant cover and bare soil cover were negatively related to the species occurrence (based on the soil moisture dataset). *Cryptostegia grandiflora* cover was higher in finer textured soils, was positively related to the degree of erosion, canopy cover, bare soil cover and tree height, and was negatively related to rock cover and woody plant cover (full dataset). Several of these relationships were also observed in the soil moisture dataset where *C. grandiflora* cover was higher on fine textured soils, and positively correlated with erosion, woody plant ground cover, bare soil cover, canopy cover and tree height, and negatively related to rock cover.

Table 1. Results from best subsets modelling relating the occurrence and cover of *Cryptostegia grandiflora* to abiotic and biotic predictor variables, where all combinations of predictor variables were tested using generalized linear mixed effect models, with the best models identified from the lowest AIC values. Coefficients represent the effect of predictor variables after the application of the logit link function in the models. Results are shown for models based on the full dataset and on the subset of quadrats for which soil moisture data were available ("soil moisture dataset"). Transect was included as a random effect in all models. Soil texture was the only categorical variable in these models, and showed sandy soils had a negative impact on the probability of *C. grandiflora* occurrence. See Appendix F for summaries of all the other variable combinations with AIC differences of < 2 from the best ranked models.

Occurrence of *C. grandiflora*			
Full dataset	Predictors	Coefficient ± SE	P value
Deviance explained = 41%	Distance from river	-0.165 ± 0.040	<0.001
N = 129	Soil texture	-1.842 ± 1.092	0.091
	Erosion	2.306 ± 0.934	0.014
Soil moisture dataset			
Deviance explained = 20%	Distance from river	-0.165 ± 0.070	0.018
N = 73	Moisture	-0.021 ± 0.015	0.154
	Erosion	3.854 ± 1.723	0.025
	Bare soil	-1.237 ± 0.632	0.050

Cover of *C. grandiflora* in occupied plots			
Full dataset			
Deviance explained = 56%	Soil depth	0.111 ± 0.057	0.049
N = 53	Leaf litter	1.691 ± 0.730	0.021
	Non-woody plant cover	-3.545 ± 1.530	0.021
Soil moisture dataset			
Deviance explained = 65%	Distance from river	0.140 ± 0.084	0.096
N = 44	Soil depth	0.084 ± 0.059	0.154
	Moisture	0.023 ± 0.015	0.117
	Leaf litter	2.312 ± 0.952	0.015
	Non-woody plant cover	-3.657 ± 1.706	0.032

3.4. Discussion

Results from fine-scale surveys showed that *C. grandiflora* is widespread and abundant along this section of the Mogalakwena River. The species' density ranged from 0 to > 4400 plants/ha and its cover reached up to 90 % in some quadrats. Most individuals of *C. grandiflora* were located close to the river, with higher densities found in proximity to natural and artificial dams in the river, indicating that access to consistently higher soil moisture could be the reason for the higher abundance of the species. Few occurrences of *C.*

grandiflora were observed beyond the surveyed 30 m areas and these were generally in small streams where occasional flooding occurred during the rainy season. Elsewhere in *C. grandiflora*'s invaded range, initial invasion is similarly limited to riparian areas, although expansion into adjacent upland areas has occurred in some systems (Grice, 1996; Luizza et al., 2016; Rodrıguez-Estrella et al., 2010; Australian Weeds Committee, 2012).

Variation in the density, occurrence and cover of *C. grandiflora* was found to be related to several biotic and abiotic parameters, broadly representing water availability, soil conditions, disturbance and competition. Soil moisture has previously been recognized as a key determinant of the distribution and performance of *C. grandiflora*, particularly water availability to seeds prior to germination (Grice, 1996; Balducci, 2015). The results from this study similarly highlight the important influence of soil moisture, affecting both *C. grandiflora* occurrence and cover. Consistent with previous studies (Dale, 1978; Grice, 1996), *C. grandiflora* cover was positively related to soil moisture. Interestingly, however, *C. grandiflora* occurrence was negatively related to soil moisture. This may reflect the inclusion of distance from river in the best fit model, since soil moisture tends to decline away from the river (i.e. soil moisture and distance from the river do not vary independently). As a result, the negative relationship probably reflects the influence of soil moisture after accounting for the effect of distance (i.e. higher than expected soil moisture away from the river may inhibit the occurrence of *C. grandiflora*). The unexpected positive relationship between *C. grandiflora* cover and distance from the river appears to reflect the relatively early state of invasion in this area, as it is driven by just six large individuals that established further than 30 m from river. Closer to the river some quadrats have similarly high cover, but mean cover in the first three distance intervals is lowered by the presence of very small *C. grandiflora* individuals in some quadrats (i.e. low cover of *C. grandiflora* in some quadrats close to the river results in a lower average cover for this species closer to the river). As the higher abundance of seedling close to the river grow and increase their mean cover, this relationship may change from positive to negative.

