Towards understanding alien floristics within an urban matrix: The case of Durban, South Africa

by

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ABSTRACT

Invasive alien plant species (IAPs) represent a major threat to biodiversity loss and ecosystem functioning globally. Alien species can take advantage of changes in ecosystems brought about by natural and non-natural disturbances and compete with indigenous species for resources. Urban areas are becoming increasingly susceptible to plant invasions due to increasing anthropogenic activity levels as urban human populations increase and changing climatic conditions that favour alien species. If uncontrolled, IAP impacts can bring about the transformation of natural habitats and exclusion of indigenous species. Given the limited financial and human resources available for IAP monitoring and control in developing countries like South Africa, increased efforts to monitor the prevalence of IAPs more efficiently and identify the drivers of invasiveness within cities is urgently needed to prioritise urban green spaces and species for monitoring and control interventions.

Frameworks to monitor alien invasions, identify their drivers and impacts and prioritise sites and species for control of alien plants have been limited in the urban context, particularly within developing countries such as South Africa. Where these frameworks have been developed, there are challenges of them not being equally effective at different geographic scales and across different habitats. Furthermore, these frameworks often also suffer the weakness of not capturing the multi-dimensionality of plant invasiveness. This inspired the current study, which aimed to inform the design of an evidence-based framework that aids in prioritising urban green spaces and alien species for monitoring and control interventions by carrying out a set of inter-related investigations that addressed the following research questions: (1) What are the major environmental drivers of alien species (particularly IAPs) distribution? (2) Are alien and indigenous plant functional diversity (FD) and alien-indigenous co-occurrence patterns influenced by non-natural disturbance? (3) What is the influence of non-natural disturbance on the alien and indigenous soil seed bank (SB) floristics? and (4) Can selected seed physical and/or chemical traits be used as potential indicators of IAP persistence in natural SBs? These research questions were addressed using a case study approach: plants occurring within selected natural green spaces in an urban matrix in the rapidly developing city of Durban (eThekwini Metropolitan Area [EMA]), located within the Maputaland-Pondoland-Albany biodiversity hotspot in subtropical KwaZulu-Natal, South Africa.

Classical vegetation survey techniques were used to identify and quantify (in terms of richness, density and diversity) aliens within 30 natural green spaces in the study area. Levels of non-natural disturbance were quantified using a scoring matrix, and soil SB samples were collected from each site. Cumulatively, 80 alien plant species were identified, of which 35 are presently categorised as IAPs in the EMA. Once it was established that IAP species richness and density were significantly positively related to disturbance level, selected parameters measured (viz. alien species richness and density) were used to develop an Alien Invasive Index (AII), the utility of which was validated in terms of its ability to discriminate between sites with low and high levels of invasiveness. The findings demonstrate the value of integrating the data generated using vegetation surveys and Geographic Information Systems to monitor and prioritise urban green spaces for alien control interventions. Importantly, the results suggest that the AII could assist in identifying invasive plant hotspots within urban areas.

In a related study, alien and indigenous floristic patterns were probed further by comparing alien and indigenous species richness, density, diversity (alpha and functional), and species co-occurrence levels at the 30 sites in relation to non-natural disturbance levels. The ratio of alien to indigenous species was 1:1.5, with Asteraceae being the most dominant family. The relationship between species richness and alpha diversity differed for alien and indigenous species. Alien species were found to have higher FD, except for reproductive mode. Additionally, FD was significantly related to disturbance levels, alien species richness, and alien plant density. Co-occurrence data showed that alien-indigenous species pairs co-occur at high levels in urban spaces. Three notable alien-indigenous pairs (*Centella asiatica-Conyza sumatrensis, Centella asiatica-Solanum mauritianum* and *Bidens pilosa-Commelina erecta*) co-occurred at more than 40% of sites, while two alien-alien pairs (*Solanum mauritianum-Lantana camara* and *Conyza sumatrensis-Tagetes minuata*) co-occurred at more than 50% of sites. The positive interactions between different alien species identified here contribute to the growing amount of evidence that supports the Invasional Meltdown Hypothesis (IMH). The results also showed that non-natural disturbance might lead to high levels of alien plant species diversity and facilitatory alien-alien and alien-indigenous species interactions. Understanding co-occurrence patterns could help design alien control programmes that focus on reducing alien-alien facilitation.

For the study examining alien and indigenous species soil SBs in relation to non-natural disturbance across the 30 sites, samples collected were processed using a modified seedling emergence method, incubated under greenhouse conditions (with irrigation), and monitored for one year. Germinants were identified and quantified, and comparisons were made between the soil SB and standing vegetation (SV). Cumulatively, 70 species belonging to 20 families were identified within the SB, with a higher presence of indigenous (60%) than alien species (40%). Overall, the SB flora was dominated by graminoids. Of the 70 species found in the SB, 69 were shared with the SV. Irrespective of the disturbance level, indigenous was higher than alien plant density within the SB. The findings of this study have implications for managers of urban green spaces since alien species in SBs could exploit niches created by disturbances, promoting urban invasions.

In the final investigation, seeds of five IAPs were buried for two years at an experimental site to mimic seed burial within natural SBs. Additionally, the seeds of these species were characterised in terms of selected morphological and anatomical (seed mass, seed size, seed coat thickness) and chemical traits (estimated lipid content and changes in lipid melting properties). This study was designed to assess whether seed physical and/or chemical traits can be used as potential indicators of IAP persistence in natural SBs. Batches of buried seeds were exhumed every three/six months for viability (germinated seeds + seeds that stained positively following a Tetrazolium Chloride Test). Seed mass, size and coat thickness differed significantly across species, with *Canna indica* having the biggest and heaviest seeds of all species and the thickest seed coat. *Solanum mauritianum* had the smallest and lightest seed, with one of the thinnest seed coats. Results showed decreases in viability for four species (*Canna indica*, *Melia azedarach*, *Senna didymobotrya*, and *Ricinus communis*), while *Solanum mauritianum* maintained a 100% viability throughout the experimental period. However, while the viability of *C. indica*, *R. communis*, and *S. didymobotrya* was dominated by germinable seeds before burial, as viability declined with an increase in burial time, viability was dominated by seeds that were not germinable but stained positively. *Melia azedarach* differed slightly, where viability declined with burial time, but the majority of the seeds that were viable remained germinable. The longest ageing rate based on P50 was observed for *C. indica* (lowest estimated lipid content), while *M. azedarach* had the shortest ageing rate (highest estimated lipid content). Decreases in germination over time for *C. indica*, *R. communis*, *M. azedarach*, and *S. didymobotrya* led to changes in either/both enthalpy of melting of the lipid, and the temperature of the lipid melt, which could be related to different seed deterioration mechanisms when buried.

This study did not identify significant relationships between the seed physical and/or chemical traits and SB longevity using the traits investigated. This could be explained by the relatively low number of species and traits studied and/or the phenotypic plasticity associated with seed post-harvest physiology in wild species. Nevertheless, the study gave rise to the beginnings of a conceptual continuum of IAP seed bank longevity, which, once populated with data for more species, could supplement the criteria currently used for assessing species invasiveness.

As mentioned earlier, alien plant invasions are a major challenge for developing countries, particularly in urban settings. In countries like South Africa, the management of IAPs is complicated by heterogeneous combinations of non-natural disturbances, site-specific levels of disturbance intensity, and diverse vegetation types and associated species richness. The results clearly show that IAPs thrive under high levels of non-natural disturbance in urban green spaces and that alien and indigenous species can co-occur in various vegetation types. The AII was able to identify alien hotspots within the study area and may represent a useful tool for conservation practitioners/land managers. *Lantana camara* and *Solanum mauritianum* emerged as the most problematic IAPs currently in the study area. It was also evident that disturbance levels play a role in soil SBs of alien and indigenous species richness and plant density, and some problematic IAPs, notably *S. mauritianum*, can persist in SBs for long periods due to morphological, anatomical, and chemical traits. The results generated were used to design a multi-disciplinary and multi-dimensional framework that aids in prioritising sites and species for alien plant monitoring and control within urban areas. The methods proposed for assessing the prevalence and drivers of alien plant species and the indicators identified as potential indicators of their impacts in the framework can assist land managers, practitioners, and researchers develop recommendations and actions for alien plant monitoring and control in urban areas. The framework is designed to supplement and aid, and not replace, existing EMA policies/guidelines for alien plant control by preceding their planning and preparation phases. It could also help in developing new approaches to monitoring alien plant species in urban spaces.

PREFACE

The experimental work described in this dissertation was carried out in the School of Life Sciences, University of KwaZulu-Natal, Durban, from July 2016 to July 2019, under the supervision of Dr. Syd Ramdhani and Prof. Sershen Naidoo.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

DECLARATION 1: PLAGIARISM

I, Minoli Appalasamy, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
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Minoli Appalasamy **Date:** 27/01/2021

DECLARATION 2: PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis (include publications in preparation, submitted, in press, and published and give details of the contributions of each author to the experiment work and writing of each publication)

Publication 1: Appalasamy, M. and Ramdhani, S., 2020. Aliens in the city: Towards identifying non-indigenous floristic hotspots within an urban matrix. Flora, p.151631.

- Author contributions: MA, SR, and S conceived the idea. MA collected and analysed the data. MA led the writing with contributions from SR and S.

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I can do all things through Christ who strengthens me
Philippians 4:13.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF ABBREVIATIONS

1/D	Simpson's inverse index
A	Air
AII	Alien invasive index
AM	Ante meridiem
ANOVA	Analysis of variance
B	Birds
C	Central
CABI	Centre for Agriculture and Bioscience International
CR	Cumulative alien species richness
CD	Cumulative alien plant density
cm	Centimeter
CO_2	Carbon dioxide
DEA	Department of Environmental Affairs
D'MOSS	Durban Municipal Open Space System
DSC	Differential scanning calorimetry
E	East
EMA	eThekwini Municipality
FEG	Field emission gun
GIS	Geographic information systems
GLM	Generalised linear model
H	Humans
H	Shannon's index
h	Hour
H'	Shannon's exponential index
IAPS	Invasive alien plant species
IAPs	Invasive alien plants
ID	Invasive alien plant density
IL	Illinois
IMH	Invasional Meltdown Hypothesis
IR	Invasive alien species richness
KZN	KwaZulu-Natal
LC	Least concern
m	Meters
m/s	Meters per second
MD	Maryland
MPA	Maputaland-Pondoland Albany
N	North
n	Number of species/ sample size
NEMBA	National Environmental Management: Biodiversity Act
NIH	National Institute of Health
NMDS	Non-metric multidimensional scaling

P	Probability
P50	Lethal dose 50
PAST	Paleontological Statistics
PC	Principle component
PCA	Principle component analysis
PCs	Principle components
POSA	Plants of Southern Africa
S	South
SA	South Africa
SANBI	South African National Biodiversity Institute
SD	Standard deviation
SD	Functional diversity
SEM	Scanning electron microscopy
SPSS	Statistical Package for Social Science
SSB	Soil seed banks
SV	Standing vegetation
T0	Time interval 0 months
T0.5	Time interval three months
T1	Time interval six months
T1.5	Time interval nine months
T2	Time interval 12 months
T3	Time interval 18 months
T4	Time interval 24 months
T5	Time interval 30 months
TAG	Triacylglycerol
Tg	Triacylglycerol
TTC	2,3,5-triphenyl tetrazolium chloride
TTZ	Tetrazolium test
UK	United Kingdom
UPGMA	Unweighted pair group method with arithmetic mean
USA	United States of America
W	West
WC	Water content

CHAPTER 1
General Introduction

1.1. Preamble

Earth's climate is changing rapidly, with anthropogenic activities exacerbating the rate of this change (Jain and Hayhoe, 2008; Xi-Liu and Qing-Xian, 2018). Climate change is associated with elevated atmospheric CO_2 concentrations and temperature, altered rainfall patterns (periods of drought or floods), and other climatic events that will affect the distribution, diversity, persistence, and survival of species (Hannah et al., 2002; Thomas et al., 2004; Pearman et al., 2008; Wilsey, 2020; Kramer et al., 2020). Anthropogenic threats associated with globalisation, such as land-use change (Oliver and Morecroft, 2014), can act independently, or interact with climate change, to affect species distribution and survival and phenomena such as biological invasions (Bezeng et al., 2020) that can themselves threaten global biodiversity.

South Africa (SA) is a megadiverse country with three global biodiversity hotspots (Hoveka et al., 2020). Climatic factors such as temperature and rainfall are major determinants of vegetation distribution and predicted changes in these factors threaten the integrity of a number of vegetation types across the country (Sykes, 2009; van Wilgen et al., 2020a), and climate change poses a threat to biomes such as grassland have already undergone several structural changes (Ziervogel et al., 2014). Additionally, many vegetation types in SA are severely impacted by alien plant species, with many of these being aggressively invasive (Richardson et al., 2020a). Alien plant invasions threaten indigenous biodiversity, ecosystem services and are becoming a feature of urban green spaces within SA and globally (van Wilgen et al., 2020a). The growing area of research around the biological, climatic, and anthropogenic drivers of alien plant invasion motivated the present study, which works towards understanding alien floristics within an urban matrix: The case of Durban, South Africa.

1.2. Problem Identification: Alien plants and the Anthropocene

As alluded to above, changes in climate together with biological invasions are major drivers of biodiversity loss and changes to ecosystem servicing globally (Walther et al., 2009; Vilà and Hulme, 2017; Shrestha and Shrestha, 2019). Climate change affects biological invasions in three ways: (1) change vectors and pathways, (2) alter the abiotic habitat of the new environment, and/or (3) change biotic interactions in the new environment (Robinson et al., 2020). Importantly, many invasive alien plants (IAPs) have been found to benefit more from increased temperature and atmospheric CO_2 than indigenous species, which may increase the spread of IAPs (Liu et al., 2013; Leishman and Gallagher, 2015) and influence the distribution of all plant species (Bellard et al., 2012; Shrestha and Shrestha, 2019) and species assemblage patterns (Leishman and Gallagher, 2015). Furthermore, many IAPs are opportunistic species that thrive in harsh environments, including those open to natural and non-natural disturbances. Urban natural green spaces are increasingly seen as novel ecosystems given the high levels of transformation and disturbance they experience and their susceptibility to non-natural climatic conditions, and alien species propagule inputs through anthropogenic activities such as transport.

World trade, travel and tourism have all increased, causing the movement of species out of their natural ranges (Blackburn et al., 2011; Gallardo and Aldridge, 2013). Blackburn et al. (2011) proposed a framework for biological invasions in which species have to overcome a series of barriers to get through to a new stage. Pathways of introduction lead to the presence of alien species from one geographic location to another (Blackburn et al., 2011; Padayachee et al., 2017). According to the authors, cities are a network of vectors that facilitate the movement of alien species within environments and in surrounding natural areas (McLean et al., 2017; Padayachee et al., 2017). Port cities, such as Durban, are seen as sources of alien species immigration, where introduced species disperse and spread into the surrounding landscape (Pysek, 1998; Alston and Richardson, 2006). The Durban Harbour is a major port for Africa and is known to be the main point of entry for many alien species (Liggitt, 1983; Leslie and Spotila, 2001). Large parts of the EMA have been subject to intensive sugar cane farming since the 1880s (Lewis 1990) up until the present day. Intense agricultural activity (e.g. associated with sugar cane farming) creates disturbances that promote alien introductions (Masters and Norgrove 2010; Bhagwat et al. 2012).

Many cities worldwide, including those in developing regions, have reported an increased presence of IAPs, with some suggesting that cities may represent ‘hotspots’ for alien species (Mehraj et al., 2018). In order to make informed decisions on biodiversity management within urban green spaces, including the removal/control of alien plant species, more knowledge is required on urban floristics in the context of species richness, density and diversity, family and species ordering, and alien-indigenous plant interactions and traits (O'Donnell et al., 2012, Shrestha and Shrestha, 2019).

1.3. Rationale and motivation for this study

Native biodiversity in many parts of the world, including South Africa, are threatened by IAPs, which pose a threat to ecosystems, health, economy, and agriculture (Shackleton et al., 2007; Pimentel et al., 2009; Vilà et al., 2010; Vilà and Hulme, 2017). Invasive alien plants have the ability to increase carbon assimilation rates (Le Maitre et al., 1996), change the status of nutrients found in soil (Vitousek and Walker, 1989), increase flammability (Anable et al., 1992), and hence alter the fire regimes of ecosystems they invade (Higgins et al., 1999), further threatening native species (Musil, 1993; Meyer and Florence, 1996). Invasive alien plants can also change habitat suitability for native animals (Steenkamp and Chown, 1996) and have secondary effects on ecosystem functioning, such as biomass accumulation (Vitousek and Walker, 1989). In fynbos, for example, IAPs can increase plant water use, which reduces surface run-off (Le Maitre et al., 1996; 2020). Invasive alien plants are therefore widely accepted as one of the greatest threats to biodiversity loss (Didham et al., 2005) and ecosystem functioning (Rouget et al., 2004; Le Maitre et al., 2020). The invasive species are also known to take advantage of changes in ecosystems, such as habitat disturbance (Didham et al., 2005; van Wilgen et al., 2020a), and their impacts are sometimes irreversible as they bring about permanent habitat loss (IUCN/SSC/ISSG, 2000).

Plants are seen as the most suitable indicators of localised conditions as they are immobile and sensitive in terms of physiological reactions to atmospheric change compared with animals (Wuytack et al., 2011; Appalasamy et al., 2017). Didham et al. (2005) hypothesised that the dominance of IAPs is an indirect consequence of habitat modification, which drives the loss of native species in that area. Habitat modification is often attributed to the fact that many IAPs are phenotypically plastic, meaning they have the ability to change their phenotype in response to a changing environment (Strayer et al., 2006; Richardson et al., 2020b). Phenological traits may give insight into IAPs entering new environments as phenology combines biotic factors (viz. growth and development) with abiotic factors (Lieth, 1974; Wainwright and Cleland, 2013). Studies report plasticity as a trait that enables IAPs to thrive under a range of abiotic conditions in novel environments where growing conditions differ from that of the alien's native range (Droste et al., 2010; Wainwright and Cleland, 2013). The dominance of IAPs can also be linked to their physiological, morphological, and reproductive traits (Pyšek and Richardson, 2008; Chrobock et al., 2011). Invasive alien plants can germinate fast and in high numbers, even under conditions that may not be deemed suitable for growth (Cervera and Parra-Tabla, 2009; Schlaepfer et al., 2010; Chrobock et al., 2011). Under periodic climatic changes, IAPs have the upper hand in early germination, whereby they suppress indigenous seedlings that germinate later (Wainwright et al., 2012; Wainwright and Cleland, 2013).

Invasive alien plants not only grow faster, but they produce higher seed sets and utilise more nutrients more effectively than indigenous and even other alien species (Pyšek and Richardson, 2008; Rejmanek et al., 2013; van Kleunen et al., 2015). Indigenous species are able to co-occur, grow and reproduce in environments invaded by aliens; however, the alien species should have similar characteristics to indigenous species (van Kleunen et al., 2015). On the other hand, successful aliens may also differ from indigenous species if indigenous species have not yet adapted to novel environments or conditions which alien species have exploited (van Kleunen et al., 2015). Invasive species have been reported to decrease indigenous species abundance, displace them, or even drive them to extinction (Takakura et al., 2009). In order to understand functional and ecological interactions between alien and indigenous species, a closer look at their functional diversity is required (Carbonell et al., 2017). Competitive interactions decrease species co-existence and increases their functional diversity (Chesson, 2000; Schleuter et al., 2010). Alien species exhibiting a greater number of functional traits than indigenous species allow them to occupy various habitats, even those in which biotic and abiotic factors may negatively influence their success and recruitment (Osunkoya et al., 2005).

Importantly, IAPs have the ability to change soil seed bank dynamics either directly by adding seeds of varying density and persistence and also indirectly by changing biotic and abiotic conditions in an area; including the above-ground vegetation, as well as in competitive interactions at different stages of plant development (Gioria et al., 2012; Gioria and Pyšek, 2016). It is crucial to predict IAPs recruitment potential in seed banks and assess their invasiveness across biomes in order to predict vegetation dynamics in the future (Gioria et al., 2014; Gioria and Pyšek, 2016). The distribution of seeds within the soil seed banks could be due to the morphological structure of seeds, physiological characteristics, and chemical composition (Gioria and Osborne, 2009). These traits allow seeds to remain viable within the soil for some time (Merritt et al., 2014) and the longevity of seeds that are able to persist is essential in the formation of persistent soil seed banks (Thompson et al., 1997; Oliveira et al., 2015).

1.4. This study

As mentioned above, this study was motivated by the need to understanding the ecology of alien plant species in relation to prevailing environmental conditions and a lack of data on alien and indigenous plant floristic patterns along environmental gradients within urban natural green spaces. This study focuses on understanding alien floristics within an urban matrix (specifically, the eThekwini Metropolitan Area [EMA]), which is located within the Maputoland-Pondoland-Albany Hotspot in subtropical KwaZulu-Natal, South Africa. The focus on this area is based on the fact that it is both highly biodiverse and susceptible to IAPs (Roberts and O'Donoghue, 2013). As in other rapidly growing cities in the world (Kowarik, 2011), IAPs are accepted as one of the greatest threats to biodiversity loss and ecosystem functioning within the EMA (eThekwini Municipality, 2019). In support of global thinking around alien plant invasions, local plant scientists believe that alien species found in the region are taking advantage of changes in ecosystems brought about by natural and non-natural disturbances and may be outcompeting indigenous species for resources. Their presence and potential impacts have been reported in a number of studies conducted in the region (Shackleton et al., 2016; Potgieter et al., 2020), but a comprehensive and systematic assessment of alien and indigenous plant floristics for this highly biodiverse region was lacking at the time of this study. Pathways of introduction and alien seed dispersal by animals were beyond the scope of the study; however, they are discussed where relevant (i.e. where interesting patterns were seen).

Terminology used in plant ecology are sometimes difficult to apply in studies on urban systems, given that vegetation sampling methods used in plant ecology have to be adapted to suit their peculiarities. Hence, it is worth defining the terms used in this study (Table 1.1.) right at the outset.

Table 1.1: List of terminology and descriptions of indices used throughout the thesis

Term	Definition	Reference
Species richness	The absolute number of species in an assemblage or community	Lincoln et al. (1982)[i] Wang et al. (2021)[ii]
Species/plant	The number of individuals or	Lincoln et al. (1982)[i]

density	observations within a given area or volume	
Species cover	The area of ground covered by vegetation of a particular plant species; expressed as a scale or as a percentage	Lincoln et al. (1982)[i]
Species abundance	The total number of individuals of a taxon or taxa in an area, volume, population or community; absolute abundance, often measured as cover in plants	Lincoln et al. (1982)[i]
Species diversity	A measure of the number of species and their relative abundance in a community; low diversity refers to a few species or unequal abundances	Lincoln et al. (1982)[i] Wang et al. (2021)[ii]
Shannon's exponential (*H'*)	An index of diversity that places emphasis on species richness and suggests that one community is more/less diverse than the other	Nagendra (2002)[ii] Wang et al. (2021)[ii]
Simpsons inverse (*1/D*)	An index of diversity that places emphasis on evenness and suggests that one community is more/less diverse than the other	Nagendra (2002)[ii] Petersen et al. (2020)[ii, iii]
Sørenson coefficient (S)	A measure of the similarity in species composition between two communities, calculated as $S = 2c/(a+b)$, where a and b are numbers of species in communities A and B, respectively and c the number common to both	Lincoln et al. (1982)[i] Luz de la Maza et al. (2002)[ii]
Jaccard's	A measure of the similarity in species	Dunn and Everitt (1982)[i]

coefficient	composition between two communities (*A* and *B*) calculated as $S_j = a/(a + b + c)$, where *c* is the number of species common to both, and *a* and *b* are numbers of species occurring only in communities *A* and *B*, respectively	Luz de la Maza et al. (2002)[ii]

[i] = application to natural systems
[ii] = application to urban systems
[iii] = application to aliens

1.5. Aims and objectives

The current study aimed to inform the design of a framework that aids in prioritising urban green spaces and aliens for monitoring and control interventions by carrying out inter-related investigations that addressed the following research questions:

(1) What are the major drivers of alien species (particularly IAPs) distribution?

- (a) Determine if alien plant distribution, species richness (number of species), and density are related to urban land use patterns and levels of non-natural disturbance?;
- (b) Identify specific land-use features and/or types of non-natural disturbance that drive invasiveness;
- (c) Evaluate whether or not selected floristic parameters can be used to develop an Alien Invasive Index (AII) for identifying invasive alien hotspots.

(2) Are alien and indigenous plant functional diversity and alien-indigenous co-occurrence patterns influenced by non-natural disturbance?

- (a) Determine if species (alien and indigenous) richness, density and diversity (alpha and functional) are related to anthropogenic (including levels of non-natural disturbance) factors and/or vegetation type;
- (b) Compare alien and indigenous functional diversity (FD) and its' influence by non-natural disturbance;
- (c) Identify patterns of alien-alien and alien-indigenous species co-occurrence.

(3) What is the influence of non-natural disturbance on alien and indigenous soil seed bank (SB) floristics?

- (a) Determine the floristic richness and density (alien and indigenous) of seed banks;
- (b) Measure the ratio of alien to indigenous plant species;
- (c) Explore floristic similarities between soil SB and standing vegetation (SV);

(d) Test the influence of non-natural disturbance on soil seed bank vegetation.

(4) Can selected seed physical and/or chemical traits be used as potential indicators of IAP persistence in natural SBs?

(a) Measure seed morphological, physiological, and physico-chemical characteristics of five selected IAPs;

(b) Assess seed longevity patterns of seeds over a two year burial period;

(c) Determine seed viability of intact seeds post burial.