Even though soil moisture was strongly positively related to *C. grandiflora* occurrence and cover, results also identified the influence of soil texture, soil depth, leaf litter, erosion, bare soil and non-woody ground cover. Several of these variables are also indirectly linked to soil moisture balance, suggesting that the mechanism by which these variables affect *C. grandiflora* may be through the availability of soil moisture (following e.g. Dale, 1978;

Balducci, 2015), although their effects could also be via other mechanisms. For example, soils with higher clay content (and therefore higher water holding capacity) were positively correlated to the density and occurrence of the species, and the cover of *C. grandiflora* increased with the depth of the soil (related to the volume of water stored). Additionally, leaf litter had a significant positive correlation with *C. grandiflora* cover, suggesting that litter does not inhibit germination or establishment (as suggested by Facelli and Pickett, 1991), but instead may provide protection from desiccation (Dale, 1978).

Disturbance plays a crucial role in structuring plant communities and can often favour the establishment of invasive species (Hobbs and Mooney 1986; Rejmánek, 1989; Hobbs and Huenneke 1992). In riparian habitats, periodic flooding alters the vegetation structure by forming gaps in the non-woody ground cover and provides favourable, resource-rich conditions for the establishment of species (including invasive species; Renöfält et al., 20105; Brown and Peet 2003). The reduction of native plant species cover by grazers and increased erosion due to trampling also facilitates the establishment of invasive species in riparian areas (Hobbs et al., 1992; Keeley et al., 2003). The results from this study match with these general patterns, with *C. grandiflora* density and occurrence higher in areas with greater erosion. The unexpected negative relationship between *C. grandiflora* occurrence and bare soil, however, suggests that *C. grandiflora* may not benefit from all types of disturbance (although the presence of bare soil may also reflect processes other than disturbances). In consequence, examining the influence of other types of disturbance (in addition to soil erosion) may be useful for determining the overall importance of disturbance for the distribution and invasion success of *C. grandiflora*.

In practice, understanding the influence of biotic and abiotic variables on the performance of alien species at fine scales allows the implementation of practices that aid in concentrating monitoring efforts and effective control measures to manage invasive species (Richardson et al., 2004; Pyšek and Hulme, 2005; Davies and Sheley, 2007; Latimer et al., 2009). The results from this research revealed that the drivers influencing *C. grandiflora* occurrence differed from those most strongly correlated with the cover of the species. Erosion and bare soil had weaker influences on *C. grandiflora* cover than on species occurrence, suggesting that this species can occur in moist, disturbed areas but possibly requires conditions of high leaf litter, low non-woody plant cover and deep soils with high moisture to initially establish. Given that the prevention of this species' spread is challenging due to *C. grandiflora*'s large potential dispersal distance, abundant seed production, and the cost associated with control once established, early detection of occurrences in areas of relatively high soil moisture and erosion before individual plants reach reproductive maturity might be the best form of management (Grice, 2006; Australian Weeds Committee, 2012; Balducci, 2015).

From an applied perspective, this study suggests two options for reducing the probability of establishment of *C. grandiflora*: by increasing non-woody vegetation cover and by decreasing soil erosion. However given the disturbance caused by periodical flooding in the riparian zone, neither of these options are likely practical. Indeed, adequate soil moisture and the occurrence of disturbances are likely key requirements for *C. grandiflora* invasions within climatically suitable regions. Therefore the hydrology of the site may limit the management options for the species in riparian areas that have already been invaded.

The factors driving a species distribution at one spatial scale are likely to influence patterns at another scale (Pauchard and Shea 2006). Indeed, predictions of broad-scale distribution patterns may be improved by incorporating information for finer scales, and fine-scale distributions may be constrained by broad-scale factors (Levin, 1992). Thus, a comprehensive multi-scale approach can contribute more a detailed understanding of the invasion process than a broad- or fine-scale study in isolation, and can assist in identifying more efficient and effective management strategies (Stohlgren et al., 1998; Mack, 2000; Pauchard and Shea 2006; Latimer et al., 2009). Ultimately these fine-scale results will act as a component in a multi-scale approach to assess the invasive status and predict the potential distribution *C. grandiflora* in southern Africa, providing an indication of the habitats that may be vulnerable to *C. grandiflora* invasion within broader, climatically-suitable regions.

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3.6. Appendix:

Appendix B

Table B1: Monthly rainfall data (mm) from 2012 to 2016, supplied by the South African Weather Service from the Saamboubrug Police station (22.5700°S 28.5800°E; 25 km from the Mogalakwena study site).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
2012	79	5.5	21	0	0	0	0	0	0	41	11	89.5	247.0
2013	243	0	11.5	25	0	0	0	0	0	31.4	49	49.5	409.4
2014	65.5	121	89	0	0	0	0	0	0	0	22.3	71.4	369.2
2015	17	27.5	60	0	0	2	0	0	28	0	12.5	0	147.0

Table B2. Spearman rank correlation of the four sets of soil moisture measurements recorded during 2014 and 2015. All four sets of readings were significantly positively correlated ($p < 0.05$ for all comparisons) and therefore only data from the first set of measurements was used in analyses.

	October 2014	March 2015	August 2015
July 2014	0.87	0.76	0.72
October 2014		0.80	0.76
March 2015			0.67

Appendix C

Table C1. Pearson's correlation between all predictor variables. All correlations < -0.5 and > 0.5 are highlighted in bold.

Full dataset	Soil depth	Erosion	Leaf litter	Ground cover woody	Ground cover non woody	Bare soil	Canopy cover	Rock cover	Tree height
Distance	-0.46	-0.21	0.26	0.05	0.10	-0.25	0.07	0.15	-0.01
Soil depth		0.15	-0.17	-0.11	-0.12	0.05	0.06	-0.21	0.06
Erosion			-0.63	-0.22	-0.40	**0.79**	-0.46	0.12	-0.42
Leaf litter				0.33	0.08	**-0.66**	**0.54**	-0.25	0.41
Ground cover woody					0.06	-0.28	0.21	-0.07	0.07
Ground cover non woody						-0.49	-0.03	-0.01	0.06
Bare soil							-0.43	0.12	-0.34
Canopy cover								-0.26	**0.65**
Rock cover									-0.21
Tree height									

Soil moisture subset	Soil depth	Moisture	Erosion	Leaf litter	Ground cover woody	Ground cover non-woody	Bare soil	Canopy cover	Rock cover	Tree height
Distance to river	-0.31	-0.37	0.12	0.06	0.00	-0.11	0.02	0.05	0.17	0.08
Soil depth		0.28	0.01	-0.14	-0.10	0.00	-0.14	0.05	-0.17	0.01
Moisture			0.05	-0.13	0.03	0.03	-0.04	-0.27	-0.06	-0.33
Erosion				**-0.62**	-0.18	**-0.53**	**0.77**	-0.47	0.26	**-0.52**
Leaf litter					0.28	0.04	**-0.65**	0.51	-0.13	**0.51**
Ground cover woody						0.04	-0.27	0.21	0.03	0.10
Ground cover non-woody							**-0.54**	0.09	-0.04	0.12
Bare soil								-0.48	0.20	-0.40
Canopy cover									-0.20	**0.72**
Rock cover										-0.19

Appendix D

Table D1. The relationship between *C. grandiflora* density and soil texture (clay and loam vs sand) and erosion.