1.6. Study area

Biodiversity is spatially variable, and spatial data is lacking for species-rich areas around the world (Midgley et al., 2002). Some cities within SA do have urban open space planning programmes such as the Durban Metropolitan Open Space System (D'MOSS), which help in monitoring and conserving biodiversity (McConnachie et al., 2008). Urban open space planning began in Durban in the 1970s with a focus on protecting conservation-worthy areas (Boon, 2010). The D'MOSS programme initiated in 1989 aimed to produce a sustainable open space system by integrating ecological, social and economic factors (eThekwini Municipality, 2007). There are > 14 000 recognised D'MOSS sites across the EMA (eThekweni Municipality, 2018). Without proper management, these green open spaces may become hubs for IAPs to exploit, especially in disturbed or unmaintained habitats (McConnachie et al., 2008). Green spaces without local diversity or that are not pristine could promote environmental problems rather than act as a buffer or mitigate urban environment issues. Data on IAPs found in KZN, and the EMA exist in various types of literature (viz. National Environmental Management: Biodiversity Act ([NEMBA] Act no. 10 of 2004), Alien and Invasive Species List 2020 [Department of Environmental Affairs, 2020]) and online sources (New Plants of Southern Africa [NewPOSA] website of the South African National Biodiversity Institute (SANBI, 2019a)) but since these datasets are usually designed to show distribution patterns at the national level, while provincial and localised patterns of invasion cannot be easily discerned at a finer scale. This is true for a number of municipalities across the country. However, spatial data for IAPs in specific areas are sparse for many of these green spaces across the country, including D'MOSS within the EMA.

It is estimated that 78% of the South African population reside in cities and surrounding peri-urban and rural areas (South African Cities Network [SACN], 2016), with Johannesburg being the largest, followed by Cape Town and Durban (Statistics South Africa, 2011). The city of Durban, in the eThekwini Municipality (EMA), covers a total of 2556 km^2 and has a population size of 3.92 million, which increased at a rate of 1.4% between 1996 and 2010/2011 (eThekwini Municipality, 2019). The EMA, in KZN, is a biodiverse region situated in the middle of the Maputaland-Pondoland-Albany biodiversity hotspot (Fig. 1.1), with high levels of urbanisation, habitat loss, species endemism and alien invasion (Roberts and O'Donoghue, 2013).

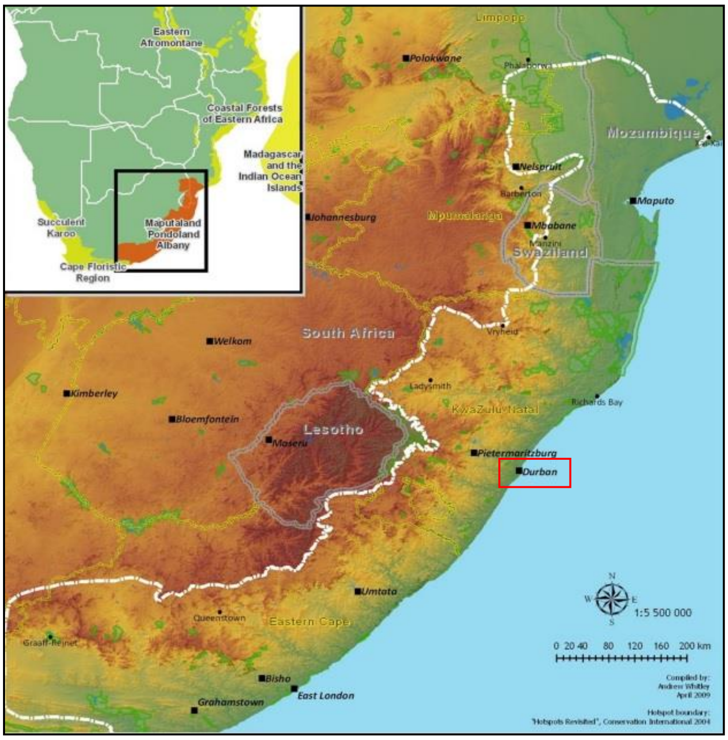

Figure 1.1: Map showing the Maputaland-Pondoland Albany hotspot (white boundary) and the positioning of the eThekwini Municipality (red box). Source: Critical Ecosystem Partnership Fund, www.cepf.net/sites/default/files/final_mpah_ep_1.pdf

The eThekwini Municipality contains the savanna and the Indian Ocean Coastal Belt biome, and also boasts a range of vegetation types, viz. Eastern Valley Bushveld, KwaZulu-Natal Coastal Forest Belt (vulnerable), KwaZulu-Natal Hinterland Thornveld, KwaZulu-Natal Sandstone Sourveld (endangered), Mangrove Forest, Ngongoni Veld (vulnerable), Northern Coastal Forest (endangered), Scarp Forest (vulnerable), Subtropical Dune Thicket, Subtropical Seashore Vegetation, and Swamp Forests (Scott-Shaw and Escott, 2011; eThekwini Municipality, 2019). One third of the municipality is represented by an open space system (Durban Municipal Open Space System [D'MOSS], Fig. 1.2) which has high biodiversity value (eThekwini Municipality, 2019). Threats to the biodiversity of Durban and the broader EMA include the transformation of natural areas and the introduction of IAPs (eThekwini Municipality, 2019), both of which play a role in decreasing indigenous plants in the city (viz. land degradation by human intervention, alien plants outcompeting indigenous species). Various parts of KZN exhibit both high levels of biodiversity and susceptibility to both disturbance and alien invasion (Roberts and O'Donoghue, 2013).

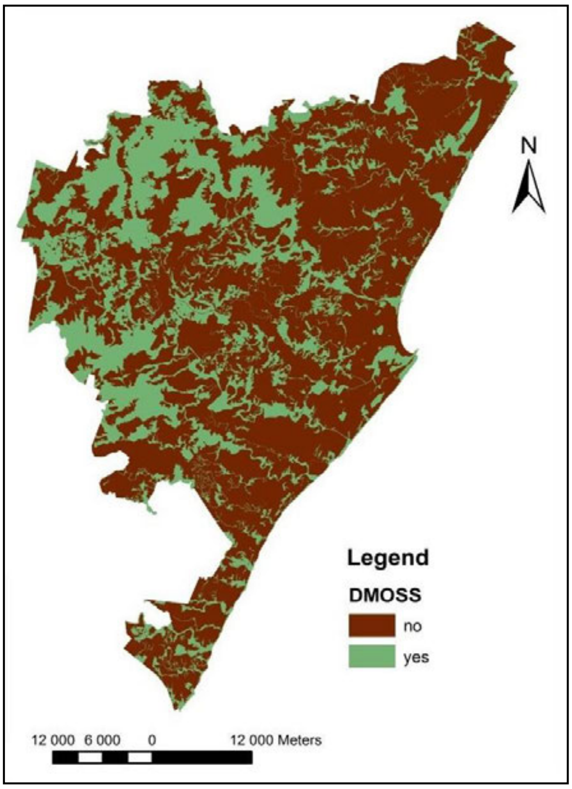

Figure 1.2: Map showing D'MOSS (shaded in green) in the EMA. Source: Pillay, 2014 (Unpublished M.Sc. dissertation).

The EMA is home to a range of ecosystems (terrestrial and aquatic) and vegetation rich in plant and animal diversity due to its varied micro-climates, geology, soils and biogeographical positioning (Boon et al., 2016). Many green spaces across the EMA are poorly maintained (92.43% not formally managed), and only 7.03% of D'MOSS are legally protected (eThekwini Municipality, 2019). Combined with rapid urbanisation in the municipality and disturbances by anthropogenic activity, these rich biodiverse areas are at risk of alien invasions (Roberts, 2008). The biodiversity of the municipality is said to be highly threatened and has less national and global interest, with lower levels of investment from provincial, national, and international non-governmental organizations (Rebelo et al., 2011; Boon et al., 2016). Green spaces across the EMA are mainly exposed (i.e. have no fencing or gated access) and vulnerable to human (viz. informal settlements, non-natural disturbance, grazing) and alien presence.

1.7. Significance of study

The current study area is situated in a biodiversity hotspot and focuses on natural green spaces across an urban matrix. This study is necessary in order to examine the level of non-natural disturbance across D'MOSS and to identify invasive and emerging aliens present, which will allow proper control measures to be instituted by the municipality to have insight on IAPs and their threat to indigenous vegetation. For over a century, various control mechanisms have been used as a management tool for the removal of plants such as IAPs (Hill et al., 2020). The study will also highlight the functional traits and the co-existence between alien and indigenous species, which will address the Invasional Meltdown Hypothesis (IMH). In addition to the IMH, the current study will also provide insight into the diversity-invasibility hypothesis proposed over 60 years ago. Furthermore, knowledge on the persistence of alien seeds within the soil seed bank is limited, and this poses concern as SA has approximately 10 million hectares of land invaded (Poona, 2008; Witkowski and Garner, 2008). The current study focuses on the seed longevity of five IAPs within open green spaces of an urban matrix, and this will provide meaningful information required for alien related projects that focus on control and restoration. With the growing concern for scientific knowledge on the impact of biological invasions (Esler et al., 2010; Foxcroft et al., 2020), the current study may assist in the development of national policies and management strategies by means of a proposed evidence-based framework that prioritises urban green spaces and alien species within them for monitoring and control interventions. South Africa provides opportunities to explore invasions due to its long history and high numbers of IAPs (Abrahams et al., 2019; Foxcroft et al., 2020), therefore results from the current study could feed into current control programmes, biodiversity conservation efforts and expand on the growing body of research that exists.

The significance of the work is based largely on the fact that it has yielded baseline and novel data for alien flora within an urban area that is located within a biodiversity hotspot in a country that has not applied some of the contemporary methods in invasion biology to understand plant invasions. In this regard, the following are considered the most important novel contributions of the study:

1. Developing a typology to assess non-natural disturbance in natural urban green spaces;
2. Developing an Alien Invasive Index (AII) for prioritising urban green spaces for alien plant control;
3. Showing the utility of integrating spatial and floristic data for prioritising species and areas for alien plant control;
4. Assessing the value of using functional diversity (FD) to understand species invasiveness;
5. Characterising the soil seed bank for alien flora in relation to standing vegetation;
6. Carrying out the first seed burial study for invasive alien plants (IAPs) that attempts to relate seed longevity to chemical characteristics (more specifically lipid profiles).

1.8. Outline of thesis

The thesis is presented in six chapters and structured primarily to address four research questions, which make up the major chapters (chapters 2 – 5). The four major chapters have been designed for submission to peer-reviewed journals (Chapter 2 has been published in the journal Flora).

Chapter 2 identifies non-indigenous invasive hotspots within an urban matrix. Classical vegetation survey techniques were used to identify and quantify aliens within 30 natural green spaces. Levels of disturbance were quantified through a scoring matrix. The AII was used to identify hotspots and emerging hotspots of invasion.

Chapter 3 explores alien and indigenous floristic ordering, plant diversity and co-occurrence patterns. Alien and indigenous species were identified and quantified during classical vegetation surveys across green spaces. Species richness, density, diversity (alpha and functional), and co-occurrences were calculated and analysed.

Chapter 4 assesses the effects of disturbance on alien and indigenous seed bank floristics. Soil samples were collected at each of the 30 sites within the study areas. Soil samples were left under shaded greenhouse conditions and monitored for one year. Germinants were identified and quantified, and comparisons were made with soil SB and SV.

Chapter 5 explores factors governing seed bank longevity in selected IAPs. Seeds of five IAPs were buried for two years, and batches were exhumed every six months for viability and germination tests. Seed wall thickness and oil contents within seeds were examined to determine seed deterioration over time.

Chapter 6 critically discusses the aim and objectives of the research, highlighting major findings from the study. It summarises the study and proposes an evidence-based framework that aids in prioritising urban green spaces and aliens within them for monitoring and control, which can complement and facilitate existing IAP control guidelines and policies. Additionally, the chapter examines the limitations of this study and presents recommendations for future research.

CHAPTER 2

Aliens in the city: Towards identifying non-indigenous floristic hotspots within an urban matrix

This chapter is based on

Appalasamy, M., Ramdhani, S. and Sershen (2020). Aliens in the city: Towards identifying non-indigenous floristic hotspots within an urban matrix. Flora, 269. doi.org/10.1016/j.flora.2020.151631. (Accepted).

ABSTRACT

Urban natural green spaces are becoming increasingly impacted by anthropogenic disturbances, promoting alien plant invasions. Using a rapidly developing city in South Africa as a case study, we attempted to relate richness and density and ordering of alien plant species to urban land-use patterns and anthropogenic factors to identify drivers of invasiveness. Vegetation surveys were used to identify and quantify (in terms of richness and density) alien species within 30 natural green spaces. Floristic characteristics were then related to levels of non-natural disturbance and land-use. Based on the relationships observed, selected floristic parameters were used to develop an Alien Invasive Index to identify 'invasive alien hotspots.' Collectively, 80 alien plant species (from 30 families) were found, 35 of which were invasive. The most speciose families were Asteraceae > Fabaceae > Verbenaceae. Their representatives, specifically the invasive shrubs *Lantana camara* (Verbenaceae) and *Chromolaena odorata* (Asteraceae), and alien herbs *Conyza sumatrensis*, *Bidens pilosa*, and *Tagetes minuata* (Asteraceae), were the most dominant in terms of frequency across sites and density. A Principal Component Analysis showed invasive alien species richness to be most strongly related to level of disturbance. The Alien Invasive Index could discriminate between sites with low and high levels of invasiveness, and its suitability was validated by the fact that sites with very high index values were in close proximity to informal settlements. The study demonstrates the value of combining classical *in situ* vegetation surveys and overlay analysis using Geographic Information Systems for prioritising green spaces and alien species for management in cities that are limited in terms of financial resources.

2.1. INTRODUCTION

Urban plant invasion is a global phenomenon that has been reported to have implications on human health, fire regimes, indigenous biodiversity, water resources, and safety and security risks (Pyšek and Richardson 2010; Potgieter et al., 2020 and references therein). Alien species, formally defined as species whose presence in a region is associated with anthropogenic actions allowing them to overcome fundamental biogeographical barriers (Richardson et al., 2011), have become a major focus in invasion science (Novoa et al., 2020). When alien plants are successful in establishing reproductive populations, they are classified as naturalised, and once they spread their range into new regions, they can become invasive (Blackburn et al., 2011; Razanajatovo et al., 2016). Identifying the biotic and abiotic factors that drive this invasiveness remains a major challenge in invasion biology and has hindered our ability to prevent, manage, and predict invasions.

Urbanisation brings about changes in land-use and is a major driver of change in natural vegetation patterns (Seto et al., 2011; Concepcion et al., 2015). This scenario applies to many developing cities (Cobbinah et al., 2015; Potgieter et al., 2020) and other parts of the developing world (Cobbinah and Amoako, 2012), where non-natural disturbances are a common feature of urban ecosystems and influence alien plant invasions through changes in intensity and frequency (Keeley and Brennan, 2012; Potgieter et al., 2020). Non-natural disturbances such as mowing, soil extraction, and dumping, as opposed to natural disturbances such as fire and tree falls, and distance from human habitation, have been shown to have a major influence on the presence of alien species in urban green spaces (Sullivan et al., 2005; Muratet et al., 2008). Anthropogenic disturbances can promote alien invasion by destroying indigenous plants through regeneration failure (Hobbs and Yates, 2003), and successful alien plant invasions appear to be more common in anthropogenically-altered rather than natural habitats (Niemela, 1999; Follak et al., 2018). Anthropogenic disturbances can create edges open to invasion (Hobbs and Yates, 2003) and also give rise to dispersal corridors that promote alien plant invasion (Lake and Leishman, 2004; Alston and Richardson, 2006). However, there are some idiosyncrasies concerning disturbance-induced plant invasion. In urban grasslands, alien plant invasions have been linked to disturbances related to cultivation, grazing, and trampling (Tyser and Worley, 1992; O'Connor and van Wilgen, 2020), which though present in some cities (e.g., Durban in South Africa [Drury et al., 2016]) are less frequent in urban forests.

In developing countries, urban areas are increasing tremendously (Rouget, 2015), and by 2030 the urban threshold (i.e., minimum population threshold of an area classified as urban) of 50% will very likely be exceeded (Boon et al., 2016). As cities (built-up areas) and urban populations grow within these countries, many natural urban green spaces are becoming increasingly fragmented (Alston and Richardson, 2006), transformed, degraded, and eroded of biodiversity (Zhao et al., 2010; Concepcion et al., 2015; Richards et al., 2017). The conservation of the remaining habitats (and biodiversity within them), which are often surrounded by human settlements (Hobbs and Yates, 2003), will be of vital importance (Godefroid and Koedam, 2007; Zhao et al., 2010; Ricardson et al., 2017) in the face of climate change given that anthropogenic factors, land-cover alteration, and urban design geometry contribute to an increase in urban surface and atmospheric temperatures (Abutaleb et al., 2015). In this regard, understanding the interplay between social and ecological systems in modulating plant invasions in urban landscapes is important (Gill and Williams, 1996; Alston and Richardson, 2006; Terzano et al., 2018; Potgieter et al., 2020).

While numerous studies have developed indicators for quantifying levels of biodiversity (e.g., Ferreira et al., 2005; Matzdorf et al., 2008) and biodiversity hotspots in particular (Schmidt et al., 2014), there have been fewer efforts to develop indices or indicators for ranking areas based on levels of alien plant invasion (Crossman et al., 2011) within urban landscapes. Nevertheless, there is growing agreement that cities may be ‘alien hotspots’ (Kühn et al., 2004; Celesti-Grapow et al., 2006). There are reports from the developing world (e.g., Kateregga and Sterner, 2007) that prevalence of known drivers of invasiveness (e.g., levels of disturbance [Godefroid, 2001]) and indicators of alien plant impacts should be considered in such an exercise (Gaertner et al., 2009; Hejda et al., 2009). A few studies have also attempted to develop indices of invasiveness to prioritise riparian zones for alien plant eradication and control in rapidly urbanising countries such as South Africa (e.g., van Wilgen et al., 2007), but this has not been applied across biomes/habitat types. This is due to the complexity of dealing with issues around invasion biology, such as the lack of alien distribution data in developing cities, levels of transformation, and urban heterogeneity, amongst others. This is the case for many rapidly developing African cities, such as Durban in South Africa, where there are often no formal systems for prioritising areas or species for control and eradication operations despite national guidelines (e.g., National Environmental Management: Biodiversity Act [NEMBA, Act no. 10 of 2004]), and Alien and Invasive Species List 2016 (Department of Environmental Affairs, 2016).

A demand for more land for settlement, agriculture, transport, and infrastructure (Rouget, 2015) in cities like Durban has been accompanied by the introduction and increased presence of numerous alien plant taxa over the last four decades (Alston and Richardson, 2006; Bhagwat et al., 2012). Approximately 900 alien plant species have established in natural areas of South Africa, c. 600 of which have become invasive, dispersing into natural ecosystems (van Wilgen, 2018). South Africa has invested extensive resources into trying to control invasive alien plants (IAPs) (van Wilgen et al., 2008), but despite these efforts, cities such as Durban continue to exhibit high levels of alien plant invasion thought to be linked to increasing urbanisation, pollution and habitat loss (Roberts and O'Donoghue, 2013). This, together with the fact that Durban is situated in the middle of a biodiversity hotspot (Maputaland-Pondoland-Albany) made the city an ideal case study that addressed the following research questions in the context of alien plants in an urban matrix: (1) Are alien plant distribution, species richness (number of species) and density related to urban land use patterns and levels of non-natural disturbance? (2) If so, what are the specific land-use features and/or types of non-natural disturbance that drive invasiveness? (3) Can selected floristic parameters be used to develop an Alien Invasive Index (AII) for identifying invasive alien hotspots? Knowledge of how land-use changes and the associated non-natural disturbances may directly or indirectly impact on IAPs within these green spaces would allow for more focused and effective control programmes (Adam et al., 2017) within cities.

2.2. METHODS

2.2.1. Study site selection

As mentioned above, the city of Durban in KwaZulu-Natal, South Africa, was selected here as the case study area, in which 30 green spaces within the eThekwini Metropolitan Area (EMA) were surveyed (Table A1, Appendix A). The EMA covers 2556 $km^{2,}$ and green spaces (c. 33% of this area) are interspersed between industrial areas and housing (formal and informal). There are > 14 000 green spaces across the EMA which form part of the Durban Metropolitan Open Space System (D'MOSS) (eThekwini Municipality, 2017), and site selection involved a combination of remote spatial techniques and *in situ* verification: Hawth's Tool extension in ArcGIS was used to generate random points [Miller et al., 2012]) and ground-truthing (i.e., visiting the random sites generated) was employed to establish site suitability, respectively. More specifically, overlay analysis (using roads, informal settlements, industry, and housing layers) in ArcMap (version 10.3, ArcGIS) and ground-truthing were used to establish whether the sites were > 10 000 ha in size, accessible by road, and not located in steep, inaccessible riparian zones. If sites were unsuitable/inaccessible, the nearest random point was selected, followed by ground-truthing. Throughout this process, 30 sites were deemed suitable for investigation. The randomised selection tool used ensured that site selection accommodated all five sectors of the EMA (viz. North, South, East, West, and Central), with a minimum of six sites in each sector (see Table A1, Appendix A for sites within each sector), ensuring good coverage of the study area. However, while sites occurred in all four major vegetation types within the EMA, viz. forest, grassland, savanna, and thicket, it was not possible to survey the sites evenly across these vegetation types without reducing the degree of coverage of the study area.

2.2.2. Vegetation surveys and quantification of sampling effort

At each of the 30 sites, eight 5 × 5 m quadrats were laid out more than 10 m apart and at least 2 m from any mowed/concrete/tarred curb edges. Sampling was conducted over a two-year period (2016 and 2017), with 15 sites (n = 120 quadrats) being sampled each year. At each site, four quadrats were sampled in autumn-winter (May-June) and four in spring-summer (November-December) to capture seasonal changes in the vegetation (Sershen et al., 2019). Within each quadrat, the abundance (number of individuals or clumps in the case of some shrubs, due to their growth form) and cover area (%) were recorded for all non-graminoid life forms (viz. trees, shrubs, herbs), while only cover area (%) was recorded for graminoid taxa due to their clonal habit (Kambaj et al., 2018). Flowering or fruiting plant specimens were collected from quadrats at each site over the two years for identification purposes, and herbarium vouchers were deposited at the Ward Herbarium (Westville Campus, University of KwaZulu-Natal).

Data from eight quadrats at each of the 30 sites (n = 240) were used for all analyses, including species accumulation curves, which were constructed using abundance data in EstimateS 9.0 (Colwell, 2013) to determine whether the sampling effort was adequate. Graminoids were not included in the species accumulation curves since only percent cover data were available. The percentage sampling effort was calculated by dividing the number of species found *in situ* by the projected number of species based on the Chao2 estimator. Sampling completeness was achieved when the sampling effort reached a minimum of 80% (e.g., Moro et al., 2014).

2.2.3. Identification and categorisation of flora and species/family ordering

Plant species were identified using field guides (Boon, 2010; Pooley, 1998) and other published literature. Nomenclature and taxonomic authorships follow the New Plants of Southern Africa (NewPOSA) website of the South African National Biodiversity Institute (SANBI, 2019a). Alien taxa categorisation was based on the National Environmental Management: Biodiversity Act ([NEMBA] Act no. 10 of 2004) and Alien and Invasive Species List 2016 (Department of Environmental Affairs, 2016) of South Africa. The Act recognises Category 1 – 3 IAPs species: (1) may not be grown and must be controlled; (2) are of commercial or utility value, which may only be grown with a permit under controlled circumstances; and (3) may have amenity value and which may be grown, but not planted, propagated, imported or traded, or grown within 30 m of watercourses. Descriptions of all non-declared alien species were based on the Weeds and Invasive Plants website (WIP, 2016). In some cases (especially for naturalised exotics), the alien status was determined using SANBI (2019b). Alien species not described in any of the above-mentioned sources were regarded as 'non-categorised' alien taxa.

In the present study, alien species (in terms of density) and family representation (in terms of richness) were ranked to identify the top three (dominant) species and families across all sites (after Jones et al., 2017). For this ranking, density for individual families and species was summed at site level and averaged for the study area.

2.2.4. Levels of non-natural disturbance and proximity to land-use types

Levels of non-natural disturbance were assessed at all sites during the last year of sampling using a scoring matrix (Table A2, Appendix A) based on the following typology: footpaths and trampling, livestock browsing, wood harvesting, agriculture, resource abstraction, solid waste dumping, effluent input, and non-natural burning. At each site, eight types of non-natural disturbance typically associated with urban green areas in South Africa (McConnachie et al., 2008; Potgieter et al., 2020) were ranked in terms of the proportion of the site they affected (see Table 2.1). This was assessed via three parallel walked transects (approximately 50-100 m apart) across the length of the site. The scores for the eight disturbance types were then summed (at site level; maximum score = 40) and expressed as a percentage of the potential maximum score (40). These percentiles were then used as the 'Disturbance Level Value' (DLV), an integrated indicator of disturbance intensity at each site, and plotted as a boxplot (SPSS Inc., Version 25, Chicago, IL), to delimit five disturbance classes: very low (≤ 24), low (25 – 28), medium (29 – 30), high (31 – 39), and very high (≥ 40).

Table 2.1: Disturbance type, indicators considered, and scale with associated scoring range for assessing non-natural levels of disturbance at sites

Disturbance Type	Indicators considered	Scale and associated scoring range*
Footpaths and trampling	Paths and trampled vegetation	0: Absent 1: ≤19% 2: 20 - 39% 3: 40 - 59% 4: 60 - 79% 5: ≥80%
Livestock browsing	Browse line and/or damage to foliage	0: Absent 1: ≤19% 2: 20 - 39% 3: 40 - 59% 4: 60 - 79% 5: ≥80%
Wood harvesting	Cut branches and/or remaining tree stumps	0: Absent 1: ≤19% 2: 20 - 39% 3: 40 - 59% 4: 60 - 79% 5: ≥80%
Agriculture	Signs of active planting, harvesting	0: Absent

	and/or clearing for planting	1: ≤19% 2: 20 - 39% 3: 40 - 59% 4: 60 - 79% 5: ≥80%
Resource abstraction	Signs of human removal of soil, water and/or stone	0: Absent 1: ≤19% 2: 20 - 39% 3: 40 - 59% 4: 60 - 79% 5: ≥80%
Solid waste	Evidence of dumping	0: Absent 1: ≤19% 2: 20 - 39% 3: 40 - 59% 4: 60 - 79% 5: ≥80%
Effluent	Evidence of stormwater, household and/or industrial effluent (including consequent erosion)	0: Absent 1: ≤19% 2: 20 - 39% 3: 40 - 59% 4: 60 - 79% 5: ≥80%
Burning	Planned: evidence of firebreaks, localised burning site (confirmation by municipal workers who carry out controlled burns), Working for Fire	0: Absent 1: ≤19% 2: 20 - 39%

	personnel present at site or in the vicinity of site; Unplanned: no evidence of firebreaks, burnt waste such as paper, wood, plant biowaste and/or plastic that was used to make a fire that burned surrounding vegetation	3: 40 - 59% 4: 60 - 79% 5: ≥80%

*Scoring range was based on the proportion of the site affected by the disturbance

A spatial proximity tool ("generate near table" [ArcMap, version 10.3, ArcGIS]) was used to measure the distance (m) of each quadrat to the closest land-use feature (roads, informal settlements, housing, industry) (after Doriwala and Shah, 2010). The sites were also mapped (in ArcMap) to show their relative proximity to housing, industry, and informal settlements and location within the study area in relation to the five sectors described earlier.