Predictors	**Coefficient ± SE**	**P value**
Soil texture: Sand < Clay & Loam	-0.187 ± 0.083	0.024
Erosion	1.305 ± 0.108	<0.001

Appendix E

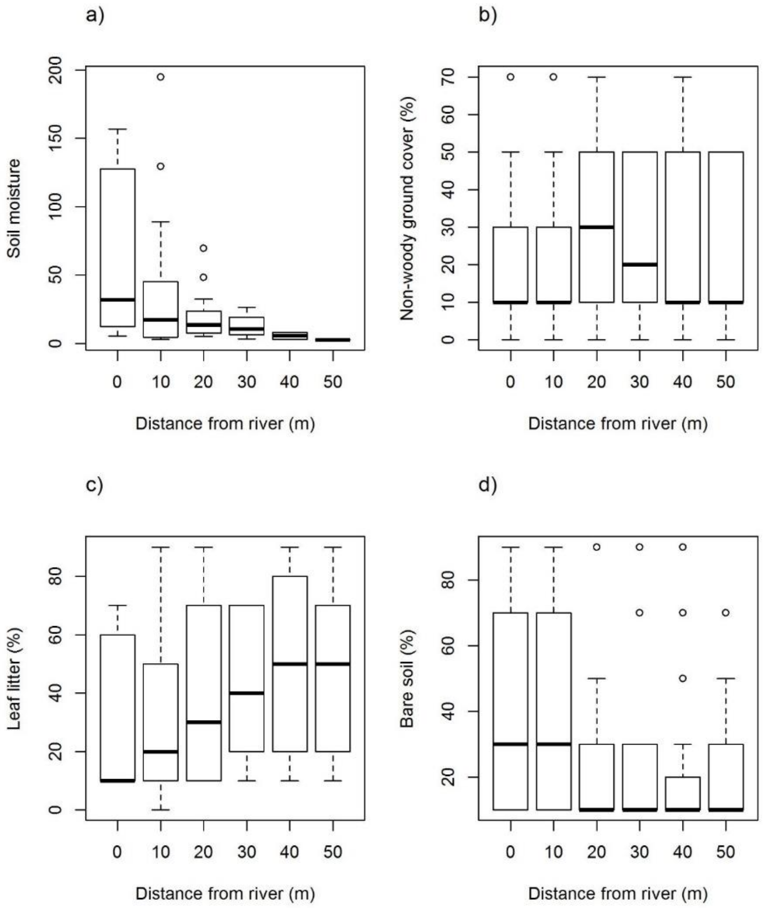

Figure E 1: The relationship between the distance from the Mogalakwena River and a) the volumetric water content within the soil (i.e. % soil moisture), b) non-woody ground cover; c) leaf litter cover and; d) bare soil cover per plot. Boxplots indicate median (thick line), inter-quartile range (box), range (whiskers), and outliers (empty circles).

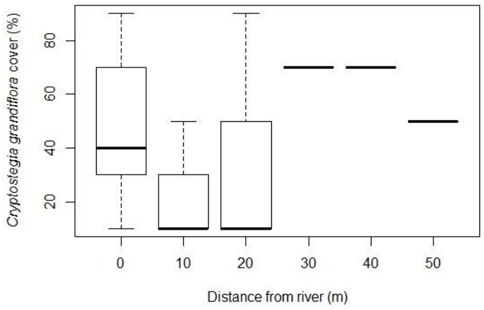

Figure E 2: The relationship between *C. grandiflora* cover and the distance from the Mogalakwena River for all plots where the species was present (i.e. where *C. grandiflora* cover > 0 %). Boxplots indicate median (thick line), inter-quartile range (box) and range (whiskers). Distance 0 – 10 m (n = 24), distance 10 – 20 m (n = 22), distance 20 – 30 m (n = 4), distance 30 – 40 m (n = 1) and, distance 40 – 50 m (n = 1).

Appendix F

Table F 1: Results from best subset modelling of the occurrence and cover of *C. grandiflora* (using the full dataset and the soil moisture dataset). All models reported here differ by < 2 from the AIC value of the best model. The coefficients of all continuous predictors, and the ranking of all factor levels for categorical predictors, are shown. Across all models the direction of all coefficients and the ranking of all factor levels were consistent. 'S' = Sand and 'C'= Clay.

Occurrence of *C. grandiflora* (modelled using the full dataset)

Model rank	AIC	Distance	Soil depth	Soil texture	Erosion	Leaf litter	Ground cover woody	Ground cover non- woody	Bare soil	Canopy cover	Rock cover	Tree height
1	86.902	-0.166		S>C	2.307							
2	87.297	-0.184		S>C	2.255						0.501	
3	87.862	-0.176		S>C	2.559		0.596					
4	88.127	-0.161		S>C	2.135			-0.394				
5	88.219	-0.151			1.428							
6	88.219	-0.168			1.927		0.786					
7	88.266	-0.193		S>C	2.472		0.608				0.484	
8	88.359	-0.169		S>C	2.745				-0.305			
9	88.482	-0.181		S>C	2.063			-0.420			0.522	
10	88.496	-0.184		S>C	2.906			-0.786	-0.693		0.551	
11	88.499	-0.167		S>C	2.510	0.268						
12	88.514	-0.164		S>C	2.853			-0.696	-0.595			
13	88.574	-0.186		S>C	2.521	0.384					0.528	
14	88.621	-0.187		S>C	2.768				-0.351		0.500	
15	88.623	-0.156	0.013	S>C	2.238							
16	88.723	-0.154			2.326			-0.717	-0.740			
17	88.852	-0.166		S>C	2.325							0.029
18	88.890	-0.165		S>C	2.314					0.026		

Occurrence of *C. grandiflora* (modelled using the soil moisture dataset)

Mod rank	AIC	Distance	Soil depth	Soil texture	Soil moisture	Erosion	Leaf litter	Ground cover woody	Ground cover non- woody	Bare soil	Canopy cover	Rock cover	Tree height
1	66.768	-0.1651			-0.0213	3.8542				-1.2372			
2	67.031	-0.1029				2.8873				-0.9485			
3	68.316	-0.1719			-0.0248	3.825				-1.3471			-0.119
4	68.387	-0.1804			-0.0223	3.8087				-1.2398		0.306	
5	68.421	-0.168			-0.0235	3.7808				-1.3636	-0.1876		
6	68.577	-0.1625			-0.0208	3.792			-0.355	-1.3343			
7	68.682	-0.1711			-0.0215	3.8893		0.2749		-1.1976			
8	68.708	-0.1611	0.0086		-0.0222	3.7717				-1.2073			
9	68.712	-0.102				2.8305			-0.4116	-1.0593			
10	68.745	-0.1635		S>C	-0.0214	3.8355				-1.2794			
11	68.753	-0.1658			-0.0219	3.8448	-0.0762			-1.2789			

Cover of *C. grandiflor*a in occupied plots (modelled using the full dataset)

Mod rank	AIC	Distance	Soil depth	Soil texture	Erosion	Leaf litter	Ground cover woody	Ground cover non-woody	Bare soil	Canopy cover	Rock cover	Tree height
1	30.711		0.111			1.691		-3.545				
2	31.179		0.115			1.496		-3.662				0.232
3	31.258	0.073	0.122			1.925		-3.142				
4	31.673		0.119			2.621		-3.080	0.960			
5	32.161		0.112		1.385	2.327		-3.125				
6	32.285		0.124	S>C		1.545		-3.727				
7	32.293		0.115			1.459		-3.540		0.250		
8	32.401		0.169	S>C		2.783		-3.133	1.450			
9	32.622	0.050	0.119			1.667		-3.243				0.169
10	32.636		0.111			1.644		-3.557			-0.255	
11	32.663	0.062	0.129			2.581		-2.841	0.729			
12	32.677		0.106			1.720	-0.124	-3.518				
13	32.704		0.122			2.080		-3.260	0.625			0.197

Cover of *C. grandiflora* in occupied plots (modelled using the soil moisture dataset)

Mod rank	AIC	Distance	Soil depth	Soil texture	Soil moisture	Erosion	Leaf litter	Ground cover woody	Ground cover non- woody	Bare soil	Canopy cover	Rock cover	Tree height
1	29.327	0.140	0.084		0.023		2.312		-3.657				
2	29.639		0.092				1.754		-3.516				
3	30.095	0.136	0.094		0.028		1.996		-3.730				0.257
4	30.424	0.067	0.104				1.956		-3.167				
5	30.489		0.098				1.561		-3.645				0.205
6	30.590	0.160	0.125		0.027		2.359	0.884	-4.371				
7	30.726		0.073		0.015		1.541		-4.379				0.292
8	30.819		0.072		0.010		1.747		-3.781				
9	30.856		0.100				2.539		-3.188	0.815			
10	31.013	0.144	0.089		0.023		1.985		-3.306		0.261		
11	31.021		0.102	S>C			1.592		-3.730				
12	31.139	0.131	0.090		0.022		2.732		-3.407	0.501			
13	31.228	0.133	0.087		0.023	0.703	2.603		-3.476				
14	31.260	0.148	0.082		0.023		2.255		-3.509			-0.280	
15	31.296		0.095			1.050	2.223		-3.221				
16	31.326		0.095				1.560		-3.522		0.212		