2.2.5. Alien invasive index and identification of invasive alien hotspots

The total number of IAPs, non-invasive aliens as well their densities at each of the 30 sites surveyed were used to formulate an Alien Invasive Index (AII):

$$AII = \left(\frac{IR}{CR}\right)\left(\frac{ID}{CD}\right)$$

Expression 1

Where IR = invasive alien species richness at site (measured as number of species at a site), CR = cumulative alien species richness (sum of all sites), ID = IAP density at site (measured as the abundance of species at a site/area), and CD = cumulative alien plant density (sum of all sites)

Factors included in the index calculation were shown to be significantly related to each other (see below Results). The decision to exclude disturbance level was based on the skewed distribution of values for this parameter. The site-specific AII values were then used to identify 'invasive alien hotspots' across the study area by plotting the values in a boxplot and delimiting four classes of increasing invasion: 1 = low (≤ 0.018), 2 = medium (0.019 – 0.024), 3 = high (0.025 – 0.067) and 4 = very high (≥ 0.068). The 30 sites were then overlaid (using ArcMap) on the human settlement layer for the city and tagged with the level of disturbance for the site to generate a map that can be used to spatially represent existing invasive alien hotspots (high to very high AII), emerging hotspots (medium AII) and sites of early invasive detection (low AII).

2.2.6. Statistical analysis

Data for all sites (eight quadrats in each of 30 sites yielding n = 240 quadrats) were pooled prior to all statistical analyses (carried out in SPSS, Version 25). All data were tested for normality using the Shapiro Wilks/Kolmogorov-Smirnov test. Non-parametric data were log/arcsine (for percentages) transformed where necessary. To determine the most important variables, a PCA was conducted with the following variables: alien (invasive and non-invasive) plant floristics (richness and density), distance to land-use feature class layers (viz. distance to roads, industry, and informal settlements), and disturbance level. The Scree plot of the eigenvalues for all components was used to determine the number of principal components (PCs) to retain, i.e., those before the last inflection point of the graph. A non-parametric correlation test (Spearman rank) was used to test for the following relationships amongst the following parameters: AII, alien plant floristics, and disturbance level.

2.3. RESULTS

2.3.1. Land-use patterns across the study area and site environmental characteristics

The gradient of non-natural disturbance that was generated via *in situ* assessments indicated that all sites exhibited some level of disturbance. Disturbance level values (DLV) at sites ranged from 21 – 47%. There were various combinations of disturbance types across sites, but footpaths or trampling and effluent (storm water, urban, industrial) were the most (observed at 93% of sites) and least (observed at 3% of sites) commonly observed disturbances, respectively (data not shown). The distribution of sites (n = 30) across the five disturbance classes were defined using a boxplot as follows: 16.67% of sites with very low, 36.67% with low, 16.67% with medium, 26.67% with high, and 3.33% with very high levels of disturbance (Table A1, Appendix A). When DLV for sites within a sector were averaged, there were no significant differences across sectors. Sites in the east were mainly disturbed by solid waste dumping and had a higher presence of built-up areas. Sites in the south were disturbed mainly by human footpaths and solid waste dumping and were not in close proximity to built-up areas as in the north (data not shown). Central regions were more prone to fires and had the highest disturbance due to high levels of solid waste dumping. Sites in the north and west regions were further away and isolated from the main city centre, and sites in the west were not usually in close proximity to housing. The main source of disturbance in the outer west sector was cattle grazing. In terms of the 30 sites investigated here, the most frequent vegetation type was forest for the north and south sectors and savanna for the east, west, and central sectors.

2.3.2. Floristics and levels of invasiveness

Cumulatively, 80 alien species (invasive and non-invasive) were found at study sites (Table A3, Appendix A). These species belong to 30 families, with the top three families being Asteraceae (n = 18), Fabaceae (n = 12), and Verbenaceae (n = 5). These three families contributed 35 species (46%) to the total number of alien species found, and the mean family richness (all sites combined) was relatively low (4 ± 0.39) but ranged widely (4 – 16) across sites. The top five sites in terms of family richness were sites 16 (n = 16), 2 and 9 (n = 15), 3 (n = 14) and 1 (n = 13), and the bottom-ranked sites were 27 (n = 7), 20 and 29 (n = 6), 28 (n = 5), and 4 (n = 4). North and south sectors had the highest presence of IAPs, and both had forest vegetation predominately (Table A1, Appendix A).

Thirty-five of the alien species found could be categorised (Category 1 – 3) according to the NEMBA typology (see Methods section): n = 29 for Category 1; n = 4 for Category 2 and n = 2 for Category 3. Furthermore, seven naturalised exotics, and 28 non-declared aliens were found. This implies that 35 (44%) of the aliens found within the study area are considered invasive. The mean number of IAPs per site was equivalent to nine but ranged widely (3 – 16) across sites. The top five sites based on IAPs presence were sites 2 (n = 16; forest), 9 (n = 14; thicket), 25 (n = 14; savanna), 6 (n = 13; savanna), and 13 (n = 13; forest), while the five bottom ranked sites were sites 11 (n = 5; savanna), 21 (n = 5; grassland), 28 (n = 4; savanna), 29 (n = 4; grassland), and 4 (n = 3; forest).

Alien species richness (invasive and non-invasive) across sites ranged from 9 – 25 species (Fig. 2.1), with a mean richness of 18.0 ± 4.2. The top five most speciose sites were 2 (n = 25; forest), 3 (n = 24; thicket), 6 (n = 24; savanna), 13 (n = 22; forest) and 18 (n = 22; thicket), and the five bottom ranked sites were 27 (n = 9; grassland), 28 (n = 9; savanna), 4 (n = 10; forest), 29 (n = 11; grassland), and 21 (n = 12; grassland).

Alien plant density (invasive and non-invasive) across the study area ranged from 0.07 to 3.76 individuals/m^2 (Fig. 2.1), with a mean density of 0.97 ± 0.75 individuals/m^2. Site 7 (grassland) had the highest non-invasive alien (n = 3.76 individuals/m^2) and IAP (n = 1.82 individuals/m^2) plant density. The top five ranked sites in terms of total alien density were sites 7 (3.76 individuals/m^2; grassland), 20 (2.53 individuals/m^2; savanna), 10 (1.80 individuals/m^2; savanna), 23 (1.68 individuals/m^2; savanna), and 5 (1.55 individuals/m^2; grassland), and the bottom ranked sites were 14 (0.35 individuals/m^2; forest), 4 (0.33 individuals/m^2; forest), 16 (0.31 individuals/m^2; savanna), 29 (0.14 individuals/m^2; grassland), and 17 (0.07 individuals/m^2; savanna). The top five alien species in terms of density were *Tagetes minuata* L. (5.71 ± 5.88 indivduals/m^2), *Rumex crispus* L. (5.32 ± 1.17 individuals/m^2), *Bidens pilosa* L. (2.80 ± 2.31 individuals/m^2), *Conyza sumatrensis* (Retz.) E. Walker (2.80 ± 0.81 individuals/m^2) and *Lantana camara* L. (2.60 ± 1.2 indviduals/m^2). One of these species is recognised as invasive (*L. camara*) while the remaining four species are not. The five bottom ranked species were *Passiflora subpeltata* Ortega, *Sonchus oleraceus* L., *Trichocereus macrogonus* (Salm-Dyck) Riccob., *Verbena brasiliensis* Vell. and *Xanthium strumarium* L. (all 1 ± 0 individual/m^2).

The frequency of occurrence across sites for individual alien species ranged from 3 – 25%, with the average frequency being 20%. Alien species with the highest frequency across the sites were *L. camara* (87% of sites; invasive), *Chromolaena odorata* (L.) R.M.King & H. Rob. (77% sites; invasive), *C. sumatrensis* (77% of sites, not declared), *B. pilosa* (73% of sites, not declared), and *T. minuata* (70% of sites, not declared) (Table A4, Appendix A).

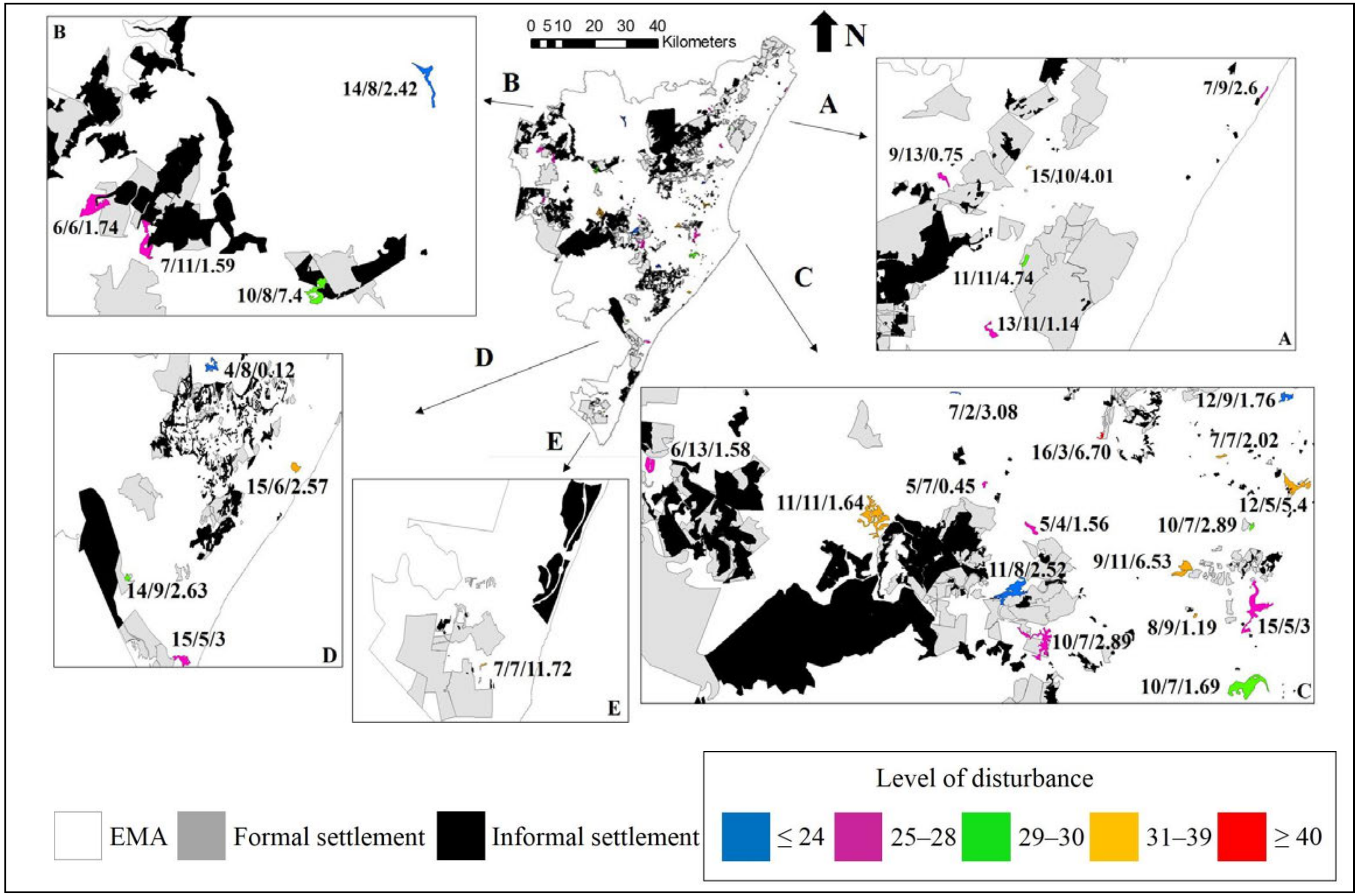

Figure 2.1: Distribution of alien species (including invasive alien plants [IAPs]) across the Durban Metropolitan Open Space System sampling sites (coloured polygons) within the eThekwini Municipality. Each coloured polygon represents a level of disturbance: blue = very low; purple = low; green = medium; yellow = high; red = very high. A – E represents parts of the study area in greater detail. Values associated with each site represent invasive alien species richness, alien species richness, and invasive alien plant density (individuals/m^2), respectively.

2.3.3. Identifying hotspots of invasiveness in relation to environmental parameters

Across sectors, alien species richness was significantly different between the central and north sectors but comparable among other sectors (P = 0.033, ANOVA). Alien plant density and family richness were comparable across sectors (P = 0.248 and P = 0.101 [ANOVA], respectively) (Table 2.2). When all sites within a sector are considered (Fig. 2.1), the highest aggregate (sum) of non-invasive alien species was as follows: north (n = 130) > west (n = 111) > south (n = 107) > east (n = 105) > central (n = 85). When the five sectors are ranked in terms of IAPs aggregate, the west sector drops two places in rank: north (n = 61 species) > south (n = 57 species) > east (n = 51 species) > west (n = 47 species) > central (n = 45 species). Despite these differences, the data suggest that both invasive and non-invasive alien species were present in high numbers across sites, in all five sectors.

The top five ranking sites in terms of alien species richness ranged between medium (29 – 30) and high (31 – 39) levels of disturbance, while the bottom sites ranged between very low (≤ 24) and low (25 – 28) levels of disturbance. The top five ranked sites in terms of IAPs richness ranged between very low (≤ 24) and very high (≥ 40) levels of disturbance, and the bottom five sites ranged between very low and high levels of disturbance.

The five sectors ranked as follows in terms of AII values (calculated based on Expression 1, Methods): east (0.047 ± 0.03) > west (0.037 ± 0.03) > north (0.036 ± 0.03) > central (0.030 ± 0.03) > south (0.02 ± 0.02) (Table 2.2). However, there were no significant differences in mean AII value across sectors (P = 0.721, ANOVA), and no significant correlations between AII and floristics parameters or level of disturbance (data not shown at sector scale). When individual sites in the study area were compared there were significant differences (P < 0.001, t-test) in the AII, and values were distributed across the four defined AII classes as follows: 20% (sites 2, 3, 7, 9, 19 and 25) were very high (labelled 'class 4'), 30% (sites 1, 8, 10, 13, 14, 18, 22, 24 and 30) high (labelled 'class 3'), 20% (sites 6, 11, 20, 23, 26 and 27) medium (labelled 'class 2'), 30% (sites 4, 5, 12, 15, 16, 17, 21, 28 and 29) low (labelled 'class 1') (Fig. 2.2). This means that 50% of the sites (spread across all vegetation types) can be classified as alien hotspots, i.e., class 3 or 4 sites in terms of AII, while the remaining 50% (spread across all vegetation types) represent emerging invasive alien hotspots (class 2) and early invasive detection sites (class 1). However, when DLV at individual sites was plotted against AII values, a weak relationship was observed (R^2 = 0.1) and it showed that only 20% of sites were actually in the very high class (i.e., alien hotspots)

(Figure A1, Appendix A). When site data were pooled, the AII was significantly positively correlated with levels of disturbance (Table A5, Appendix A).

Table 2.2. Alien species richness, alien plant density, family richness, and Alien Invasive Index (AII) for all five sectors.

Sector	Alien species richness (number of species at a site)	Alien plant density (individuals/m^2)	Family richness	Alien Invasive Index (AII)
North	21.67 ± 3.14 [a]	0.94±0.52 [a]	20 ± 5.28 [a]	0.036 ± 0.03 [a]
East	17.5 ± 2.26 [ab]	1.42 ± 1.24 [a]	16 ± 3.14 [a]	0.047 ± 0.03 [a]
South	17.83 ± 4.26 [ab]	0.57 ± 0.49 [a]	17 ± 4.08 [a]	0.02 ± 0.02 [a]
West	18.5 ± 3.67 [ab]	1.24 ± 0.73 [a]	17 ± 3.72 [a]	0.037 ± 0.03 [a]
Central	14.17 ± 4.75 [b]	0.69 ± 0.27 [a]	13 ± 1.17 [a]	0.030 ± 0.03 [a]

Values represent mean ± SD (n = 6 sites per sector) and are significantly ($P < 0.05$) different when labelled with different letters (one-way ANOVA).

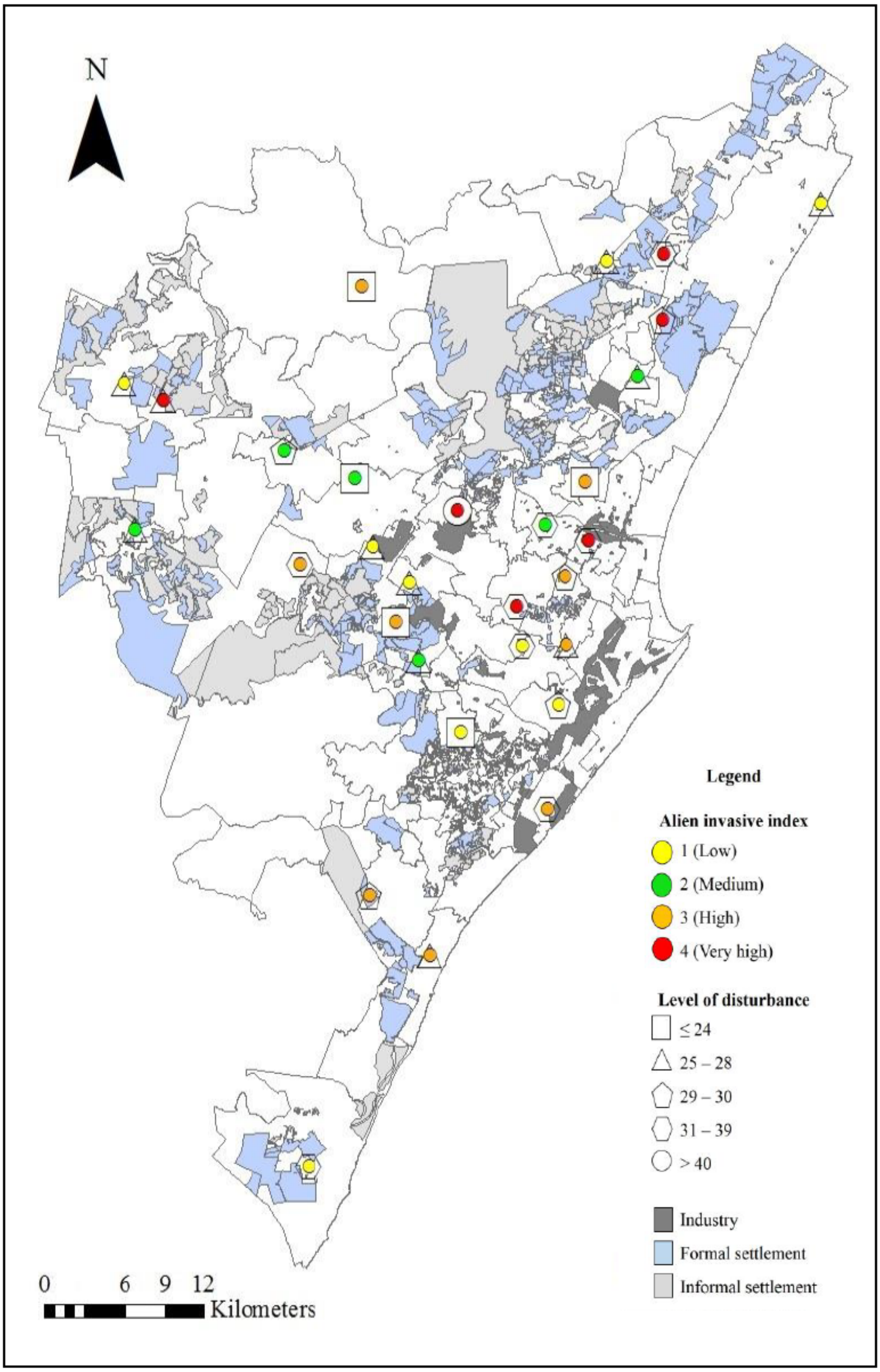

Figure 2.2: Alien Invasive Index (AII) highlighting sites that are invaded. Classes of AII range from 1 (low: 0.001 – 0.018), 2 (medium: 0.019 – 0.024), 3 (high: 0.025 – 0.067), and 4 (very high: 0.068 – 0.094). All red dots are indicative of invasive alien hotspots across all sites in the EMA, and shapes represent the level of disturbance (%).

Four parameters (referred to as principal components 1 – 4 henceforth) accounted for 76% variance in the data. In Figure 2.3, only the first three PCs are shown. Distance to roads (PC1) accounted for 29% variance in the data and was highly positively related to IAP density, non-IAP density, and total alien plant density (see Table A6 for R^2 values, Appendix A). Total plant density loaded most high for PC1. Level of disturbance (PC2) accounted for 50% of the variance and was highly positively related to invasive alien species richness and density and total species richness. Total species richness loaded most high for PC2. Distance to informal settlements (PC3) accounted for 64% of the variance and was highly positively related to non-invasive alien species richness and plant density and distance to industry. Non-invasive alien species richness loaded most high for PC3. Distance to industry (PC4) accounted for 76% of the variance and was highly positively related to level of disturbance, and negatively related to distance to informal settlements. Level of disturbance loaded most high for PC4 (see Table A6 for R^2 values, Appendix A).

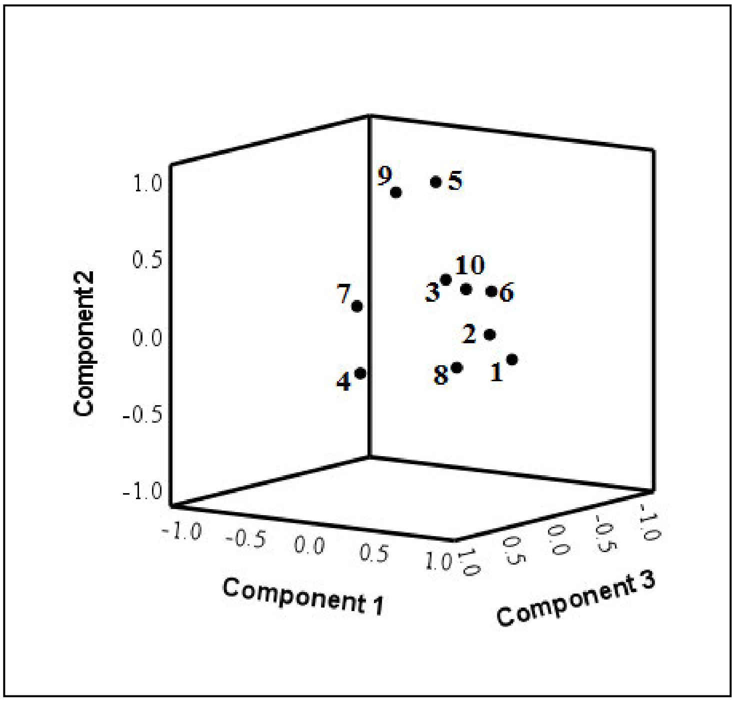

Figure 2.3: Principal component analysis (PCA) plot for the first three components. Each number (1 – 10) represents a principle component used in the PCA: 1 = distance to roads; 2 = levels of disturbance; 3 = distance to informal settlement; 4 = distance to industry; 5 = invasive alien species richness; 6 = IAPs density; 7 = non-invasive alien species richness; 8 = non-IAP density; 9 = total alien species richness; 10 = total alien plant density. The cumulative % of variance were as follows: PC1 = 29%; PC2 = 50%; PC3 = 64%.

2.4. DISCUSSION

2.4.1. Alien floristics in the study area

Using a rapidly developing city in South Africa as a case study, this study sought to develop an approach to identifying alien plant hotspots within an urban matrix. Despite the fact that just 30 of 2915 recognised green spaces in the city were sampled, 80 alien species (invasive and non-invasive) were recorded, and the richness and density of these species were compared with a number of anthropogenic factors. According to a recent report (eThekwini Municipality, 2018), there are a total of 106 IAPs found in the city of Durban. This is a relatively high number for an area of 2556 km^2; since, on average, 260 alien species were found across 54 European cities (Pyšek, 1998a). However, it must be noted that most of the species featured in the above-mentioned report for Durban (eThekwini Municipality, 2018) were based on surveys of parks and nurseries and not systematic assessments of alien species richness and density/abundance. This is largely because South Africa, like many countries in the developing world, faces increasing environmental challenges, which include urbanisation, rising numbers of informal settlements, limited infrastructural and service provision and, unemployment while trying to maintain the quality and quantity of green spaces (Pillay and Pahlad, 2014).

2.4.2. Taxonomic and life form coverage, and family/species ordering of alien flora in the study area

Even though alien species were present in all 30 of the sites sampled, species richness varied greatly across sites (Fig. 2.1). However, despite these inter-site differences at the species level, 46% of the species found belonged to just three (viz. Asteraceae, Fabaceae, and Verbenaceae) of the thirty families recorded. Asteraceae and Fabaceae are considered large Angiosperm families, consisting of > 20 000 species globally (Angiosperm Phylogeny Website [APW], 2019). Asteraceae and Fabaceae were also part of the top three dominant families for alien richness in urban areas of other studies (e.g., Pauchard and Alaback, 2004). Recent floristic studies for grasslands and forests within the city have shown Asteraceae and Fabaceae to be dominant alien families (Drury et al., 2016; Kambaj et al., 2018).

Of the five most dominant species in terms of frequency across sites, both *L. camara* (Verbenaceae) and *C. odorata* (Asteraceae) are invasive shrubs, whilst the remaining three species are alien herbaceous Asteraceae species (*C. sumatrensis*, *B. pilosa*, and *T. minuata*). South Africa has 170 of the global list of 622 invasive alien trees (357) and shrubs (265)

(Richardson and Rejmánek, 2011). *Lantana camara* is considered invasive due to its ability to reduce indigenous species diversity and richness, decrease soil fertility and alter ecosystem services (Taylor et al., 2012). This is based on its ability to produce allelochemicals (Sharma et al., 2005; Taylor et al., 2012), rapid growth rate, short life cycle, high reproductive potential, and competitive ability (Kohli et al., 2006). Globally, *L. camara* is a common and very challenging invasive species to manage (Goodall and Erasmus, 1996). Like *L. camara, C. odorata* produces allelopathic chemicals (Goodall and Erasmus, 1996) and is an aggressive pioneer species, particularly in disturbed habitats, and a prolific seed producer (Erasmus, 1985; Goodall and Erasmus, 1996). Similarly, the high frequency of some of the other species mentioned above is based largely on their reproductive strategy (Pérez-Fernández et al., 2019) and ability to colonize disturbed areas (Taylor et al., 2012) which are major contributors to invasiveness. *Conyza sumatrensis,* for example, thrives in abandoned arable land, road edges, and close to roads and railways and produces vast amounts of achenes (> 200 000 per individual) with high dispersal potential in the air (Anastasiu and Memedemin, 2012). *Bidens pilosa* also has allelopathic properties, and each plant produces approximately 80 floral heads with up to 3000 seeds per individual, and has the ability to invade various habitats, including disturbed areas, roadsides, and open spaces (Mahmoud et al., 2015). *Tagetes minuata* has small seeds that attach easily to the fur of animals, thereby aiding in dispersal, and produces secondary anti-herbivory metabolites (Martinez-Ghersa et al., 2000).

Interestingly, the three most dominant families in terms of species richness (Asteraceae, Fabaceae, and Verbenaceae) were also the most dominant in terms of density. All three of the dominant alien taxa in terms of density (*T. minuata* [Asteraceae], *R. crispus* [Polygonaceae], and *B. pilosa* [Asteraceae]) are non-declared alien herbs within the city. In fact, 56% of the aliens recorded were herbs, and as alluded to above there were very few (15%) of the alien species recorded in this study were trees. The reasons for the dominance of these species are similar to those made for species that were most frequent across sites; for example, *T. minuata* has allelopathic properties (Arora et al., 2015), *R. crispus* has very high seed production, multiple flowering times in one year, quick establishment from seed, high germination rates, and can regenerate vegetatively ([viz. cuttings] Pino et al., 1995) and sexually (Pérez-Fernández et al., 2019).

2.4.3. Drivers and hotspots of invasiveness

Urbanisation is associated with a number of disturbances that promote the introduction, spread, and impacts of aliens (Pyšek, 1998a; Alston and Richardson, 2006; Botham et al., 2009; Potgieter et al., 2020). In this study, all 30 sites sampled exhibited some level of disturbance, with the most commonly observed types of disturbance being solid waste dumping, trampling, footpaths, and fires (planned vs. unplanned), which have been associated with alien invasions (Berry et al., 1994; O'Connor and van Wilgen, 2020).

In the present study, the PCA reduced the 10 variables considered to four principal components. Level of disturbance (PC2) was strongly related to IAP richness. It is well established that alien species richness can increase in response to anthropogenic activity and disturbances (e.g., Hobbs and Huenneke, 1992; Celesti-Grapow et al., 2006), and this relationship is modulated by the structure, activities, and land-use practices associated with the built-up areas within an urban matrix (Niemala, 1999; Godefroid and Koedam, 2007; Potgieter et al., 2020). Protected areas have a low number of non-natural disturbances, and their boundaries act as a filter to invasive alien species (Wilson et al., 2020). However, green spaces in the current study were mainly unprotected with minimal management and were therefore exposed to non-natural disturbance such as footpaths, solid waste dumping, settlements, grazing, and agriculture. Disturbance from agricultural fields (such as constant trampling and footpaths) pose problems for alien spread (van Rensburg et al., 2018), and studies have found that alien plants are significantly more abundant at sites adjacent to these fields and urban areas (Meek et al., 2010; Wilson et al., 2020). Anthropogenic disturbance has been reported to increase invasibility in South African ecosystems (van Wilgen et al., 2020). In the current study, sites were susceptible to non-natural disturbance (increased invisibility) causing invasibility to increase. The invisibility of sites (how susceptible they are) can therefore be used as a management tool in future studies.

As in many developing countries (Berry et al., 1994), Durban hosts both formal and informal housing settlements (Meth, 2013). As you move towards informal settlements in the current study, non-invasive species richness and density decreased. This may be explained by the fact that informal settlements usually occupy smaller areas of public green spaces, and space around settlements don’t have much vegetation cover (McConnachie and Shakleton, 2010; Potgieter et al., 2020). Combined with a lack of basic needs available for people at these settlements, the cutting down of plant species (including invasives) occurs to assist with fuel for fire or shelter (Potgieter et al., 2020). As more species decrease close to informal settlements, more space becomes available for constructing more settlements. Therefore, fewer alien species are found closer to settlements than further away.

There was a significant positive relationship between distance to roads (PC1) and IAP density, non-IAP density, and total alien plant density. These patterns are potentially an artefact of the sampling regime (quadrats were laid at least 2 m from any mowed/concrete/tarred curb or road edge/verge). The curb maintenance methods presently employed within the city involve clearing/grass cutting at edge features, and these edges represent potential dispersal corridors that were not sampled. Other studies (e.g., Tyser and Worley, 1992; Lake and Leishman, 2004; Alston and Richardson, 2006; Follak et al., 2018) have shown that disturbances from transport routes produce dispersal corridors that promote alien plant invasion.

Controlling alien invasion, particularly in the cities of developing countries with limited resources, requires the rapid identification and continuous monitoring of alien plants, as well as prioritization of areas and species for clearing. Cities are believed to host alien invasive hotspots, but this is very rarely described quantitatively (but see Kühn et al., 2004; Celesti-Grapow et al., 2006). While it is common to define hotspots by the mere number of aliens species present ([viz. alien species richness]; Celesti-Grapow et al., 2006), this study attempted to develop and use AII to identify hotspot of invasiveness. Muratet et al. (2008) attribute these hotspots to the central positioning of cities to major transport routes, while other studies assert that human activities and the associated disturbance lead to increased alien establishment in cities (Hobbs and Huenneke, 1992; Potgieter et al., 2020). The current study supports this assertion by showing that IAP richness was strongly related to the presence of informal settlements and, by implication had high disturbance levels. Furthermore, the study showed that apart from the drivers of invasiveness identified by the PCA (level of disturbance, distance to informal settlements, distance to roads), the AII developed could be used to identify six hotspots of invasiveness (sites 2, 3, 7, 9, 19 and 25 [AII class 4 in Fig. 2.2]). The very high index of invasiveness at four (2, 7, 9, 25) of these six sites could be attributed to high (31 – 39) to very high levels (≥ 40) of disturbance, while the fifth site (3) has a medium level of disturbance (Fig. 2.1). It should also be noted that sites 2, 7, 9, and 25 were also subject to high levels of solid waste dumping (which included garden refuse), while site 25 is situated in a densely populated urban area (with many home gardens).

Highly disturbed natural green spaces are prone to the establishment of garden-escapees from adjacent or nearby parks and gardens (Pyšek, 1998a; Botham et al., 2009), and the dumping of garden refuse can also lead to the spread of alien species (Foxcroft et al., 2008).

The utility of the AII developed in this study in identifying alien hotspots within an urban matrix is validated by the fact that it was significantly positively correlated with disturbance. However, it must be mentioned that the highest-ranked site (site 19) in terms of this index was subject to low (26) levels of disturbance. A potential reason for this anomaly may be the high density (0.81 individuals/m^2) of *Populus* x *canescens* (Aiton) Sm. (Salicaceae), which was also unique to this site. This species is known to form dense stands (through profuse suckering) in moist areas and propagates vegetatively, limiting its ability to spread (Henderson, 1991). The dense stands and high numbers of mature individuals suggest that this is an established population and likely to have occupied the site for several years, or possibly decades. The index was also useful in identifying emerging alien hotspots, viz. sites belonging to class 2: 6, 11, 20, 23, 26, and 27. These sites exhibited fairly low means for disturbance level, invasive alien species richness, and density compared with class 4, but a higher non-invasive alien species richness and density.

2.5. CONCLUSION

The present study set out to determine whether alien plant species richness and density were related to urban land-use patterns and levels of non-natural disturbance and which were the drivers of invasiveness, with the intention of developing an index to identify hotspots of invasiveness. A wide range of alien taxa were recorded, many of which are recognised as invasives globally. There was some taxonomic bias at the family level in terms of representation (46% of all species belonged to Asteraceae, Fabaceae, and Verbenaceae), frequency across sites, and densities. Of the five most dominant species identified, two were invasive (*L. camara* [Verbenaceae] *and C. odorata* [Asteraceae]), and three were non-invasive (*C. sumatrensis*, *B. pilosa*, and *T. minuata* [Asteraceae]), suggesting the invasive potential of the latter three. The major driver of invasiveness in these urban green spaces appears to be disturbance. The AII developed included IAP species richness and density, cumulative alien species richness, and cumulative alien plant density as variables and was useful in identifying alien hotspots. The AII was strongly related to level of disturbance and should be applied to other cities in South Africa and globally to assess its utility in prioritising sites for alien species control. In terms of Durban, the established alien hotspots identified using the AII and the dominant species (*L. camara* and *C. odorata*) represent an immediate management priority. The traits that promote the invasiveness of these dominant species (invasive and non-invasive) should also be investigated, despite the enormity of the task to generate a comprehensive understanding of the factors that drive alien invasiveness within cities. Finally, the findings show the value of combining classical *in situ* vegetation surveys and overlay analysis using GIS for prioritising green spaces and alien species for management in cities that are limited in terms of financial resources.

CHAPTER 3

Understanding alien and indigenous floristic ordering, plant diversity, and co-occurrence patterns in a subtropical urban matrix

ABSTRACT

Alien-indigenous plant interactions are poorly understood in urban settings, but there is consensus that anthropogenic activities can affect indigenous plant species directly through disturbance and/or indirectly by promoting the presence of alien species. This motivated the present study, which investigated alien and indigenous floristic ordering (richness, density and life-form), diversity (alpha and functional diversity [FD]), and degree of co-occurrence within a subtropical urban matrix in South Africa. Thirty natural green spaces across the eThekwini Municipal Area were assessed for species richness (number of species), density (invasive and non-invasive aliens and indigenous species), and various diversity measures. Floristic data were then related to levels of non-natural disturbance. Positive species co-occurrence interactions were examined between aliens only and alien-indigenous pairs to identify potential mutually beneficial interactions between species pairs. A Principle Component Analysis (PCA) was conducted to identify relationships among floristic ordering, non-natural disturbances and diversity (functional only). Cumulatively, 201 species (from 59 families) were found, of which 121 were indigenous. The relationship between alpha diversity and species richness differed for alien and indigenous species: alpha diversity was significantly negatively related to alien species richness and significantly positively related to indigenous species richness). Alien species had significantly higher FD values for univariate FD (life form, life cycle, dispersal syndrome) compared with indigenous species FD values for all categories; however, aliens exhibited a lower FD for reproductive mode. There were 20 positive alien-alien co-occurrences ranging from three and 19 sites, with two pairs co-occurring (*Lantana camara* and *Solanum mauritianum*) at > 50% of sites. There were 27 positive alien-indigenous co-occurrences ranging from three to 14 sites, with three pairs co-occurring (*Conyza sumatrensis* and *Centella asiatica*) at ≥ 40% of sites. Co-occurrence data shows that alien-indigenous co-occurrence can occur at high levels in urban spaces, and there are indications of species-specific interactions, possibly facilitatory. The PCA showed that combined FD of species is more strongly related to levels of disturbance and both alien species richness and density. This suggests that anthropogenic induced changes in FD within habitats could influence their susceptibility to alien invasion. Co-occurrence data could be valuable in understanding alien and indigenous functional interactions in urban green spaces. The value of FD in understanding these interactions could not be fully established here given the limited number of traits assessed, but the results suggest that anthropogenic induced changes in FD within habitats could influence their susceptibility to alien invasion. More

detailed studies on competitive and facilitatory interactions between alien and indigenous species and plant FD within urban green spaces are needed since classical theories around the relationship between diversity and invasibility may not hold for disturbed/transformed ecosystems.

3.1. INTRODUCTION

Globally, urban areas cover only approximately 3% of the earth's terrestrial surface (Iswoyo et al., 2018), but rapid urban growth threatens biodiversity and presents numerous conservation challenges such as habitat loss and alien plant invasions (Antrop, 2004; Hansen et al., 2005, Kowarik, 2011; Potgieter et al., 2020). This is largely because cities in many developing parts of the world are often situated in close proximity to areas rich in biodiversity (e.g. Curitiba in Brazil, Mexico City in Mexico, and Cape Town in South Africa [Marchese, 2015; Gaertner et al., 2016]). Natural green spaces within these cities are diverse in terms of size, vegetation, environmental conditions and exposure to disturbance (Fuller and Gaston, 2009; Sister et al., 2010), but generally provide a range of ecosystem services which include filtering systems, removing/reducing air, water and noise pollution (Escobedo et al., 2011; Groenewegen et al., 2006; Wolch et al., 2014) and providing suitable habitats for fauna (particularly pollinators [May, 2019; Daniels et al., 2020]). Cities are, however, becoming increasingly overcrowded and polluted (Blanco et al., 2009; Wolch et al., 2014), impacting negatively on the integrity of natural green spaces within urban matrices (Pillay and Pahlad, 2014). Apart from anthropogenic pressures, urban green spaces are often plagued by invasive alien plants (IAPs) that threaten indigenous species and ecosystem functioning (Vitousek et al., 1997; Bjerknes et al., 2007; Relva et al., 2010; Le Maitre et al., 2020). Increasing levels of anthropogenic disturbance, a common consequence of urban development, generally lead to an increase in the number of alien species (Kowarik, 1995; Relva et al., 2010; Appalasamy et al., 2020). Disturbances such as waste dumping, footpaths, grazing and trampling by large herbivores (mainly on the outskirts of the city centre) have been shown to favour the emergence of alien species that are usually well-adapted to disturbance (Hobbs and Huenneke 1992, Wiser and Allen 2006; Relva et al., 2010). Remnant patches of forest within urban areas are particularly susceptible to plant invasions due to increased edge effects and propagule pressure from the surrounding urban matrix (Cadenasso and Pickett, 2001; Duguay et al., 2007; Mavimbela et al., 2018).

The well-established relationship between urbanisation and increased prevalence of IAPs has prompted increasing interest in describing, understanding, and predicting plant invasions. In this regard, studies have shown that alien plants can comprise as much as 32-53% of the total flora in cities (Zhao et al., 2010; Kowarik, 2011), making cities 'alien hotspots'. The increased mobility of people and goods can contribute to the creation of these alien hotspots in cities (Seebens et al., 2017), but it is largely unclear how alien and indigenous species interact and impact each other and contribute to the transformation (in terms of species richness and structure) of natural vegetation in urban green spaces. The IMH (Simberloff and van Holle, 1999; Simberloff, 2006) suggests that alien species facilitate each other, increase their chances of survival, and can supposedly lead to the reduction of indigenous species abundance, which benefits alien species through competitive release (Simberloff and Von Holle, 1999; Braga et al., 2018). However, there is limited understanding of how functional and ecological interactions between co-occurring indigenous and alien plants influence the success of biological invasions under conditions of dynamic environmental change and stressors associated with urban matrices (Carbonell et al., 2017).

Community assembly frameworks show patterns of species co-occurrences to be based on both neutral (e.g., dispersal limits) and niche-based processes (Weiher et al., 2011). Abiotic stressors may increase the segregation of species into different habitats (abiotic filtering) (Shipley et al., 2006), resulting in a greater functional similarity between co-existing species (Gutierrez-Canovas et al., 2015; Carbonell et al., 2017). Under low-stress conditions, species can exploit resources and habitats, thereby facilitating the co-existence of ecologically diverse species (Spasojevic and Suding, 2012; Carbonell et al., 2017). Invasive species may also compete strongly against ecologically related or trait-based comparable indigenous species under similar conditions (Violle et al., 2011), causing a change in the patterns of co-existence and performance of indigenous species (Chase and Leibold, 2003). When species interact in a similar niche, the weaker of the two species are out-competed and excluded from the community (Reitz and Trumble, 2002; Carbonell et al., 2017). According to Mavimbela et al. (2018), competition in the same niche may be due to the influence of disturbance on resources.

Competitive interactions (niche separating and limiting similarity) prevent the co-existence of similar species (MacArthur and Levins, 1967; Chesson, 2000), and strong competitive interactions result in more functional diversity (FD) than would be expected by chance (Weiher and Keddy, 1995; Schleuter et al., 2010). However, as alluded to above, anthropogenic disturbances can also cause shifts in ecosystem dynamics, including plant species richness, species ordering (Kowarik, 2011), competitive interactions and FD (Biswas and Mallik, 2010; Laliberté et al., 2013). Understanding vegetation changes brought about by plant invasions and predicting species invasiveness within specific urban environments is challenged by the fact that classical/traditional ecological theories around species diversity and FD are potentially complicated by the presence of anthropogenic disturbance. Of particular interest to the present study are reports that the relationship between species diversity and FD varies with disturbance intensity (Biswas and Mallik, 2011; Carreño-Rocabado et al., 2012). It is also not clear whether changes in this relationship can be used as an indication of the degree of or susceptibility to alien invasion associated with a site. The depth of the studies needed to answer such questions is, however, often limited by the lack of and/or limited trait data. This situation is compounded in areas with rich flora, and short-term studies do not allow sufficient time to collect trait data for hundreds of species. In these instances, the value of more 'simple' traits such as reproductive mode, i.e. the ability of species to reproduce sexually, asexually or via a combination of these (Zhang and Zhang, 2007), could be explored in the context of species alien-indigenous interactions, co-occurrence, and diversity-disturbance relationships.

Managing alien plant invasions and protecting indigenous biodiversity within urban green spaces does, and will, increasingly require human intervention such as alien plant control and indigenous species reintroduction (Mugwedi et al., 2017). This remedial engineering in invaded landscapes will require an understanding of alien-indigenous plant assemblages in urban settings, particularly in terms of how they may be influenced by anthropogenic and climatic factors. More specifically, this will require answering some fundamental research questions in the context of alien and indigenous floristic interactions and ordering within urban green spaces: (1) Is species (alien and indigenous) richness, density and diversity (alpha and functional) related to anthropogenic (including levels of non-natural disturbance) factors, and/or vegetation type? (2) How do alien and indigenous FD compare, and is this influenced by non-natural disturbances associated with urban areas? and (3) What is the degree of co-occurrence between alien-alien and alien-indigenous species?

The rapidly developing city of Durban, in South Africa, was used as a case study to address the above research questions. Selected natural green spaces (unplanted and not subject to agricultural activity) across the city were characterised in terms of alien and indigenous plant species richness, density and diversity (alpha and functional), and co-occurrence, in relation to levels of non-natural (anthropogenic) disturbance.

3.2. METHODS

3.2.1. Study sites and vegetation surveys

The description of the study area and methods used for site selection have already been described in Chapter 2 (Section 2.2.1). The study area and sites are shown in Figure 3.1. Furthermore, the details of vegetation surveys carried out at each of the thirty sites selected is given in Section 2.2.2. of Chapter 2.

3.2.2. Identification and categorisation of flora

Plant species recorded as part of the vegetation surveys at each site were identified using field guides (Pooley, 1998; Boon, 2010) and other published literature. Nomenclature and taxonomic authorships follow the New Plants of Southern Africa (NewPOSA) website of the South African National Biodiversity Institute (SANBI, 2020a), while conservation status of the species follows SANBI's Red List of South African Plants (SANBI, 2020b). The categorisation of alien taxa (non-invasive and invasive) was based on the National Environmental Management: Biodiversity Act ([NEMBA] Act no. 10 of 2004), Alien and Invasive Species List 2020 (Department of Environmental Affairs, 2020).

Species ordering is an important tool that can be used in comparative floristic studies (Jones et al., 2017). In the present study, alien and indigenous species and family representation (in terms of species richness) were ranked to identify the top three (dominant) species and families across all sites. Species (richness, density) and family ranking was summed at site level and averaged for the entire study area.

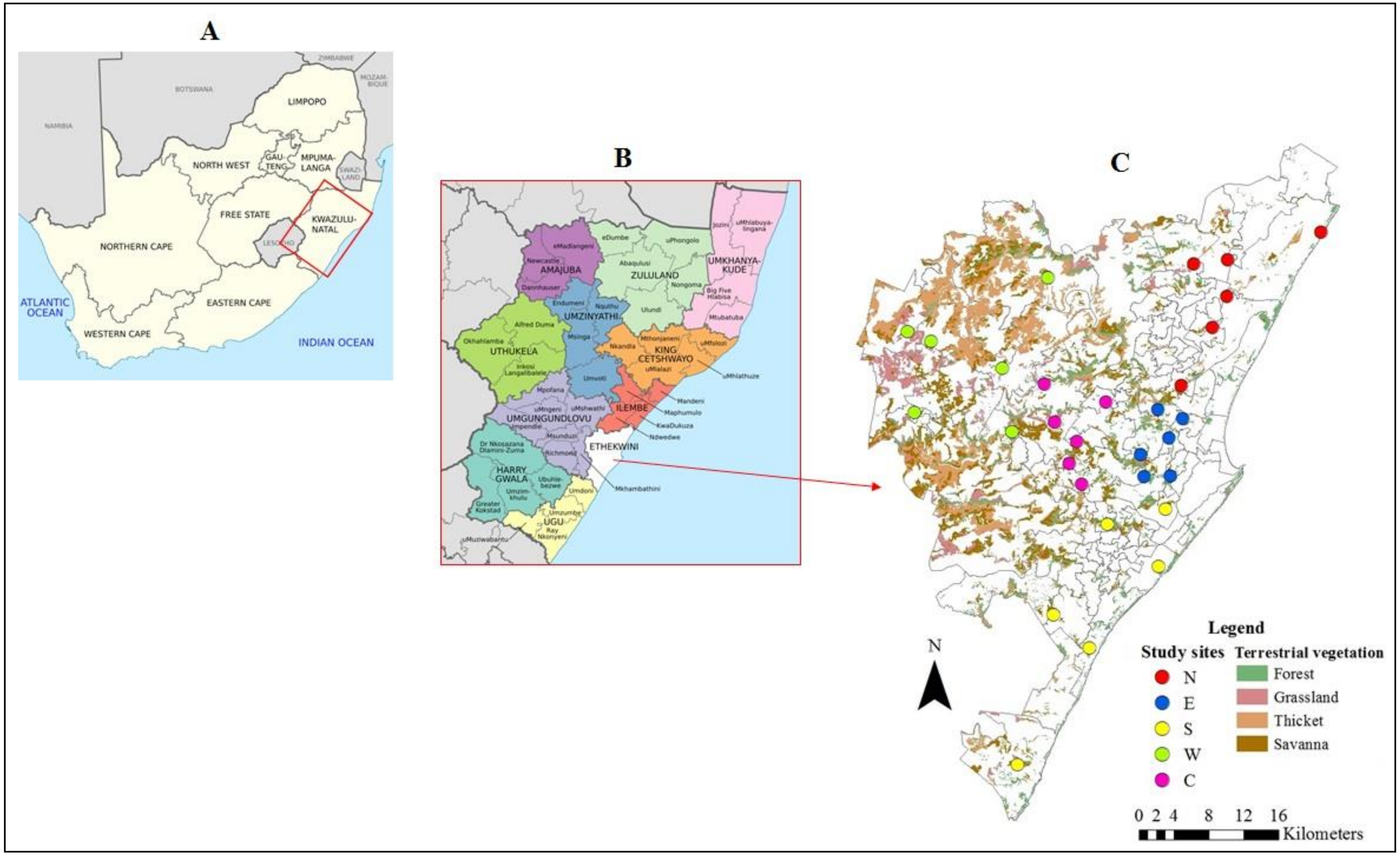

Figure 3.1: The province of KwaZulu-Natal in South Africa (A) within which the study area, the eThekwini Municipality (B), is located and the study sites (dots) in the eThekwini Municipal Area (C) sampled for alien and indigenous vegetation. Polygons are shaded based on the vegetation type they represent. Dots are coloured based on the sector of the city they were located in (N: north; E: east; S: south; W: west; C: central).

3.2.3. Alpha species diversity and functional diversity

Alpha diversity was calculated using EstimateS 9.0 (Colwell, 2013). Both Shannon's exponential (*H'*) and Simpson's inverse (*1/D*) indices were calculated to compare diversity across all 30 sampling sites based on quadrat data (n = 240 quadrats). The two indices of alpha diversity used in the present study measure diversity on the basis of species richness (Shannon's exponential index) and evenness (Simpson's inverse index) (Lincoln et al., 1982; Santini et al., 2017): the higher the species richness, the higher the Shannon's index and the lower the Simpson's inverse index, the higher the evenness (Luis, 1996; Drury et al., 2016).

Functional diversity (FD) was estimated in R statistics (R Core Development Team, 2014) using a script written by Shan Kothari from the University of Minnesota (available at https://github.com/ShanKothari/DecomposingFD). The metric proposed by Scheiner et al. (2017) was used to express FD, effectively integrating measures of trait evenness, trait dispersion, and species richness. Functional diversity was estimated for each site using four categorical traits: dispersal syndrome (air, wind, human, animal), life form (herb, shrub, tree), reproductive mode (both sexual [seed, achene], or asexual (using vegetative subterranean organs [e.g. rhizomes]) and life cycle (annual, perennial), following Murphy et al. (2006). All categorical traits were classified as binary (0 = absent; 1 = present). Functional diversity was calculated using each trait individually (univariate), as well as using all traits in conjunction (multivariate), since traits may respond differently to the same environmental gradient (Spasojevic and Suding, 2012). In this study, FD was estimated for three data subsets: alien species only, indigenous species only, and all species combined (alien and indigenous).