CHAPTER 4

4.1. General summary

The aim of this project was to assess the potential risk posed by C. grandiflora and C. madagascariensis by determining the drivers of the species distributions, and to suggest possible management options. Central to this assessment was, first, to delimit the species' current extent through collating occurrence data from available resources (including GBIF and SAPIA) and field surveys in Botswana, Namibia and South Africa (Chapter 2). Secondly, to predict the potential distribution of both Cryptostegia species, thereby highlighting currently unoccupied areas that are climatically suitable and could be at risk of invasion in the future (Chapter 2). Finally, the environmental factors related to fine-scale variation in the distribution, density and cover of C. grandiflora were identified for an invasive population along the Mogalakwena River (Chapter 3).

Cryptostegia grandiflora is widespread in southern Africa, with at least five invasive populations of this species existing. In contrast, few *C. madagascariensis* plants were recorded, none of which occurred outside of cultivation. Using these occurrence records in conjunction with other published occurrence records for the species (from both their native and invaded ranges), species distribution modelling was used to investigate the influence of climatic parameters on the distribution of *C. grandiflora* and *C. madagascariensis* to predict their potential ranges. Mean temperature of the coldest quarter most strongly influenced habitat suitability for the species, with optimal temperatures ranging between 15° and 25°C. Consistent with observations from the surveys, the predicted range of *C. grandiflora* was considerably larger than that of *C. madagascariensis* in southern Africa. Climatically suitable areas for *C. madagascariensis* were restricted to Mozambique, the Kariba dam region (Zimbabwe) and a small area in the north-eastern corner of South Africa (Pafuri section of Kruger National Park). In contrast, most of Mozambique and large portions of the northern provinces of South Africa and southern Zimbabwe were predicted to be suitable for *C. grandiflora*. The differences in the potential ranges between the two species suggest that *C. grandiflora* can potentially occur in areas too dry for *C. madagascariensis*. While coarse-scale species distribution modelling can reveal broad regions climatically suitable for the species, *C. grandiflora* has been observed in areas predicted to be climatically unsuitable, suggesting suitable microclimates within otherwise unsuitable areas can provide conditions conducive to *C. grandiflora* establishment and survival.

At fine-scales the distribution of *C. grandiflora* was patchy, with much spatial variability in the cover and density of the species. However, the species highest densities were consistently found in close proximity to artificial irrigation dams where monospecific stands appeared to outcompete native vegetation. Additionally, the species was largely limited to riparian areas, with a clear trend for lower cover further from the river. *Cryptostegia grandiflora* was more likely to occur in soils with higher clay content, high levels of erosion and higher bare soil cover. In contrast, the species cover was greater in deeper soils with more leaf litter and less non-woody plant cover. These results revealed that the performance of *C. grandiflora* is related to several biotic and abiotic variables, and that the drivers influencing *C. grandiflora* occurrence differed from those most strongly correlated with the cover of the species. Erosion and bare soil cover were related to *C. grandiflora* occurrence, but not cover, suggesting that this species can occur in moist, disturbed areas but possibly achieves optimal growth under conditions of high leaf litter, low non-woody plant cover and deep soils with high moisture. Understanding the influence of these biotic and abiotic variables allows the implementation of practices that aid in concentrating monitoring efforts and effective control measures. For example, areas with higher moisture levels and frequent disturbance should be the focus for monitoring, with the implementation of such targeted surveys reducing both costs and time.

4.2. Conclusions

Both *Cryptostegia* species are successful invaders in several countries and have caused significant economic and ecological damage where they have established (McFadyen and Harvey, 1990; Kriticos et al., 2003). Their fast growth rates, adaptable growth forms and large dispersal range contribute to their invasiveness (Grice, 1996; Brown et al., 1998; Tomley, 1998; Bebawi and Campbell, 2002; Australian Weeds Committee, 2012). Both species currently occur in many tropical and subtropical regions across the globe, but the results from this study additionally show that where sufficient moisture is locally available (e.g. in riparian areas) and minimum temperature are above 15°C, *Cryptostegia* can establish in semi-arid areas (e.g. parts of Brazil, Ethiopia and southern Africa). As a result, this suggests that both species could potentially pose a significant risk to southern Africa.