3.2.4. Level of disturbance and proximity to land-use types

Levels of non-natural disturbance were assessed at all sites during the last year of sampling using a scoring matrix (see Chapter 2, Table A2, Appendix A) based on the typology and scoring system described in Section 2.2.4. (Chapter 2). The scores for the eight disturbance types were then summed (at site level; maximum score = 40) and expressed as a percentage of the potential maximum score (40). These percentiles were then used as the 'Disturbance Level Value' (DLV), i.e. an integrated indicator of disturbance intensity at each site, and plotted as a boxplot (SPSS Inc., Version 25, Chicago, IL), to delimit five disturbance classes: very low (≤ 24%), low (25 – 28%), medium (29 – 30%), high (31 – 39%), and very high (≥ 40%).

The 'generate near table tool' in ArcGIS 10.3 was then used to measure the distance (m) of each quadrat to the closest land-use feature (roads, informal settlements, housing, industry) (after Doriwala and Shah, 2010). The site-to-feature distance values were then analysed as described below. The sites were also mapped (in ArcMap version 10.3, ArcGIS) to show their relative proximity to housing, industry and informal settlements and location within the study area in relation to the five sectors shown in Figure 3.1.

3.2.5. Species co-occurrence

The presence-absence data of all species across the 30 sites were used to generate a co-occurrence matrix. Species co-occurrences were then tested for three co-occurrence patterns (random, positive, and negative) using the 'COOCCUR' package in R (Veech, 2013; R Core Development Team, 2014). This analysis utilized a probability-based approach to assess the likelihood of each species pair occurring more or less frequently than expected, under the assumption that species are distributed independently (Veech, 2013). Only positive co-occurrences were examined at two levels: alien-alien and alien-indigenous. This was done to determine which species pairs co-occur together at more sites than expected and if each species pair were randomly distributed.

3.2.6. Statistical analyses

Data for all sites (eight quadrats at each of 30 sites yielding n = 240 quadrats) were pooled prior to all statistical analyses, which were carried out in SPSS (SPSS Inc., Chicago, IL) and R (R Core Development Team, 2014). All data were tested for normality using the Shapiro Wilks/ Kolmogorov-Smirnov test. Non-parametric data were log or arcsine transformed where necessary. A Principle Component Analysis (PCA) was used to test for relationships among floristic, disturbance, and land-use variables: alien and indigenous floristic ordering (richness and density), diversity (functional only and not alpha), distance to land-use feature class layers (viz. distance to roads, housing, rivers and informal settlements), and disturbance level. Due to the large number of non-zero loadings in the first attempt, it was impossible to interpret variable associations clearly. Therefore, two successive PCA's were run to understand variable interactions by truncating the number of PC loadings. The subsequent two PCA's were conducted for the following interactions: FD, non-natural disturbance and land-use, and floristic ordering and FD.

3.3. RESULTS

3.3.1. Sites and level of disturbance

Sampling sites across the EMA differed in size (10 720 – 2 431 424 m^2) and degree of disturbance; ranging from very low (16.7% of sites) and low (36.7% of sites) to medium (16.7% of sites), high (26.7% of sites) and very high (3.3% of sites) (see Table B1, Appendix B). The sites belonged to four vegetation types: forest (n = 8), grassland (n = 6), savanna (n = 12) and thicket (n = 4). Within vegetation types, disturbance levels varied across sites (Fig. 3.2). Generally, sites with thicket vegetation (least sampled vegetation type) did not experience high or very high levels of disturbance, while forest and grassland sites (intermediate sampling levels) exhibited high levels of disturbance. Sites with savanna vegetation (most sampled vegetation type) had the highest degree of disturbance. A few sites within each vegetation type exhibited very low levels of disturbance, and savanna was the only vegetation type in which all disturbance levels were represented.

3.3.2. Floristics

Cumulatively, a total of 201 species were recorded after surveying the 30 sites (see Table B2, Appendix). These species belong to 59 families with the three most speciose families (alien and indigenous species combined) being, Asteraceae (n = 36 species) > Fabaceae (n = 24 species) > Poaceae (n = 17 species). These three families hosted 38% of the total number of species recorded.

Of the 201 species, 40% were alien (see Table B2, Appendix B) and the remaining 60% were indigenous. The alien species represented 30 families while the indigenous species represented 43. The three most speciose families in terms of alien species were, Asteraceae (n = 18, 60%) > Fabaceae (n = 11, 37%) > Verbenaceae (n = 5, 17%). The most speciose families in terms indigenous species were Asteraceae (n = 18) > Poaceae (n = 17) > Fabaceae (n = 13). All the indigenous species were of 'least concern' (LC) conservation status (SANBI, 2020b), and 40% of them belonged to the top three dominant families mentioned above. There were a number (n = 32) of families with monotypic species representation for both alien (n = 12) and indigenous (n = 20) flora (see Appendix B for details).

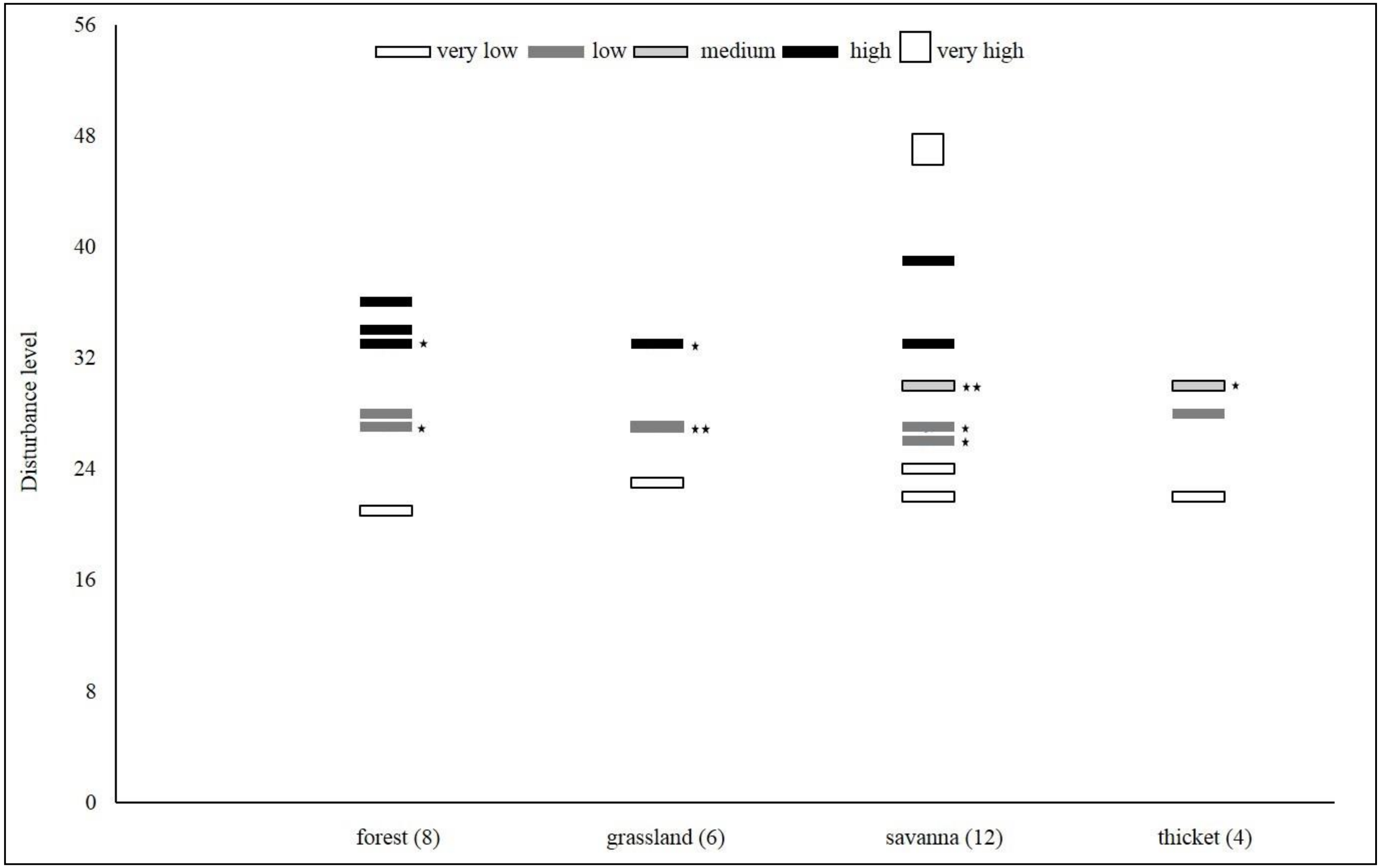

Figure 3.2: Distribution of sites (n = 30) across varying levels of disturbance for four vegetation types sampled. The number of sites belonging to each vegetation type is given within brackets on the x-axis. Disturbance levels with more than one site (within a vegetation type) are represented by one star (one additional site) and two stars (two additional sites).

When data for alien and indigenous species (n = 201) were pooled for analysis, the life form distribution (Figure 3.3) was as follows: herbs > shrubs > graminoids > trees > climbers. Within the alien taxa alone (n = 80), life form distribution again showed a high proportion of herbs, followed by shrubs, trees and climbers. Indigenous species (n = 121) exhibited a similar life form distribution trend: herbs > shrubs > trees > climbers. However, the major exception was that all graminoids (sedges and grasses; 12% of the total number of species) found were indigenous (Figure 3.3).

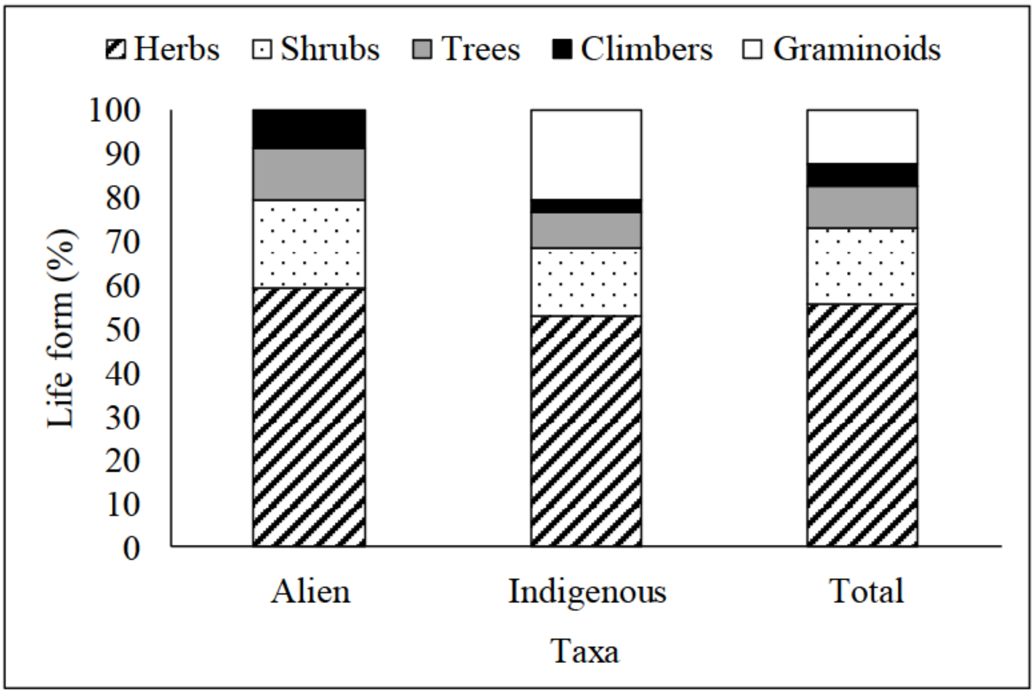

Figure 3.3: Life form distribution for alien, indigenous and total taxa. Values represent the percentage of life form within each taxa category, across 30 sites.

3.3.2.1. Species richness

Alien and indigenous species richness (i.e. number of species) ranged widely across sites, from nine to 25 species for the former and three to 28 species for the latter (Table B3, Appendix B). The average number of species per site was statistically similar ($P > 0.05$, ANOVA) between alien (18.00 ± 4.20) and indigenous (16.00 ± 5.40) taxa (Fig. 3.4A). The three most speciose sites in terms of alien flora were sites 2 (n = 25, forest), 6 (n = 24, savanna) and 18 (n = 23, thicket) while the three most species-poor sites in terms of aliens were sites 29 (n = 12, grassland), 28 (n = 9, grassland) and 27 (n = 9, savanna). The three most speciose indigenous sites were sites 18 (n = 25, thicket), 17 (n = 22, savanna) and 5 (n =

21, grassland) and the three most species-poor sites were sites 9 (n = 2, savanna), 23 (n = 8, savanna) and 27 (n = 7, savanna). It should be noted that site 18 was one of the most speciose sites, and site 27 was the most species-poor sites in terms of alien and indigenous flora. When data for alien and indigenous species were combined the three most speciose sites were 5 (n = 39, grassland), 18 (n = 38, thicket) and 7 (n = 37, grassland), while the three most species-poor sites were 11 (n = 18, savanna), 8 (n = 17, savanna) and 27 (n = 14, grassland).

3.3.2.2. Plant density

Alien plant density (for all non-graminoid taxa combined) varied widely across sites (0.07 to 3.76 individuals/m^2) and to a greater degree than indigenous plant density (0.01 to 1.19 individuals/m^2) (Table B3, Appendix B). There was no difference between the average number of individuals/m^2 for alien and indigenous flora when data for all species within each category were pooled. The top three sites in terms of alien plant density were sites 7 (3.76 individuals/m^2, grassland), 20 (2.53 individuals/m^2, savanna) and 10 (1.80 individuals/m^2, savanna), and the lowest ranking three sites were sites 16 (0.31 individuals/m^2, savanna), 28 (0.29 individuals/m^2, savanna) and 17 (0.31 individuals/m^2, savanna). The top three sites in terms of indigenous plant density were 17 (1.19 individuals/m^2, savanna), 7 (1.10 individuals/m^2, grassland) and 15 (1.00 individual/m^2, forest), and the bottom ranking three sites were sites 4 (0.12 individuals/m^2, forest), 23 (0.10 individuals/m^2, savanna), and 9 (0.01 individuals/m^2, thicket). Interestingly, site 7 (grassland) featured in the top three sites in terms of alien and indigenous plant density.

The top three alien species in terms of density were *Tagetes minuta* (3.33 individuals/m^2), *Rumex crispus* (2.86 individuals/m^2) and *Bidens pilosa* (1.77 individuals/m^2), and the bottom three ranking species were *Passiflora subpeltata, Sonchus oleraceus* and *Trichocereus macrogonus* (all 1.00 ± 0.00 individual/m^2). The top three indigenous species in terms of average density were *Berkheya speciosa* (1.03 individuals/m^2), *Cheilanthes viridis* (0.72 individuals/m^2) and *Asystasia gangetica* (0.58 individuals/m^2), while the bottom-ranked species were *Solanum incanum, Tephrosia villosa* and *Trema orientalis* (all 1.00 ± 0.00 individual/m^2).

When data for alien and indigenous species were combined (to assess total plant density), plant density ranged from 0.44 to 4.83 individuals/m^2 (average = 1.41 ± 0.88 individuals/m^2) across sites. The three families that exhibited the highest total density were Asteraceae (0.43 ± 0.71 individuals/m^2), Verbenaceae (0.35 ± 0.63 individuals/m^2) and

Malvaceae (0.19 ± 0.27 individuals/m^2), while the three families with the lowest densities were Araceae, Cannabaceae and Ebenaceae (all 0.005 ± 0.00 individual/m^2).

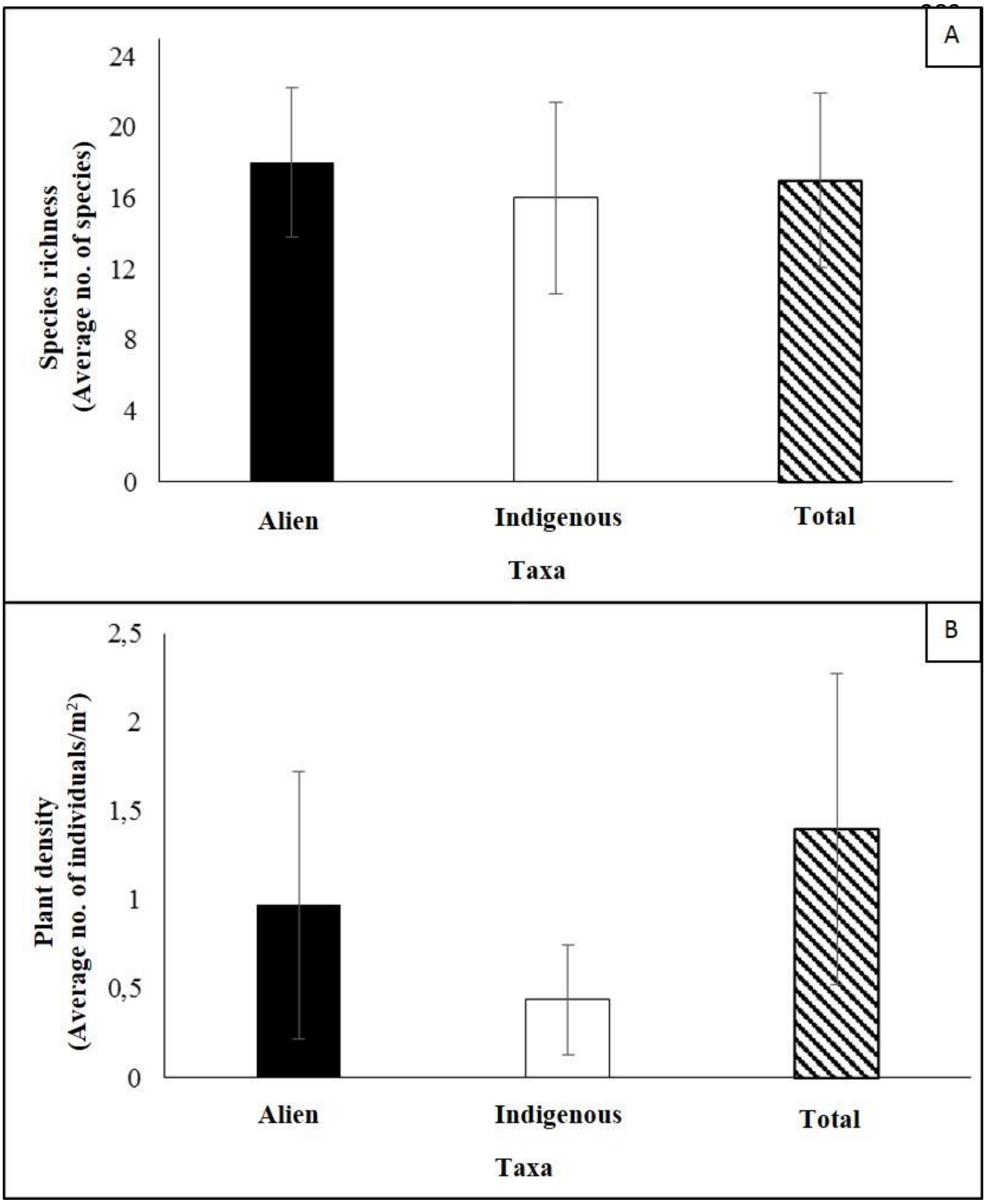

Figure 3.4: Species richness (A) and density (B) for alien and indigenous taxa with data for all sites combined. Values represent mean ± SD (n = 30 sites), and there were no significant differences between categories ($P < 0.05$, independent t-test).

3.3.3. Alpha and functional diversity

The average number of species per quadrat varied widely between sites, ranging from 5.09 (site 9, thicket) to 24.03 (site 16, savanna) and averaged at 12.19 ± 3.83 (data not shown). The variation across sites for the Shannon's exponential index was just as wide: 7.13 (site 23, savanna) to 24.86 (site 18, thicket) with an average of 15.53 ± 4.09 (see Figure 3.5 and Table B4, Appendix B). This wide inter-site variation extended to the Simpson's inverse index as well, which ranged from 3.97 (site 23, savanna) to 17.58 (site 18, thicket) and averaged at 9.97 ± 3.36 (see Table B4, Appendix B). The top three sites for the Shannon's exponential index were sites 18 (24.86, thicket), 29 (22.98, grassland) and 14 (20.41, forest), and the bottom ranking three sites were 11 (9.70, savanna), 10 (9.47, savanna) and 23 (7.13, savanna) (see Figure 3.5 and Table B4, Appendix B). The top three sites for the Simpson's exponential index were sites 18 (17.58, thicket), 29 (16.39, grassland) and 1 (14.38, forest), and the bottom three were sites 23 (7.13, savanna), 11 (6.04, savanna) and 10 (5.29, savanna) (see Table B4, Appendix B). Site 18 had the highest index values (Shannon's exponential and Simpson's inverse) and also the highest species richness (alien and indigenous species combined). Site 23 had the lowest index values (Shannon's exponential and Simpson's inverse), indicative of the low evenness, but this was not accompanied by the lowest species richness, which occurred at site 9. Alpha diversity (both richness and evenness) is significantly negatively related with alien species richness (R^2 = -0.367; $P < 0.05$; Spearman rank), and significantly positively related with indigenous species richness (R^2 = 0.434; $P < 0.05$; Spearman rank).

Alien species had significantly higher FD values than indigenous taxa for most univariate measures ($P < 0.05$, ANOVA) (see Table B5, Appendix B), excluding reproductive mode, where values were comparable for all species (alien and indigenous). Additionally, alien species had significantly higher FD values for combined traits (multivariate FD) compared with indigenous species (see Table B5, Appendix B). There were no significant trends in terms of vegetation type for alien species, and disturbance levels for alien and indigenous species. However, it is worth noting that forest vegetation had the highest FD values for aliens at sites with high disturbance. The savanna biome had the lowest FD values for indigenous species at sites with low levels of disturbance (data not shown). Examination of combined traits for all species showed that sites with the highest FD values occurred predominantly in grassland vegetation and were not affected by disturbance levels.

While the three sites with the lowest multivariate FD values were not vegetation dependent, these sites displayed relatively low levels of disturbance.

3.3.4. Principle component analysis

3.3.4.1. Floristics, non-natural disturbance and land-use

Four variables (labelled components henceforth) accounted for 68% variance in the data (data not shown). Alien species richness increased as one moved away from formal and informal housing as well as informal settlements and decreased as disturbance levels increased. As indigenous species richness increased, there was an increase in the density of indigenous species as well. Alien plant density increased as disturbance level increased (data not shown).

3.3.4.2. Functional diversity, non-natural disturbance and land-use

Two variables (i.e. components) accounted for 61% variance in the data. Functional diversity (PC1) accounted for 33% variance in the data and increased with level of disturbance but decreased as one moved away from informal settlements (see Table B6 for R^2 values). Level of disturbance loaded most high for PC1. Level of disturbance (PC2) accounted for 61% variance in data and was positively related to distance to informal settlements and FD, and negatively related to distance to roads. Functional diversity loaded most high for PC2 (See Table B6, Appendix B).

3.3.4.3. Floristic ordering and FD

When a PCA was used to test for relationships among FD and floristic ordering, three variables (i.e. components) accounted for 61% variance in the data. Functional diversity (PC1) accounted for 34% variance in the data and was positively related to alien species richness and alien plant density (see Table B7 for and R^2 values). Alien species richness loaded most high for PC1 (FD). Alien species richness (PC2) accounted for 61% variance in data and was positively related to indigenous species richness and indigenous plant density, and total plant density. Indigenous species richness loaded most high for PC2 (Alien species richness). See Table B7, Appendix B.

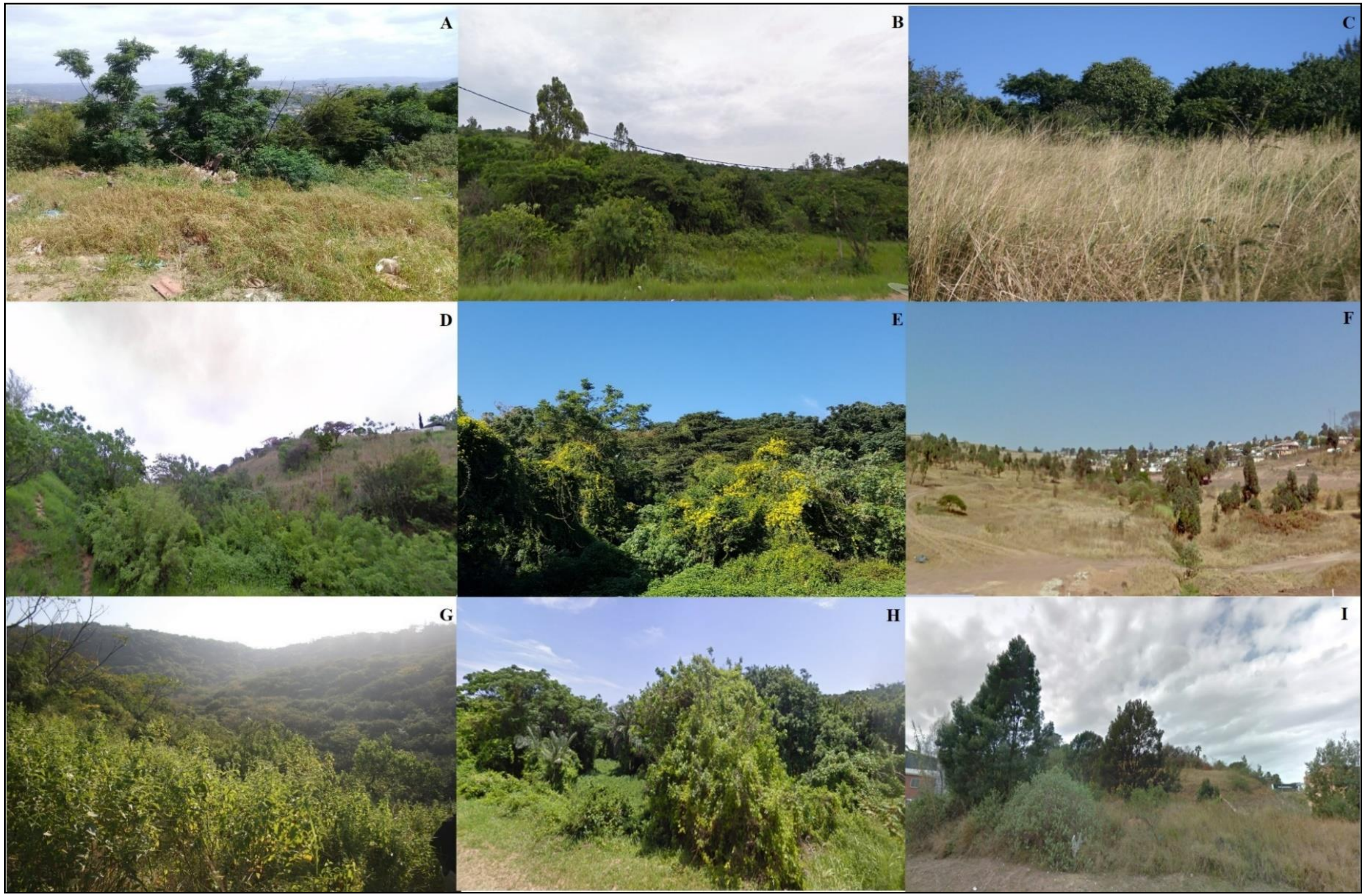

Figure 3.5: Selected sites and vegetation types (A – E) in the study area: A = site 9, thicket; B = site 18, thicket; C = site 10, savanna; D = site 11, savanna; E = site 16, savanna; F = site 23 savanna; G = site 1, forest; H = site 14, forest, I = site 29, grassland.

3.3.5. Species co-occurrence

3.3.5.1. Alien-alien interactions

A total of 20 significantly positive co-occurrences (i.e. species pairs) were observed for alien species (Table B8, Appendix B). The 20 co-occurrence relationships (the incidence of an alien species co-occurring with another alien species more than once) involved 28 individual alien species, of which 18 (64%) were IAPs. Observed co-occurrence at sites ranged from three to 19 sites, with only two pairs occurring at more than 50% of sites (predominantly forest and savanna vegetation). Three IAPs co-occurred more than once with another alien species: *Ageratum conyzoides* (n = 4) > *Tecoma stans* (n = 3) > *Ricinus communis* (n = 3). The most common species pair observed for alien species was at 19 sites for *Lantana camara* and *Solanum mauritianum*, with a positive co-occurrence ($P < 0.05$).

3.3.5.2. Alien-indigenous interactions

A total of 27 positive co-occurrences were observed between alien and indigenous species (Table B9, Appendix B). Of the 27 co-occurrence pairs, 14 interacting species were indigenous, and 23 were alien (and 11 [48%] were IAPs). Observed co-occurrence at sites ranged from three to 14 sites, with only three pairs occurring between 40 – 47% of sites (predominantly savanna vegetation). The indigenous species *Centella asiatica* co-occurred the most with other alien species (n = 3 species). The most commonly observed species pair was *Centella asiatica* (indigenous) and *Conyza sumatrensis* (non-invasive alien) (14 sites), with a positive co-occurrence ($P < 0.05$).

3.4. DISCUSSION

3.4.1. Alien and indigenous floristics

South Africa's rich floral biodiversity and serious challenges with IAPs from various parts of the world (van Wilgen et al., 2020a) is reflected by the findings of the current study: a survey of just 30 green spaces (total area of 0.075 hectares) in one city yielded 201 species of which 40% were alien (Table B2, Appendix B). The largest Eudicot family (> 25 000 species) (Hao et al., 2009a; Kenny et al., 2014) in the world, Asteraceae, was the most speciose family for both alien and indigenous species. The family is well represented globally, has numerous invasive taxa (Wu and Wang, 2005; Zhu et al., 2005), and its members exhibit a number of traits such as specialised dispersal mechanisms (viz. pappus, hooked fruit) and high reproductive rates (with high levels of apomixis) that promote dispersal and invasions (Heywood, 1989; Pyšek, 1998b). Similarly, the second most speciose family for both alien and indigenous species, Fabaceae, is a large Angiosperm family (> 19 000 species) that is widely distributed globally (Angiosperm Phylogeny Website [APW], 2018). These two families, together with the Poaceae, represent the three most dominant alien family's worldwide (Pyšek, 1998a; Pauchard and Alaback, 2004). The Poaceae family comprises of over 11 500 flowering species and is recorded as the fifth-largest flowering plant family (Hodkinson, 2018) but was not well represented in terms of both indigenous and alien flora in the area studied here, making up just 8.5% of the total species found. This corroborates a recent study which suggests that South Africa appears to be a major donor but an infrequent recipient of invasive grasses (Visser et al., 2016). On a broader scale, family level analyses are significant as regional dominance; in terms of families, can be used to gain global understanding of dominance at the family level. This becomes important when designing control measures (biological and chemical) which are sometimes more suited/effective against certain families.

Mean alien species richness and density across sites were significantly higher than indigenous species. Species richness of alien (non-invasive and invasive) and indigenous species have been correlated in many studies (Lonsdale, 1999; Stohlgren et al., 2003; Richardson et al., 2005); however, this was not the case in the current study. Alien species in the current study made up a total of 39% of species found and was similar to alien prevalence levels reported for cities in the northern hemisphere (e.g. 40.3% alien species found in 54 European cities [Pysek et al., 1998] and 20% of the total number of species recorded in Mexico City [Rapoport, 1991]) but these figures are dated. When considering South Africa, surveys of public urban green spaces within the Eastern Cape have shown aliens to make up a similarly high proportion of the total woody species complement (59.9%; of which 29% were invasive) (McConnachie et al., 2008). Other local more recent studies conducted within urban green spaces hosting natural vegetation in the study area have also reported the presence of a number of alien species: 14 aliens (of which three were invasive) in grassland (Drury et al., 2016); 61 aliens (of which 36 were invasive) in forest vegetation (Kambaj et al., 2018); and a total of nine IAPs listed as important in forest vegetation (Mavimbela et al., 2018).

As in other studies on alien plant prevalence (Ansong et al., 2019), the majority of alien species (69%) found originate from the Americas (Table B2, Appendix B), with a large proportion of them (44% of the 80 alien species) categorised as invasive in South Africa. Many of these IAPs were shrubs and trees, while the non-invasive species were mainly herbs (e.g. *Tagetes minuta, Rumex crispus* and *Bidens pilosa*) (Table B2, Appendix B). It should be noted though, that the proportional distribution of species across the four life form categories was comparable between alien and indigenous flora (herbs > shrubs > trees > climbers), with herbs being the most dominant life form (60% and 52% of species, respectively). A study conducted in the South Africa's Western Cape also found herbs to be the most dominant life form (35%) amongst the alien species found, particularly in transformed and disturbed habitats ([forest and fynbos], Baard and Kraaij, 2014). Herbs are known to be the dominant life form in alien plant studies as they are able to grow easily under a variety of environmental conditions, including in the presence of disturbance (Dogra et al., 2010; Mallik et al., 2019).

In the current study, grassland and forest vegetation generally displayed the highest combined (alien and indigenous) species richness levels, while high alien species richness was predominantly associated with forest and thicket vegetation. As mentioned earlier, recent studies on grasslands (Drury et al., 2016) and coastal forests (Kambaj et al., 2018) in the municipality have shown the presence of a number of alien and invasive species. Savanna is the most dominant vegetation type in Africa and South Africa, making up one-third (46%) of the country's vegetation (Huntley and Walker, 1982; Rutherford et al., 2006). There are indications that savanna vegetation may be particularly prone to alien invasion (Richardson et al., 2005; Rouget et al., 2015), and this appears to be the case in the present study (percentage of aliens only in each vegetation type: savanna = 94%, forest = 71%, grassland = 42%, thicket = 43%).

Apart from the above, the results did reveal one very interesting observation: grassland and forest sites exhibited the highest combined (alien and indigenous) species richness, but forests seemed to be more prone to alien species invasion than grasslands in this urban matrix. While the number of sites belonging to the different vegetation types were not comparable and limited in the present study, the interpretation of this observation may benefit from an appreciation of the diversity-invasibility hypothesis proposed by Elton (1958) c. 60 years ago. Elton hypothesised that more diverse communities should be less susceptible to invasion by exotic species. Species-rich communities may be less vulnerable to invasion as a consequence of a lower availability of vacant niches and more severe intensity of interspecific competition (Collins et al., 2007). The data obtained here suggests that the acceptance of this hypothesis may be complicated by both the vegetation type to which it is applied and/or the disturbance type and intensity acting on the system. Furthermore, the use of this hypothesis to explain patterns of diversity-invasibility requires one to consider species richness or indices involving species richness, evenness, genetic diversity (at population level), functional diversity (species distinction using trait attributes), and phylogenetic diversity (Fridley, 2011). Some of these characteristics were measured here, and this argument is expanded on in the next section by drawing on these data.

3.4.2. Alpha and functional diversity

The data obtained here indicate that sites with the lowest values for both alpha diversity indices had low richness and high evenness compared with sites that had high alpha diversity index values. It is usually assumed that evenness is an indicator of future species extinction in a community as it measures how similar species are in terms of abundance (Halloy and Barratt, 2007; Rohr et al., 2016). Additionally, it is presumed that if invasions persist, local populations of rare and low-density species will face extinction. Overall, results obtained in the study suggest that high alpha diversity (both richness and evenness) in urban green spaces is linked with low alien species richness and high indigenous species richness rather than disturbance levels. These results support Elton's biodiversity-invasion hypothesis, where high alpha diversity is associated with low invasion.

Differences in alien (higher) and indigenous species univariate functional diversity (except for reproductive mode) suggest that alien and indigenous species may be occupying different niches within ecosystems. The differences in FD may, in turn, have an influence on resource availability within these ecosystems and species richness and density (Nijs and Roy, 2000). Hejda and de Bello (2013) conducted a similar study within various vegetation types in the Czech Republic and showed invading aliens to be functionally dissimilar to indigenous species allowing alien species to occupy empty niches. Higher alien species richness in the present study suggested that FD varies in relation to species richness; the more species present, the wider the range of functional traits (Villeger et al., 2008; Hejda and de Bello, 2013). This suggestion is supported by the fact that FD was highly related to species richness and density (Table B7, Appendix B).

These results may explain why aliens in the present study are able to occupy different vegetation types at similarly high-density levels and are out-competing indigenous species at certain sites. Alien species exhibiting a greater number of functional traits than indigenous species allow them to opportunistically occupy a variety of habitats, even those in which biotic and abiotic factors may negatively influence their success and recruitment (Osunkoya et al., 2005). Alien species in this study had higher univariate scores for life form, life cycle and dispersal syndrome compared with indigenous species, which appears to be allowing them to establish in diverse (in terms of disturbance level and vegetation type) habitats in the study area. Based on Elton’s biodiversity-invasibility hypothesis, the low diversity of indigenous species afford for alien species to exploit niches (Collins et al., 2007). At present, aliens appear to exhibit relatively higher FD than indigenous species at forest sites investigated, which may explain why Bhugeloo (2020) found forest patches in the study area to house a large number of alien species. This is worrying since alien tree species, once established, can eventually transform forest habitats and develop monospecific tree stands with closed canopies (e.g. Osunkoya et al., 2005; Gairola et al., 2016; Adam et al., 2017). In addition, results of the present study suggest that alien species may be opportunistically exploiting diverse environments due to high FD of individual alien species. Future studies should include more focused investigations on the FD associated with traits that contribute to the competitiveness of alien species and the presence/expression of characters that allow plants to thrive in disturbed environments (Biwas and Mallik, 2010).

The fact that the alien plant community investigated here exhibited a low reproductive mode FD score compared with other alien traits could have been explained by the fact that the characteristics that aid in the success of aliens, particularly IAPs, are largely related to reproduction (e.g. high seed set, fast growth and shorter time to reach reproductive maturity) as reported by other studies (Ordonez et al., 2010). However, a limitation is that the current study only considered asexual and sexual reproduction, with almost all species reproducing sexually. Future studies should look in greater detail into traits related to reproductive mode and phenology (i.e. flowering time and reproduction period) as these have the potential to be very informative (e.g. Xavier et al., 2019; Pérez-Ramos et al., 2019) in understanding plant invasiveness. It is important to mention that even though alien species may not exhibit high reproductive mode FD compared with indigenous species, they may be reproductively functionally different to indigenous species allowing them to occupy niches that may not be suitable for indigenous species (Hejda and de Bello, 2013) in disturbed scenarios. For example, they may be employing reproductive mechanisms such as coppicing (e.g. of *Melia azedarach* [Khan et al., 2001; Tiwari et al., 2020]) that promote their persistence and spread in habitats with high levels of disturbance.

It is worth noting that site 5 (grassland), which had the highest FD values in terms of most of the categorical traits (dispersal syndrome, reproductive mode and life cycle), had a higher indigenous than alien species richness and density, a high species evenness and was ranked the second-highest site in terms of combined species richness. This site is in close proximity to a reforested landfill at which restoration programmes have introduced indigenous species, and the presence of alien species is controlled (Mugwedi et al., 2017). Site 27 had the lowest FD values for dispersal, life cycle and life form and had more alien species than indigenous species in terms of richness and density. A potential reason for this could be due to frequent unplanned fires at this site (author's unpublished observations) which promotes alien species (van Wilgen, 2009).

Interestingly, the PCA results found FD to increase with increased levels of disturbance and tends to argue against the Intermediate Disturbance Hypothesis (IDH), where communities with intermediate disturbance levels are known to have high species and functional trait representation (Biwas and Mallik, 2010; Biwas and Mallik, 2011). Some studies have found species functional traits to be resistant and resilient to disturbance (Roovers et al. 2004; Bernhardt-Römermann et al., 2011). Life form, for example, is seen as a good functional trait predictor of vegetation change due to disturbance, and plants with similar traits are known to respond in similar ways to short term environmental change (Bernhardt-Römermann et al., 2011). Irrespective of species (alien or indigenous), the herb life form dominated the study area. This suggests that herbaceous species (including invasive alien species) would be better suited to environments prone to anthropogenic disturbance, such as those associated with the presence of informal settlements (FD decreased as distance from informal settlements increased).

3.4.3. Effects of anthropogenic factors on floristic patterns

Although the 30 green spaces surveyed (see Fig. 3.1, and Table B1, Appendix B) here are heterogeneous in terms of a number of characteristics (e.g. size, location, vegetation type and level of disturbance), there were no significant differences in terms of levels of disturbance when the sites were compared on a sector level (data for all sites within a sector were averaged and pooled for analysis). However, some inter-site differences in disturbance levels were noted.

Levels of disturbance were negatively related to species richness, but positively related to alien plant density. Alien invasion is driven by disturbance (Potgieter et al., 2020) and is typically associated with large (often monospecific) stands of a few species (Nuñez et al., 2018). A logical explanation for the relationships observed between disturbance and species richness and alien plant density observed here is that increases in disturbance led to the dominance (in terms of density) of a few alien plants, which reduced species richness.

3.4.4. Species co-occurrences

A major focus of the current study was the phenomenon of alien-indigenous and alien-alien co-occurrence, which has been reported in a number of studies (Procheş et al., 2008; Procheş et al., 2015) but very seldom investigated in detail as attempted here. The 20 alien-alien co-occurrences observed here involved a large group of species that were not closely related: 28 species (from 28 genera) were found to occur. This included representatives of all life form categories. Only four pairs of species were from the same family (viz. Asteraceae). A large proportion of the co-occurring alien species were IAPs (64%) which co-occurred (in some cases multiple times) with other IAPs (n = 10 pairs) and non-invasive alien species (n = 10 pairs).

A closer look at the data reveals that two species frequently co-occurred (19 sites). The first of these pairs are *L. camara* and *S. mauritianum* (Category 1b invasives, NEMBA, 2020), which originate from South America (Pedrosa-Macedo et al., 2003; Goulson and Derwent, 2004), and are regarded as prominent IAPs in SA (Henderson, 1989; 2007). The seeds of both these species are dispersed by birds (Henderson and Musil, 1984), facilitating dispersal over vast areas and into remote places. The invasive potential of both *L. camara* and *S. mauritianum* is due to their ability to withstand harsh environments and exploit new habitats, and have high seed sets as a result of high pollinator visitation and superior competitive ability for resources (Takakura et al., 2009). These characteristics may collectively explain the high levels of co-occurrence recorded for these two species. Both species have a prominent presence in the savanna biome, as well as forest and grassland biomes (Henderson, 1989; Henderson, 2007; van Wilgen et al., 2012; Vardien et al., 2012; Rejmanek et al., 2016), and this may explain why both species were prominent at savanna (37%), forest (37%), and grassland (20%) sites in this study. The second most common species pair are non-invasive aliens; *Conyza sumatrensis* and *Tagetes minuta*. Both species are from the Asteraceae and also originate from South America (Table B2, Appendix B). *Conyza sumatrensis* has been discussed in further detail below (alien-indigenous section). *Tagetes minuta* is a common weed species found in cropping fields with small non-dormant seeds which form part of transient seed banks (Martinez-Ghersa et al., 2000). Dead *T. minuta* plants with viable undispersed seeds can persist above-ground, even though they don't persist below-ground, which could aid in its high co-occurrence and their ability to disperse via hooking onto animals (Martinez-Ghersa et al., 2000). In Northern Tanzania (Ngondya et al., 2019) and southern Africa (SANBI, 2020a), *T. minuta* is regarded as an invasive alien species; however, within the EMA, it is not yet regarded as invasive. In the current study, both species occupied savanna (37%), forest (21%), grassland (26%), and thicket (16%) vegetation.

The study indicated that the high levels of alien-alien co-occurrence observed (43%) also partly lends support to the Invasional Meltdown Hypothesis (IMH): IAPs are able to alter ecosystem processes, thereby facilitating invasion by other IAPs (Simberloff and Von Holle, 1999; Holzmueller and Jose, 2009). Characteristics that aid in the invasiveness of these species include their abilities to spread across widely and rapidly (e.g. *Lantana camara*) grow and reach reproductive maturity fast, thrive in disturbed areas, produce high seed sets that are viable and long-lasting (e.g. *Solanum mauritianum*), alter fire regimes (e.g. *Melia azedarach*) which may impact on fire-intolerant indigenous species and out-compete indigenous species for resources such as nutrients and space (Holzmueller and Jose, 2009).

There were also a number (27) of positive co-occurrences between alien and indigenous species (see Table B9, Appendix B), but three indigenous-alien pairs are worth mentioning given their high frequency of occurrence: *Centella asiatica* and the alien *Conyza sumatrensis* co-occurred at the highest frequency (n = 14), closely followed by *C. asiatica* and the invasive alien *S. mauritianum* (n = 13), and *Commelina erecta* and the alien *B. pilosa* (n = 12). *Conyza sumatrensis* and *C. asiatica* are both herbs (Table B2, Appendix B) that occupy savanna, forest and grassland vegetation. *Conyza sumatrensis* (Asteraceae) is an annual herb that is short-lived and is wind-dispersed, while *C. asiatica* (Apiaceae) is a perennial herb that is often accidentally dispersed via garden waste disposal/garden escapees or intentionally dispersed when introduced for medicinal purposes (Centre for Agriculture and Bioscience International [CABI], 2019). Similarly, *B. pilosa* and *C. erecta* are also both herbs, with *B. pilosa* having effective pollination mechanisms and distinctive dispersal abilities (Rocha, 1996). Unlike the previous pairs, *C. asiatica* and *S. mauritianum* do not have the same life form. *Solanum mauritianum* is a shrub that has extensive fruiting and is distributed by frugivorous birds, which intensifies its invasive potential (Witkowski and Garner, 2008). It is interesting to note that *C. sumatrensis* and *S. mauritianum* co-occurred and ranked highest for alien-alien and alien-indigenous interactions.

Similar observations have been made for *Impatiens noli-tangere* L., a native species in the Czech Republic, and the invasive *Impatiens parviflora* (Čuda et al., 2015). Daehler (2003) also highlights 79 indigenous-invasive species pairs and explains these co-occurrences are due to growing conditions (e.g. resource availability [nutrients, light, and water]) allowing indigenous species to occur equally with invasive species. Data shown in Table B10 (Appendix B) suggest that alien and indigenous species are more likely to co-occur if they have similar functional traits (viz. life form and reproductive mode), but more detailed studies are needed to understand whether this relates to resource requirements and facilitatory interactions. The positive interactions between different alien species contribute in part to the growing amount of evidence in the literature that supports the IMH: positive interactions among invaders initiate positive population-level feedback that promotes secondary invasions and leads to more impacts (Green et al., 2011). Interestingly, there are also a few reports that describe facilitatory interactions between indigenous and alien species (Rodriguez et al., 2006; Cavieres et al., 2008; He et al., 2013), which was also a finding of the present study. Apart from broadening our understanding of theories such as the IMH in the context of urban ecosystems, the findings related to co-occurrence also have practical implications in that they can help design alien control programmes that focus on alien species that facilitate each other and identify indigenous-alien interactions that require management interventions.

3.5. CONCLUSION

Functional diversity data collected within the subtropical urban matrix investigated here supported the literature in that alien plant species were functionally more diverse than indigenous species. Additionally, combined FD was significantly positively related to alien species richness and density, and the relationship between alpha diversity and species richness differed for alien and indigenous species. Alien plant species co-existed with alien and indigenous species at all the sites, and the nature of this co-existence could be due to facilitatory and/or increased susceptibility to invasion based on habitat- or species-specific characteristics.

Importantly the results showed that combined (multivariate) FD was strongly related to levels of disturbance. Future studies should examine the diversity of traits associated with plant invasiveness in greater detail, but the results presented here suggest that anthropogenic induced changes in FD within habitats could influence their susceptibility to alien invasion. In terms of co-occurrence, the presence of some indigenous species (viz. *C. asiatica*) may be facilitating the presence of IAPs – as indicated by high alien-indigenous species pairing frequencies. These observations are significant as they provide support for further research into how alien control programmes can reduce the potential for alien-indigenous facilitatory interactions. Future studies should examine competitive and facilitatory interactions between alien and indigenous species within urban green spaces, given that classical theories around the relationship between diversity and invasibility may not hold for these disturbed/transformed ecosystems. In this context, FD proved to be valuable in terms of understanding alien and indigenous functional interactions in urban green spaces open to anthropogenic disturbances. Furthermore, integrating indicators of alpha and functional diversity and species co-occurrence into the design of remedial and preventative alien plant management strategies for urban areas also proved to be valuable.

CHAPTER 4
The effects of non-natural disturbance on alien and indigenous seed bank floristics within an urban matrix

ABSTRACT

Seed banks (SBs) are essential in ecological processes, and the ability of vegetation to recover following disturbance events lies in seeds buried beneath the soil. Seed bank species richness and abundance within green spaces in urban matrices are generally poorly understood, particularly in rapidly developing countries such as South Africa, where natural vegetation is subject to anthropogenic disturbance and biological invasions. This study investigated the effects of non-natural disturbance on alien and indigenous SB floristics within an urban matrix (the eThekwini Municipal Area [EMA]) in South Africa. Seed banks were sampled at 30 natural green spaces across the EMA, and differences in seeding times across species was accommodated for by spreading sampling over the two main flowering periods in a year. These data were used to describe the SBs in terms of species ordering (richness, density, and diversity) and similarity to standing vegetation (SV). Seed bank characteristics were then related to levels of non-natural disturbance (at each site). Across all sites, the SBs showed no significant differences between alien and indigenous species richness and density. When data for all sites were pooled, Asteraceae and Cyperaceae were the most speciose alien and indigenous families, respectively, with herbs being the most dominant life form represented. *Conyza sumatrensis*, *Verbena brasiliensis,* and *Chamaecrista mimosoides* had the highest SB densities. High alpha diversity (Shannon and Simpsons index) across SBs were related to high species richness, low disturbance, and a high number of herbaceous species. However, there were no significant trends between disturbance level and species evenness. Sørenson and Jaccard similarity indices found high similarity for sites with lower disturbance levels and low similarity for sites with higher disturbance levels. Cluster and ordination analyses based on the entire SB flora found unexpected random disturbance level groupings suggesting floristic similarity is not related to disturbance regime. The PCA results suggest a link between disturbance and SB floristics: significant positive relationships between disturbance level and combined species richness and density. This could be due to disturbance events allowing for the breaking of seed dormancy in certain species. This study highlights the relationship between urban SBs with disturbance level and the role of SBs in alien invasions. The findings of this study have implications for managers of urban green spaces since alien species in SBs could exploit niches created by disturbances, promoting urban invasions. Furthermore, the results highlight the importance of considering the regeneration potential of a site afforded by the SB when urban green spaces are denuded of vegetation as a consequence of alien clearing programmes.

4.1. INTRODUCTION

Soil seed banks (SBs), or the collection of mature and viable seeds either on the soil surface, between leaf litter or buried within the soil (Swaine, 2001; Savadogo et al., 2017), are a major component of plant community dynamics (Gioria et al., 2019), and can act as reservoirs of plant propagules and genetic diversity for many species (Chesson, 1994; Clemente et al., 2007). The above-ground component captures plant diversity only partly (Margalef, 2000), and together it is only when this is considered together with the SB that one can get an estimate of the total biodiversity of a habitat, including recent past conditions (Vilà and Gimeno, 2007).

Importantly, SBs are necessary for determining floristic richness (Pakeman et al., 2005) following disturbance events (rain, grazing, anthropogenic activity, etc.) and play a role as 'primers' in secondary regrowth of plants at degraded sites depending on the severity of the disturbances (Savadogo et al., 2017). Vegetation richness and the rate at which richness develops at degraded sites are, therefore, influenced by the density and diversity of seed banks (Thompson et al., 2003). This density and diversity are variable in time and space depending on the vegetation type, land-use/land cover system and climate (Shiferaw et al., 2018a). Physical and physiological characteristics of seeds also influence their persistence in seed banks; for example, small seeds move through the soil more easily and to greater depths where they persist longer compared with larger seeds that lack hard seed coats (Shiferaw et al., 2018a). The relationship(s) between seed banks, above-ground vegetation, and disturbance are vital in understanding community dynamics and implementing essential vegetation restoration plans (Snyman, 2004; Solomon et al., 2006). Varying levels of disturbance may be used as an indicator of changes in seed persistence (Thompson et al. 1997; Kassahun et al., 2009), with both factors being directly proportional to one another (Fenner and Thompson 2005; Gioria and Osborne 2010).