The small number of occurrences, limited suitable range (mostly restricted to Mozambique) and no evidence of escape out of cultivation shows that *C. madagascariensis* is not an imminent risk to southern Africa. This, however, does not mean *C. madagascariensis* does not have the potential to become invasive, as seen in other areas. Eradication of *C. madagascariensis* has been attempted in Hawaii, where controls measures have significantly reduced the species' abundance, suggesting that complete removal of this species is a possibility (Penniman, 2011). Therefore, *C. madagascariensis* is a prime candidate for aggressive management actions and its feasibility for potential eradication target should be fully assessed. In contrast, the widespread occurrence of cultivated, naturalized and invasive populations and negative impacts of *C. grandiflora* highlights the risk this species already poses to southern Africa. In addition, the predictions of this species' potential distribution illustrate that large areas beyond the species current occurrences are climatically suitable and, therefore, that further expansion of the species range is possible. As a result, *C. grandiflora* should be targeted for urgent management actions to prevent future spread.

4.3. Management options

When considering the control options for *C. grandiflora* in southern Africa, lessons learnt from other invaded ranges, in combination with the results of this study, can aid in deciding on the most efficient and cost-effective techniques. In one of the worst affected areas in Australia, several methods (including fire, herbicide treatments, mechanical removal and biological control) have had varying levels of success. Fire is a cost-effective management tool often used in the control of invasive species (Emery and Gross, 2005) and has been successful in reducing the extent of large invasive *C. grandiflora* populations (Grice, 1997; Bebawi and Campbell, 2000). Herbicide treatments and mechanical control are also effective control techniques for smaller or isolated populations, however these techniques become uneconomical when targeting large or widespread populations (Vitelli, 1992; McFadyen and Harvey, 1990; Tomley, 1998). The introduction of "rubber vine rust" (*Maravalia crytostegiae*) in invaded areas of Queensland has been very successful causing significant reductions in *C. grandiflora* populations (Mo et al., 2000; Radford 2003; Tomley and Evans, 2004; Tomley and Evans, 2004; Tomley and Evans, 2004; Campbell and Brazier, 2016).

Finding suitable control techniques and identify populations where efforts should be focused is a crucial part in the effective management of *Cryptostegia* species in southern Africa. The extent of *C. grandiflora*'s current distribution and the number of existing invasive populations eliminates the possibility of eradication of this species in southern Africa and alternative management strategies should be investigated. Although fire is a successful method to control large *C. grandiflora* populations elsewhere (Grice, 1997; Bebawi et al., 2000), the semi-arid areas of southern Africa may be too dry to provide sufficient fuel to sustain fires (Brooks and Lusk, 2008). Additionally, burning in riparian zones may adversely impact native vegetation and wildlife (Valentine et al., 2006). Herbicide treatment will be uneconomical for larger populations and could negatively impact native vegetation and river systems. Mechanical removal through cutting stems at ground level of *C. grandiflora* along the Mogalakwena River proved unsuccessful, time-consuming and very costly (pers. obs). Therefore, given the success of *Maravalia crytostegiae* as a biocontrol for *C. grandiflora* in Australia, it could be a potentially efficient control option in southern Africa and further investigation is warranted.

As for most invasive alien species, effective management should incorporate a combination of control strategies (Hulme, 2006). The best management strategy for *C. grandiflora* in southern Africa would be a combination of methods, particularly focusing on reducing the seed production (Grice et al., 1996) and spread into uninvaded areas. In particular, areas with significant conservation and economic value, like the Kruger National Park and Mapungubwe National Park, as well as their upstream areas, which fall within the high-risk areas for both species, should be prioritised for control actions. More generally, areas downstream of invasive populations should be targeted for monitoring, with the rapid removal of any new occurrences beyond an established containment line.

Whilst many advances have been made in managing biological invasions, the introduction of species into novel areas outside of their native ranges and their associated impacts show no signs of abating (Seebens et al., 2015; Rouget et al., 2016). Minimising the damage caused by these biological invasions relies on efficient, pro-active management strategies. This study demonstrates that understanding the drivers of invasions at multiple spatial scales enables decision makers to identify efficient and cost-effective management options of emerging invaders like *Cryptostegia*.

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