The post-disturbance recovery of indigenous species at any site is based on the richness and persistence of SBs (Fourie, 2008). However, SBs facilitate the persistence of all sexually reproducing plant species (Baker, 1989), including the successful establishment of alien species in their new ranges and their persistence during unfavourable conditions (Gioria et al., 2012, 2019). Alien plant species generally produce large numbers of viable seeds, most of which are often incorporated into SBs (Gioria and Osborne 2009). Disturbance (natural/non-natural) and changes in disturbance regimes such as fires are known drivers of invasive alien plants (IAPs) (Keeley and Brennan, 2012). Anthropogenic activities are precursors of change to species richness and diversity in urban plant communities (Smart et al., 2005; Zhao et al., 2010; Potgieter et al., 2020). These communities are generally characterised by the following: high species richness (Gilbert, 1989; Schmidt et al., 2014), replacement of indigenous species with alien species (Godefroid, 2001; Wania et al., 2006; Millard, 2008), increased habitat unevenness, low stability, and increased landscape alteration toward the urban centre (McKinney, 2002). Human population increases lead to increased disturbance levels (via anthropogenic activity) and have been reported to lower density and diversity of species in most vegetation types (Shiferaw et al., 2018b).

The role that SBs play in vegetation responses to anthropogenic disturbance in urban matrices is poorly researched, but it is clear that IAPs change the richness and diversity of above- and below-ground flora by decreasing and displacing indigenous species abundance and diversity (Gioria and Osborne, 2010, 2014; Gioria et al., 2014). Alien removal programmes generally assume that there will be a natural recovery of indigenous plant species in an invaded area, but this is not always the outcome as clearing of invaded areas often leads to further decline in indigenous plant biodiversity due to secondary invasions (Fourie, 2008; Nsikani et al., 2020).

The present study investigated the effects of disturbance on alien and indigenous seed bank floristics within an urban matrix, namely the eThekwini Municipality (EMA) in South Africa (SA). The EMA sits within a biodiversity hotspot (Maputaland-Pondoland Albany [MPA]) and houses thousands of natural green spaces with varying levels of non-natural disturbance and IAP prevalence (see Chapter 2 for details). Using a subsample of these green spaces, this study addressed the following research questions: (1) What is the floristic richness and density (alien and indigenous) of seed banks? (2) What is the ratio of alien plant species to indigenous plant species? (3) What are the similarities in floristic patterns between SB and SV? and (4) Does the level of non-natural disturbance influence SB vegetation? The findings will add to the growing body of literature that shows soil seed bank species profiles are important in designing conservation recommendations within disturbed urban vegetation types (Senbeta and Teketay, 2002; Sershen et al., 2019), including the prioritisation of species and sites for management intervention such as alien control and/or indigenous species reintroduction/enrichment.

4.2. METHODS

4.2.1. Study sites

Green spaces across the EMA cover approximately 33% of terrestrial land. Within the Durban Municipal Open Space System (D'MOSS) patches, 30 sites that vary in size (>10 000 m^2), disturbance level and vegetation types (forest, grassland, savanna, thicket) were selected for investigation (see Figure 3.1, Chapter 3). These sites were not enclosed by fences or gates and were unmanaged in terms of maintenance and solid-waste dumping/clearing. The openness and accessibility (by road) of each site meant that anthropogenic activities (such as footpaths, dumping, resource abstraction, and unplanned burning) occurred at varying levels.

4.2.2. Standing vegetation (SV) sampling

Methods describing vegetation sampling and the categorisation of the flora are provided in Sections 2.2.2 and 2.2.3 of Chapter 2.

4.2.3. Soil seed bank (SB) sampling

Soil SB samples were collected on the day that SV was surveyed at a particular site and in all four seasons between March 2016 – March 2018 (autumn and winter [March – August], spring and summer [September – February] to accommodate for species that seed and/or germinate at different times of the year. Leaf debris on the soil surface was removed before excavation. At the four corners of each quadrat at a site, the top 3 cm of soil was extracted from four subplots (per plot, per site) in a 15 × 15 cm area and were placed in labelled plastic bags that were taken back to the laboratory. At the laboratory, stones, leaves, roots, and branches were discarded before the sieving of soil using a 10 mm sieve. As per Lévesque et al. (1996), pots (12 × 7 cm) were prepared using 100 g of potting soil, 200 g of sieved sample soil, and topped with a fine layer (1 – 2 mm) of river sand to prevent excessive light exposure (Sershen et al., 2019). For each sample, four 200 g subsamples were placed in two separate pots as described below. In total, 960 pots were prepared (n = 480 pots per sampling season). Additionally, ten control pots containing 200 g of potting soil and a fine layer of river sand were prepared and followed the same watering regime. Each pot contained four holes at the base for drainage, and watering occurred three times a week. Soil SBs were maintained in a shaded greenhouse to track seed germination and flowering of germinants (for identification).

As per Jensch (2004) and Sershen et al. (2019), a shaded greenhouse (covered with 60% monofilament black shade cloth) was chosen to prevent the risk of germination inhibition by high irradiation. Germinants were recorded weekly for one year (365 days), and some were removed if there was overcrowding, death, or had flowered within the pot. Germinants were identified following methods described for the standing vegetation (see above). Species were also classified into life form (graminoid, climber, herb, shrub, and tree) categories (SANBI, 2020a). In the present study, SB species (in terms of density) and family representation (in terms of richness) were ranked to identify the top-ranked (dominant) species and families across all sites (Jones et al., 2017).

Seed bank densities for each species were expressed as germinants/m^2. This was based on an extrapolation method commonly used in seed bank studies (Lévesque et al., 1996), where if the volume of soil in each pot (sub-sample) and volume of soil extracted *in situ* (sample) is kept constant across replicates, then the number of germinants in each sub-sample (pot) is converted to the predicted number of germinants that would have been present in the sample collected. Since the area of the sample collected *in situ* is known, the density of germinants can then be expressed per m^2 to allow for comparison with other published seed bank studies in which germinant/seed density is most often expressed on a per m^2 basis (Lévesque et al., 1996; Sershen et al., 2019).

4.2.4. Level of disturbance

Levels of disturbance were quantified for each site using a scoring matrix developed as part of a previous study involving these sites (see Section 2.2.4, Chapter 2). Sites were grouped (very low, low, medium, high, and very high) based on Disturbance Level Values (DLVs) generated during *in situ* assessments.

4.2.5. Data analysis

Prior to all analyses, data for the two main flowering seasons (autumn-winter and spring-summer) were pooled. Seed bank density was tested for normality, and data were compared across sites and levels of disturbance using SPSS (SPSS Inc., Chicago, IL). Data comparisons were made using an independent *t*-test (or, if not normally distributed counterpart Mann-Whitney *U* test). A Principle Component Analysis (PCA) was conducted (SPSS) to test for significant relationships between level of disturbance and soil SB floristic parameters (plant species richness and density).

Alpha diversity was calculated for SBs using EstimateS 9.0 (Colwell, 2013). Shannon's (*H*), Shannon's exponential (*H'*) and Simpson's inverse (*1/D*) indices were calculated to compare diversity across all 30 sampling sites based on quadrat data (n = 240 quadrats). The Shannon's (*H*) and Shannon's exponential (*H*') indices assessed SB species richness on a community level (across sites), whilst species evenness was assessed using Simpson's inverse index (*1/D*). Similarities in species richness between SBs and SV were assessed using the Jaccard and Sørenson indices computed in EstimateS 9.0 (Colwell, 2013). Cluster and ordination analyses across study sites of varying levels of disturbance; and sites grouped within the five disturbance levels were conducted to assess similarity in species composition. A similarity matrix using the Bray-Curtis index was generated based on presence-absence data of species in the seed bank of each site. Clustering was performed using the unweighted pair group method with arithmetic mean (UPGMA) in PAST (version 3.25, Paleontological Statistics, 2019 [Hammer et al., 2001]). Dissimilarities for plant density (germinants/m^2) were assessed using the Bray-Curtis index via a non-metric multidimensional scaling (NMDS) ordination across all sites (PAST version 3.25). The ordination was evaluated using the 'stress' coefficients (a measure of disagreement between values in the ordination space). Stress coefficients lower than 0.20 were considered as well-represented interpretations (Clarke, 1993).

4.3. RESULTS

Cumulatively, the SBs across the 30 sites yielded germinants belonging to 70 species and 20 families (Table C1, Appendix C). The top three ranking speciose families were Asteraceae > Fabaceae > Cyperaceae and Poaceae, hosting 65% of the total number of species recorded. Of the 70 species, 28 (40%) were alien, and 42 (60%) were indigenous. The top three ranking speciose families in terms of aliens were Asteraceae > Fabaceae > Verbenaceae, while Cyperaceae > Poaceae > Asteraceae and Fabaceae were the most speciose for indigenous species. Family richness (i.e. total number of families) differed significantly across sites with a wide range: 1 – 18 when all species were combined, 1 – 12 for alien species, and from 1 – 9 for indigenous species. When data for all sites were pooled for analysis, the life form distribution for SB species ranked as follows: herbs > graminoids > shrubs > trees (Fig. 4.1). Alien taxa had a higher proportion of herbs followed by shrubs and trees with no graminoids, compared with indigenous taxa, which had a higher proportion of graminoids followed by herbs, shrubs, and trees.

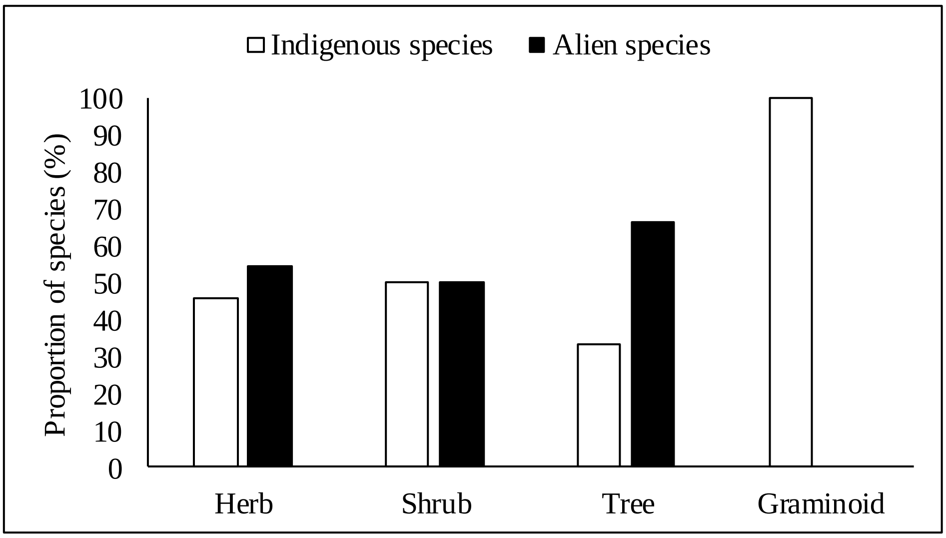

Figure 4.1: Life form distribution of indigenous and alien plant species within seed banks. Values represent the proportion (%) of species with data for all 30 sites combined (n = 960 pots).

4.3.1. Species richness in the seed bank

Sixty-nine of the 70 seed bank species found were present in the standing vegetation, with *Cyperus crassipes* Vahl. being absent in the SV. Total species richness for seed banks ranged widely, from 3 – 18 species, across sites. Similarly, indigenous species richness ranged from 3 – 12 species across sites, while alien species richness ranged from 1 – 10 species (Table C2, Appendix C). Alien and indigenous species richness were statistically different ($P < 0.05$, Mann-Whitney *U* test). The top three indigenous species with the highest densities across sites were *Cyperus esculentus* L. (n = 17 sites), *Phyllanthus polygonoides* Nutt. ex Spreng. (n = 16 sites) and *Pycreus polystachyos* (Rottb.) P.Beauv. (n = 12 sites). The top three alien species with the highest densities across sites were *Conyza sumatrensis* (Retz.) E. Walker (n = 21 sites), *Oxalis corniculata* L. (n = 18 sites) and *Galinsoga parviflora* Cav. (n = 17 sites). When SB data for alien and indigenous species were combined, the most speciose sites were found in forest vegetation, while the most species-poor sites were found in savanna vegetation. The most speciose sites for indigenous and alien species were forest and thicket vegetation, respectively, and the most species-poor sites were found in savanna vegetation (Fig. 4.2).

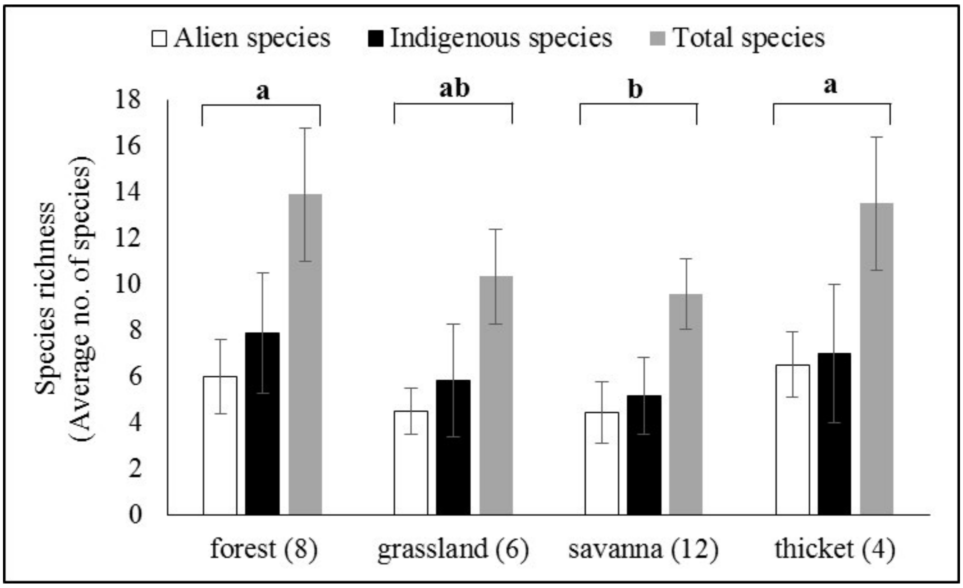

Figure 4.2: Species richness (alien, indigenous, total) across vegetation types at study sites. Values represent mean ± SD, and values in brackets represent the number of sites belonging to each vegetation type on the x-axis. Lettering indicates significant differences ($P < 0.05$, one-way ANOVA) across vegetation types when all species were compared.

Indigenous and alien seed bank richness did not differ between any of the disturbance levels (Fig. 4.3A). Total species richness (indigenous and alien combined) also did not differ across disturbance levels.

4.3.2. Plant density in the seed bank

Total (all species combined) plant density ranged from 49.39 germinants/m^2 to 301.21 germinants/m^2, with a mean density of 140.65 germinants/m^2, across sites. The top three species in terms of total density (i.e. data for all sites summed) were *Conyza sumatrensis* (alien), *Verbena brasiliensis* Vell. (alien) and *Chamaecrista mimosoides* (L.) Greene (indigenous). The bottom three ranking species in terms of density were all indigenous: *Tragus berteronianus* Schult., *Cyperus cyperoides* (L.) Kuntze, and *Digitaria longifolia* (Retz.) Pers. (Table C1, Appendix C). Indigenous plant density ranged from 6.66 to 160.85 germinants/m^2 across sites, with a mean density of 58.66 germinants/m^2. The top three indigenous species in terms of total density (i.e. data for all sites summed) were *Chamaecrista mimosoides*, *Helichrysum splendidum* (Thunb.) Less., and *Centella asiatica* (L.) Urb. The bottom-ranked three species were *Tragus berteronianus* Schult., *Cyperus cyperoides*, and *Digitaria longifolia*. Alien plant density ranged widely across sites, from

12.13 to 180.99 germinants/m^2, with a mean density (80.78 germinants/m^2), and there was no significant difference with indigenous plant density (59.87 germinants/m^2) (Table C2, Appendix C). The top three alien species in terms of total density were *C. sumatrensis*, *V. brasiliensis,* and *Mimosa pudica* L. The bottom three species were *Amaranthus dubius* Mart, ex Thell, *Malvastrum coromandelianum* (L.) Garcke, and *Bidens pilosa* L. When data for alien and indigenous species were combined, the most dense seed bank sites were found in forest vegetation with an average of 176.76 germinants/m^2, while the least dense seed bank sites were found in savanna vegetation with a mean average of 122.80 germinants/m^2.

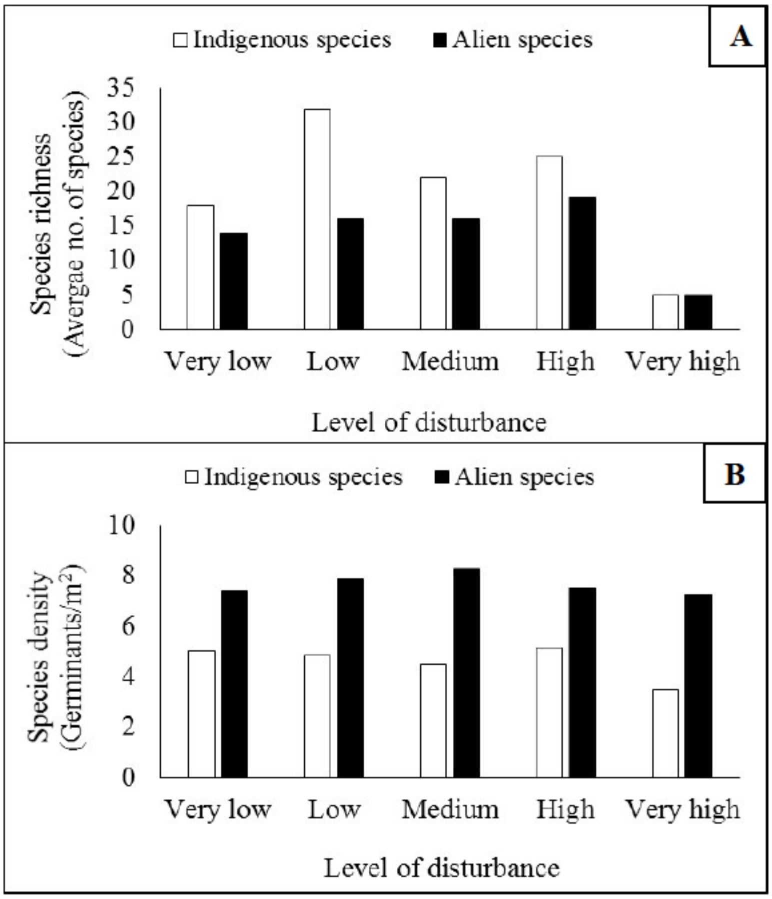

Figure 4.3 A: Species richness (indigenous and alien) and **B:** plant density (indigenous and alien germinants/m^2) across five levels of disturbance. Values for plant density represent means, and standard deviations ranged from 2.80 – 9.29. Values in brackets indicate the number of sites for each disturbance level.

Indigenous and alien plant density did not differ significantly across disturbance levels (Fig. 4.3B). There were also no significant differences across disturbance levels in terms of total plant density (indigenous and alien species combined) at individual levels of disturbance. However, Figure 4.3 seems to reflect a pattern associated with the Intermediate Disturbance Hypothesis (IDH).

4.3.3. Seed bank diversity and evenness, and standing vegetation similarity

Total species richness was highest for site 4 (forest), site 3 (thicket) and site 2 (forest), and all these sites had high *H* and *H*' indices and fairly high levels of evenness (*1/D*) (Table C3, Appendix C). There was no consistent relationship between species richness and evenness and disturbance level (site 4 = low, site 3 = medium, site 2 = high). Total species richness was lowest for sites 17 (savanna), 5 (grassland) and 16 (savanna), and all sites had low *H* and *H'* indices, with a fairly low level of evenness (*1/D*) (Table C3, Appendix C). There were no trends between species richness and evenness and disturbance level at these low ranked sites (site 17 = very low, site 5 = low, site 16 = medium).

At each site, the total SB flora were compared with the SV using the Sørenson and Jaccard similarity indices (Table C4, Appendix C). Site 4 had the highest similarity (Sørenson similarity index = 0.421, Jaccard similarity index = 0.266), followed by sites 12 (Sørenson similarity index = 0.368, Jaccard similarity index = 0.225) and 13 (Sørenson similarity index = 0.352, Jaccard similarity index = 0.214). Levels of disturbance were low for site 4 and high for sites 12 and 13. The sites with the lowest similarity between SBs and SV were sites 9 (Sørenson similarity index = 0.074, Jaccard similarity index = 0.038), 5 (Sørenson similarity index = 0.125, Jaccard similarity index = 0.066) and 25 (Sørenson similarity index = 0.139, Jaccard similarity index = 0.075). Disturbance levels for these sites ranged from low, high, to very high, respectively. In general, there were no significant trends between disturbance level and similarity (Figure 4.4). Low similarity sites were generally forest, grassland, and savanna vegetation, while high similarity sites were found in thicket and savanna (Figure 4.4). However, there were no significant trends in terms of level of disturbance and vegetation types. It is worth noting that there was also a high presence of herbs at high similarity sites and a high presence of graminoids at low similarity sites.

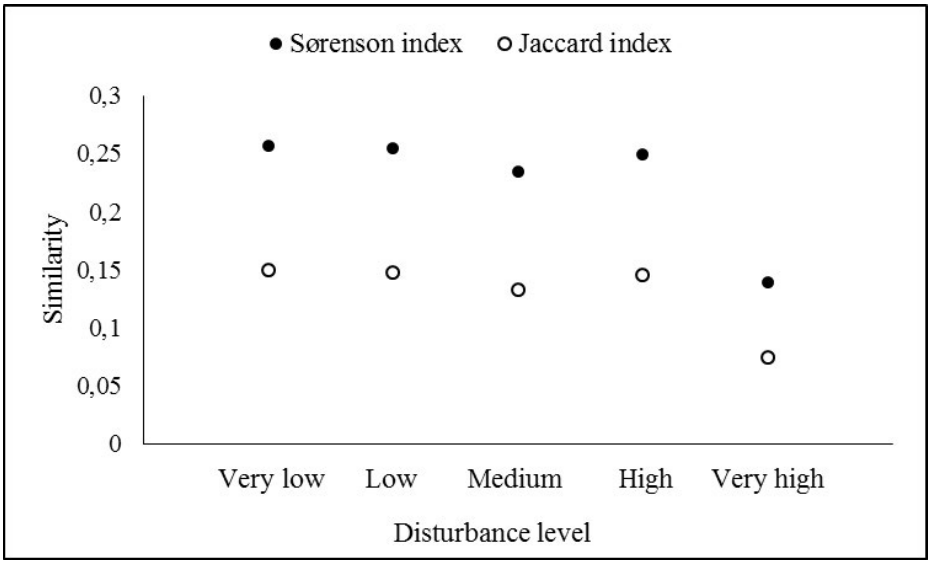

Figure 4.4: Similarity between standing vegetation and seed banks across sites with varying levels of disturbance. Values represent means for Sørenson and Jaccard indices, and standard deviations ranged from 0 – 0.10 (Sørenson index), and from 0 – 0.07 (Jaccard index). Vegetation types ranged as follows: Very low = forest / savanna / thicket; low = forest / grassland / savanna; medium = thicket / savanna; high = forest / grassland / savanna; very high = savanna.

4.3.4. Floristic similarity of seed banks

Sites were assessed for seed bank floristic similarity via a UPGMA cluster analysis. Initially, all 30 sites were analysed, but this did not show any meaningful pattern as clustering was not based on disturbance level (results not shown). The site-level data was then conglomerated into the five disturbance levels. This analysis was based on presence/absence data of the total number (n = 70) of species found (including graminoids) across the five disturbance levels. The phenogram (Fig. 4.5A) at a similarity of 0.450 has a singleton (very high disturbance sites) and a cluster of the remaining four disturbance levels.

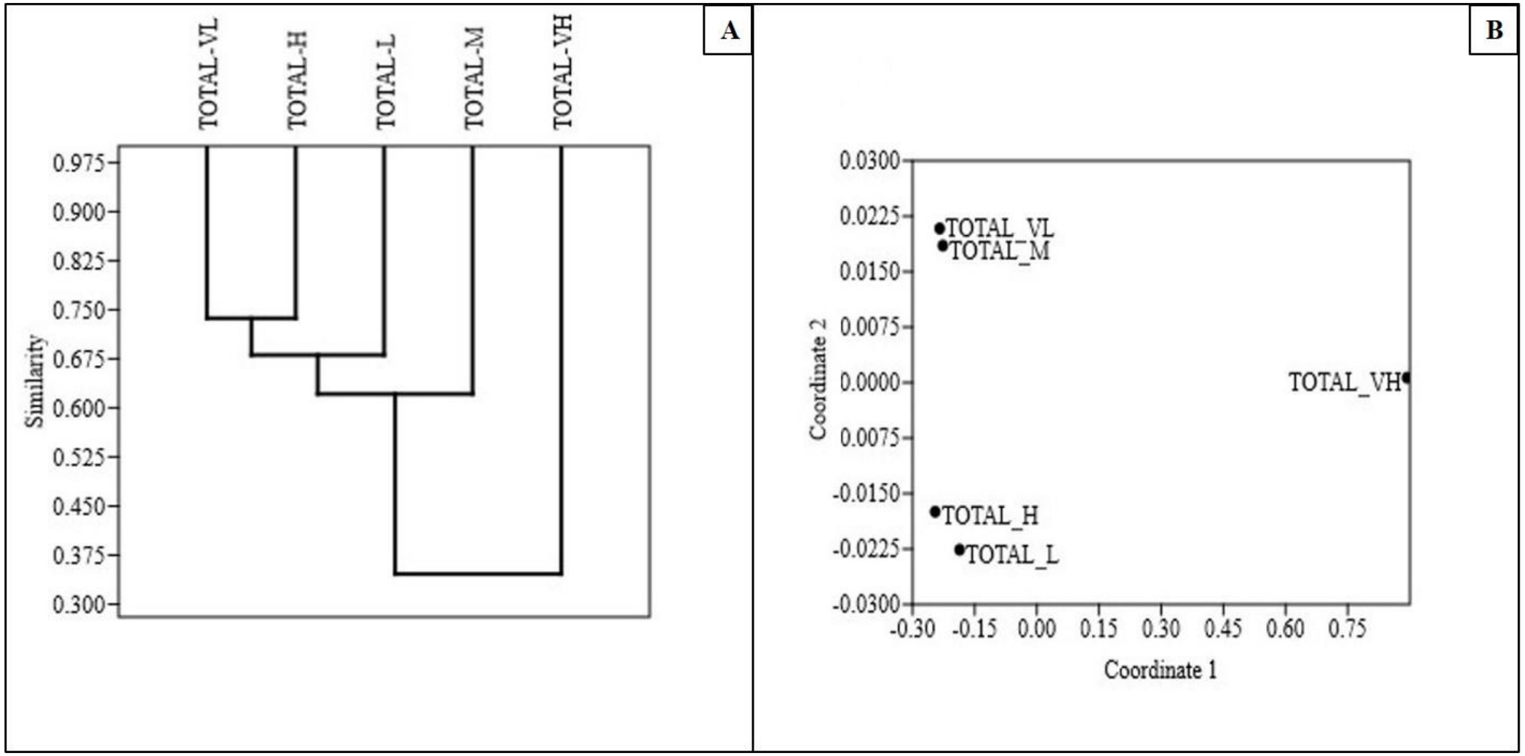

Figure 4.5 A: Unweighted pair group method with arithmetic mean (UPGMA) phenogram (using the Bray-Curtis index) for the total soil seed banks flora across the five levels of disturbance, **B:** Non-parametric multidimensional scaling (NMDS) plot (using the Bray-Curtis index) for total soil seed bank flora across various the five levels of disturbance. Stress value = 0.1612. Both analyses based on eight quadrats at 30 sites = 240 quadrats. Abbreviations for five disturbance levels: VL = very low, L = low, M = medium, H = high, VH = very high.

Within this cluster, medium disturbance level branches out followed by low disturbance level, and there is a sub-clustering of high and very low disturbance levels (similarity of 0.700). Similarly, the plant density data was conglomerated into the five disturbance classes. The NMDS analysis (Fig. 4.5B) based on density data across levels of disturbance showed that medium and very low levels of disturbance formed one group and were separated from a second group formed by high and low disturbance levels (in the ordination space). Very high disturbance levels appeared distinctly different from these two groups (Fig. 4.5B; stress value = 0.1612).

4.3.5. Relationships among soil SB characteristics and levels of disturbance

A PCA was also used to test for relationships among level of disturbance and soil seed bank characteristics (species richness and density). Two components accounted for 75% variance in the data (Fig. 4.6).

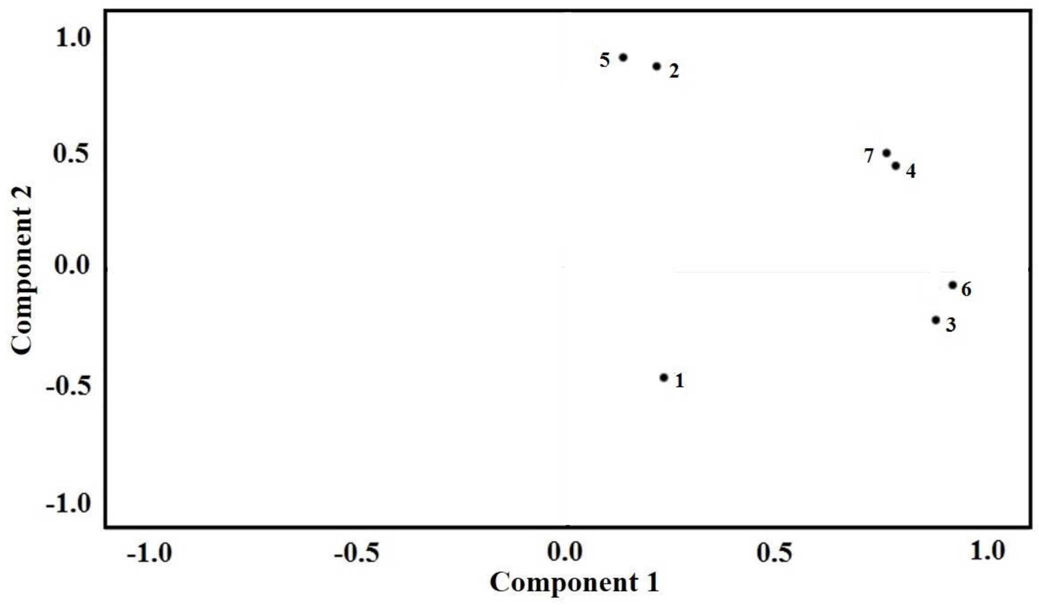

Figure 4.6: Principal component analysis (PCA) plot for the first two components. Each number (1 – 7) represents a principle component used in the PCA: 1 = level of disturbance; 2 = alien species richness; 3 = indigenous species richness; 4 = total species richness; 5 = alien plant density; 6 = indigenous plant density; 7 = total plant density. The cumulative % of variance were as follows: PC1 = 48%; PC2 = 75%.

Level of disturbance (PC1) accounted for 48% variance in the data and was highly positively related to total species richness and density, indigenous species richness and density, and alien species richness and density (see Table C5 for R^2 values, Appendix C). Total plant density loaded most high for PC1. Alien species richness (PC2) accounted for 75% of the variance and was highly positively related to indigenous species richness and density and level of disturbance, and was negatively related to alien species richness and density (PC2). Indigenous species richness loaded most high for PC2.

4.4. DISCUSSION

Results from the present study suggest that anthropogenic disturbance did influence the SB profile of natural green spaces in a subtropical urban matrix in terms of the ratio (and number) and density of alien versus indigenous species.

4.4.1. Seed bank species richness, ordering and life form representation in relation to disturbance intensity

When the results for all 30 sites sampled were pooled, SBs yielded germinants belonging to 20 families, 56 genera and 70 species which is a small proportion of species found across the EMA (< 25% of the EMA indigenous and alien flora [excluding garden ornamental aliens]) (per coms, T. Govender, retired Parks, Recreation and Culture Services, eThekwini Municipality, January 2021). Previous studies on SBs of natural green spaces within urban areas have reported lower SB species richness values: 24 in subtropical grasslands (Sershen et al., 2019), 48 in a grassy fynbos area (Fourie, 2008), and 42 in a forest area in Chile (Figueroa et al., 2020). However, it should be mentioned that all three of these studies focussed on a single vegetation type, whereas the present study sampled seed banks in grassland, forest, savanna, and thicket vegetation coupled with varying levels of disturbance. Reference to other SB studies does, however, indicate that the four highest-ranking families in this study in terms of species richness (viz. Asteraceae Fabaceae, Cyperaceae and Poaceae) are amongst the top-ranking families in SBs within urban matrices in the study area (Asteraceae, Poaceae and Fabaceae [Sershen et al., 2019]) and other parts of the world (Asteraceae and Cyperaceae [Fourie, 2008]; Asteraceae, Poaceae and Cyperaceae [Yang and Li et al., 2013]; Asteraceae and Poaceae [Figueroa et al., 2020]). It is worth noting that Asteraceae, Fabaceae and Poaceae were also dominant families in the SV at these sites (see sections 2.3.2 and 3.3.2 in Chapters 2 and 3) and are generally well represented in soil seed banks due to their high seed sets (Thompson and Grime, 1979; Sershen et al., 2019).

In the present study, four life forms were represented in the SB, but herbs were the most speciose life form, followed by graminoids, shrubs and trees. Studies have found woody species (trees and shrubs) dominating soil seed banks of tropical areas, while shrubs and herbs dominated subtropical areas (Luo et al., 2017). Other studies have also shown SBs in urban habitats to be dominated by regenerating herb and grass species (Bekele, 2000; Albrecht et al. 2011; Cui et al., 2013; Shiferaw et al., 2018; Figueroa et al., 2020). However, the general paucity of global SB studies makes generalisations regarding life form tentative. When the Shannon's and Simpson indices were used to compare species richness and evenness across sites differing in disturbance level, there were no differences, but it was interesting to note that sites exhibiting the lowest levels of diversity (in terms of both indices) had relatively fewer herb, graminoid, and shrub species than sites ranking highest for these diversity indices. Disturbance-induced changes in the SV can, in turn, bring about changes in the SB (Bordon et al., 2019). This may also explain why the Sørenson and Jaccard comparisons between SB and SV yielded higher levels of similarity at lower disturbance levels and lower similarity for higher disturbance levels (discussed below, Section 4.4.4).

4.4.2. Floristic similarity of SBs and influences from disturbance

Results for the UPGMA and NMDS analyses conducted on the SB data were not in agreement when the total SB flora across sites were grouped together within disturbance levels; there were no meaningful and/or discernible pattern(s) detected. In both analyses, the *very high* disturbance level was the outlier; however, this is very likely a consequence of under-sampling of *very highly* disturbed sites. The other disturbance levels formed random groupings based on disturbance level. The lack of agreement between the UPGMA and NMDS results are partly due to the input data with the cluster analysis drawing on binary (presence-absence) data, while the NMDS relies on density data. Besides the methodological differences, these differences may be due to the high incidence of no data, (i.e. sampling zeros) that could have contributed to differences.

In the present study, disturbance intensity was based on an integrated measure of disturbance, i.e. a disturbance index that integrated the intensity of different types of non-natural disturbance (Appalasamy et al., 2020, and explained in section 2.2.4, Chapter 2). However, different types of disturbance may have different effects on SBs, and the use of a disturbance index may not accommodate for the specific effects of each type of disturbance on species richness and density. For example, lower species floristic values (viz. seed density and richness) in sites disturbed by grazing vs sites that are not grazed is a common finding (Mayor et al., 2003; Ma et al., 2010; Savadogo et al., 2017). The current study found higher disturbance levels caused by grazing in outer-lying areas (to the west) of the city compared with levels within more central areas, closer to the city center. The intensity of grazing at sites to the west was high due to relatively large herds of cattle. The effects of grazing as a non-natural disturbance type should, therefore, not be excluded from urban studies in developing countries such as South Africa. Furthermore, since domesticated animals often move/are moved across the urban space indiscriminately they can convey plant propagules from peri-urban traditional grazing sites to green spaces closer to the city center. Before the effects of specific types of disturbances on individual species or groups of species found in SBs within urban spaces can be performed, there is a need to generate baseline data on seed banks. Such data were not in place for the study area at the time of this study. In fact, at the time of this study, the only published data on seed banks for the study area was for selected grassland sites across the EMA (Sershen et al., 2019).

As reported previously, alien species had a higher species richness compared with indigenous species (Section 3.3.2, Chapter 3) within the SV at these sites, and this was attributed to the effects of disturbance (Appalasamy et al., 2020). Due to high seed sets, alien species are also known to persist in SBs even when no longer present in SV, and emergence can be rapid in a disturbed situation with past and ongoing disturbance activities (Gioria et al., 2019). Alien species are therefore able to re-emerge even after the disturbance regime removes or progressively alters SV. The PCA (Table C5, Appendix C) found disturbance level to be positively related to species richness and density (alien and indigenous) within the SB. Increased levels of non-natural disturbance within green spaces are therefore likely to increase species richness and density within the SB. As previously reported, non-natural disturbance within urban areas increases as the proximity to the source of disturbance increases at the study sites (Appalasamy et al., 2020). Many studies have highlighted the relationship between disturbance and SBs, where highly disturbed vegetation are more likely to have higher numbers of alien species in the soil due to high seed input and their high tolerance to environmental change (Sershen et al., 2019; Figueroa et al., 2020; Bhugeloo, 2020). In urban grasslands in the study area, disturbance had significant effects on species richness and less of an impact on plant density in SBs (Sershen et al., 2019). A similar result was noted in urban forests, which observed negative effects on species richness due to disturbance levels (Bhugeloo, 2020).

4.4.3. Indigenous versus alien floristics within the seed bank

The proportion of species made up by aliens in the SB was 40% (27 species), of which 26% (seven species) are classified as invasive in the study area. The top two ranked families in terms of total alien species richness belonged to the most speciose families overall (viz. Asteraceae and Fabaceae), along with Verbenaceae. *Conyza sumatrensis* (Retz.) E.Walker (alien herb), *Oxalis corniculata* L. (alien herb) and *Galinsoga parviflora* Cav. (alien herb) had the highest frequency across all sites; and were the most common alien species in forest SBs.

In terms of life form representation, while the ranking in ascending order for the alien flora was herbs, shrubs and trees, for the indigenous flora, graminoids were the dominant life form, followed by herbs, shrubs and trees. In urban habitats, regenerating herb and grass species are known to dominate the SB (Bekele, 2000; Albrecht et al. 2011; Cui et al., 2013; Shiferaw et al., 2018; Figueroa et al., 2020) and is known to occur across different vegetation types (Shiferaw et al., 2018). However, it is worth noting that in the present study SBs at forest sites appeared to be relatively more species-rich than those within savanna sites. This could be attributed to the relatively higher levels of disturbance at savanna (viz. grazing pressure on SV [Sanou et al., 2018]) compared with forest sites in the present data set (see Chapter 3, section 3.3.1). Disturbance is said to activate the SB (Albrecht et al., 2011), i.e. the removal/disturbance of standing vegetation can create opportunities for alien seeds within the soil to be exposed to increased soil temperature, light and/or direct rain, allowing for germination and seedling establishment. As seeds germinate, they effectively deplete the seed bank.

Of the total germinants recorded in the study (all species and all sites/pots/replicates combined), 40% of these were identified as alien. High alien seed densities may be related to levels of disturbance whereby SB density increases, and ultimately this decreases the SB diversity (Grime et al., 1988; Pellissier et al., 2008). The current study found high alien species densities compared with indigenous species densities across all levels of disturbance. Surprisingly, higher plant density for alien species was found between very low to medium levels of disturbance. This may be due to alien species richness in the SV being lower at higher levels of disturbance as reported previously (see Section 3.3.4.1 of Chapter 3). These results may also be explained by the findings of Figueroa et al. (2020): low levels of disturbance are responsible for high seed densities, while high levels of disturbance are responsible for high diversity of species in the SB.

The top three species in terms of total plant density were *Conyza sumatrensis* (alien herb), *Verbena brasiliensis* (alien herb) and *Chamaecrista mimosoides* (indigenous shrub). *Conyza sumatrensis* is an annual alien herb species that ranked highest in both frequency (mentioned above) and plant density across study sites. It is highly invasive due to traits such as persistent fecundity, high germination rate, and its dispersal mechanism (Hao et al., 2009b). The high germination rates recorded for this species with over 60 000 seeds produced per plant per fruiting season accounts for its high presence in the SBs of this study in terms of density. Seeds develop within 8 – 10 days, are light in weight, and have a slow settlement speed (Hao et al., 2009b). This species was found in the soil SB of open rice fields and after burning in tropical parts of the world (Laos [De Rouw et al., 2014]). Fire is a common form of disturbance within green spaces in the study area (Drury et al., 2016) and could promote the germination and subsequent spread of this species in the city. Various *Conyza* species have also been found to be the dominant SB species in other studies in subtropical SA (Fourie, 2008; De Rouw et al., 2014). *Verbena brasiliensis* is a perennial alien herb that originates in South America and is known to have highly ruderal growing patterns (viz. high seed production), and is able to tolerate drought and disturbance (Luecke et al., 2020). This species has high reproductivity, produces between 90 000 – 100 000 seeds per mature plant in a year, and both flowering time, and seed ripening occurs concurrently, aiding in its spread (Mikeladze et al., 2017). *Chamaecrista mimosoides* is a perennial shrub that is indigenous to SA. According to SANBI (2020a), *C. mimosoides* is found in various habitats and is a common weed species in disturbed areas.

The ratio of the number of alien to indigenous species was 1:1.5 showing that there is currently a higher presence of indigenous species to alien species within the SB. This was largely a consequence of the high number of indigenous grass species found across all SBs in the present urban matrix. This is reassuring but also concerning since alien plant density was higher than indigenous plant density. These results suggest that the invasive traits of alien species, such as high seed set, are allowing them to dominate seed banks in terms of density but not in terms of diversity. High to intermediate levels of evenness, indicated by Table C3 (Appendix C), showed a high proportion of indigenous species, and lower levels of evenness at sites showed low combined species richness made up of alien species. This may be due to alien species having a higher combined plant density across sites (irrespective of disturbance level). This may also explain why many invaded stands of herbaceous IAPs in the city are dominated by a single species (e.g. *Chromolaena odorata*, *Lantana camara*, *Tithonia diversifolia*) (author's unpublished observations). However, these particular dominant IAPs in the SV of EMA were not well represented in the present study.

4.4.4. Similarity between seed bank and standing vegetation

The current study found high similarity between species richness of the SB and SV. Of the 70 species found in the SB, 69 (99%) were present in the SV except for one graminoid. In contrast, reports of low similarity between SV and the SB are common in the literature (Thompson and Grime, 1979; Scott et al., 2010; Shiferaw et al., 2018; Sershen et al., 2019). The SB and SV similarity has been linked to disturbance patterns where similarity increases with disturbance time and frequency in grasslands and decreases with time since the first disturbance in forest vegetation (Hopfensperger, 2007). In this study, sites ranking high in similarity ranged between 0.368 – 0.421 and were predominantly found at intermediate levels of disturbance, while lower levels of disturbance were found at sites ranking low in similarity (0.074 – 0.139). Results are comparable with other studies that found high similarities between SB and SV under frequent (Roberts and Boddrell, 1984; Garcia, 1995) and medium levels of disturbance (Sheferaw et al., 2018). The low similarity between SB and SV is a reflection of differences in the number of seeds produced by species, their seed dormancy patterns, longevity once shed, and life cycle (Sershen et al., 2019). Additionally, there was also a high presence of herbs at high similarity sites and a high presence of graminoids at low similarity sites. Growth forms and life cycles have been found to influence SB and SV (e.g. Pierce and Cowling, 1991), which may explain our results. The high presence of grasses at low similarity sites could be attributed to the fact that all grass species were perennial. Perennial grasses have been reported to have high dominance in SB studies, are able to germinate rapidly after a disturbance event, and have low mortality during disturbance events such as fires (O'Connor and Pickett, 1992; Sershen et al., 2019). The reason behind this is that perennial grasses are better adapted to unfavourable conditions and low to moderate non-natural disturbances (e.g. fires) within the SB and do not solely rely on seed bank processes whereby viable seeds in the soil germinate and become persistent, next-generation plants (Fenner and Thompson, 2005; Scott et al., 2010).

In a study on savanna vegetation in a South African national park, shared plant species (5.6%) were found in the SB and SV for grass-layer plants (Scott et al., 2010). This is a likely phenomenon for savanna vegetation due to poor seed dispersal and short-lived seed banks of dominating species (O'Connor and Pickett, 1992; Scott et al., 2010). However, results differ between SB and SV when woody and grass-layer plants are compared as it is rare for woody species to be found in savanna SBs (Scott et al., 2010). This may explain why the present study found a low percentage of similar plant species (above vs below-ground) in savanna vegetation, but overall found a high percentage of similar species for above- and below-ground. This high percentage was not a feature of other studies conducted at a research station in KZN, which showed lower numbers of shared species but have more unique species found in the SB (three) compared with our results (one) (Everson et al., 2009). Other dissimilarities between our study and that of Everson et al. (2009) was the presence of grass species in the SBs (26% : < 15%) and SV (12% : 75%). Due to non-natural disturbance occurring at sites, seeds of grass species are likely to fall to the ground and bury beneath the soil. Lastly, grazing could also play a role as more seeds of annual species within the SB, depending on whether grazing occurred early or late in the growing season (Aboling et al., 2008). This implies that grass species produce enough seeds to regenerate and are not reliant on persistent seed banks (Aboling et al., 2008). Perennial grasses also have both sexual and asexual reproductive strategies (Piquot et al., 1998), which may explain the results of this study.

4.5. CONCLUSION

Soil seed banks have the potential to play crucial roles in temporary continuity and succession of species in urban open spaces, as well as contribute to the floristic diversity above-ground. While most vegetation disturbance studies focus on the SV, it is becoming important also to have an understanding of SB species richness, density and diversity, in the context of anthropogenic disturbance. Disturbance, irrespective of intensity, had an effect on SB and SV similarity. These independent similarities contributed to the overall high similarity (99%) in species found between SV and SBs. In order to fully understand the relationships among the SB, SV, and disturbance, knowledge of community dynamics are required, which was a major limitation of the current study. The SBs within natural green spaces can be viewed as a seed source for plant community re-establishment. Further research into community re-establishment is needed for effective control and management strategies.

Seed banks in the study area appear to contain more indigenous species (high richness) but are dominated by alien species in terms of density. This is a concern for urban SBs (in terms of conservation and management) as alien species are unlikely to be negatively affected by disturbances, as seen in the current study and other studies. Increases in alien densities will impact urban green spaces negatively and will require increased conservation and management of these areas. Differences between alien and indigenous species within the SB were not major in terms of species richness; however, there is a chance that non-invasive alien species such as *C. sumatrensis* will become invasive over time as changes to the climate and anthropogenic disturbances increase. This is also applicable to weedy indigenous species such as *C. mimosoides* that could reduce indigenous richness and diversity. The results suggest that a lack of management at sites in the current study may have contributed to disturbance impacting negatively on indigenous species richness and density within the SB.

Future studies should be designed to examine the transient and persistent SBs within urban green spaces to get an idea of the vertical distribution of the SB. Furthermore, a better understanding of seedbanks in undisturbed sites and similar vegetation types is needed and would serve as a benchmark for comparisons with disturbed sites. Proper control of alien species and management of open spaces within the urban matrix is required as alien species may compromise indigenous species establishment, and high alien species seed rain may have a long-term effect on indigenous species within these urban vegetation types. The findings of this study have implications for managers of urban green spaces since alien species in SBs could exploit niches created by disturbances, promoting urban invasions. Furthermore, the results highlight the importance of considering the regeneration potential of a site afforded by the SB when urban green spaces are denuded of vegetation as a consequence of alien clearing programmes.

CHAPTER 5

A comparison of seed longevity in four invasive alien plant species buried in subtropical South Africa

ABSTRACT

Soil seed banks (SBs) and seed traits are important in understanding the establishment and persistence of invaders in urban green spaces and their impacts (type, extent, and time scale) on these habitats. The present study was designed to assess whether selected seed physical and/or chemical traits can be used as potential indicators of invasive alien plant (IAP) persistence in natural SBs. This involved comparing seed bank persistence in five IAP species using a burial experiment in subtropical South Africa. Seeds were collected from plants growing in urban green spaces and buried in a randomised block design for 30 months. Morphological and anatomical traits (seed mass, seed size, and seed coat thickness) were measured in freshly harvested seeds. Buried seeds were excavated at periodic intervals over 30 months and assessed for viability which was the sum of the percentage of seeds that germinated and non-germinable seeds that stained positive when subjected to a tetrazolium (TTZ) test. Thermal behaviour (specifical changes in lipid melting properties which can lead to seed deterioration) of freshly harvested and buried seeds was measured using differential scanning calorimetry (DSC). There were significant differences across all species for traits related to seed mass, seed size, seed coat thickness and estimated lipid content. *Solanum mauritianum* maintained 100% viability throughout the burial experiment but declined significantly in the remaining four species, being most severe in *M. azedarach*. In *C. indica, R. communis,* and *S. didymobotrya,* viability was dominated by germinable seeds before burial, but as viability declined with an increase in burial time, viability was dominated by seeds that were not germinable but stained positively. *Solanum mauritianum* seeds were the smallest and lightest, with the thinnest seed coat, and estimated to possess a high lipid content predominantly composed of monounsaturated fatty acid (possibly oleic). Seed longevity was highest for *C. indica* with one of the lowest estimated lipid contents and lowest for *M. azedarach,* which had the highest estimated lipid content, predominantly composed of polyunsaturated fatty acid (possibly linolenic). Decreases in germination over time for *C. indica, R. communis, M. azedarach,* and *S. didymobotrya* were associated with changes in either/both enthalpy of melting of the lipid and the temperature of the lipid melt, which could reflect inter-specific differences in the mechanism of seed deterioration when buried. The relatively low number of species and traits studied and/or the phenotypic plasticity associated with seed post-harvest physiology in wild species may explain the absence of significant relationships between the seed physical and/or chemical traits and seed bank longevity using the traits investigated. Nevertheless, the trends observed suggest that clearing programmes

need to consider seed traits, such as seed bank persistence, when prioritising species for control. The study has also given rise to the beginnings of a conceptual continuum of SB longevity for IAPs, which, once populated with more species, could serve as an additional criterion that practitioners can use for categorising species in terms of invasiveness.

5.1. INTRODUCTION

Invasive alien plants (IAPs) threaten biodiversity and natural ecosystems globally (Nel et al., 2004; Dogra et al., 2010; Carbonell et al., 2017). The introduction and subsequent invasiveness of some alien species impact terrestrial, freshwater, and marine communities (Gurevitch and Padilla, 2004), influence indigenous plant species diversity and can alter soil nutrients, water status and fire regimes (Pimentel et al., 2005; Dogra et al., 2010; Holmes et al., 2020). Alien species tend to have greater establishment success rates than indigenous species, thereby dominating invaded communities and excluding their indigenous neighbours (Kolar and Lodge, 2001; Ortega and Pearson, 2005; Dogra et al., 2010; van Wilgen et al., 2020).

The rapid spread and persistence of IAPs is usually facilitated by high reproductive output (i.e. high number of viable seeds produced) (Witkowski and Wilson, 2001; Witkowski and Garner, 2008). Fruits and seeds housed within fruits are the main dispersal units of many alien species (via wind, water and various biotic dispersal agents) into new and disturbed areas (Witkowski and Garner, 2008; Ratnayake, 2014). Once dispersed, seeds of any species (alien or indigenous) can either germinate, persist in the soil seed bank (SB) or die once viability is lost (Soriano et al., 2014). Species diversity and abundance of soil SBs, which is affected by IAPs (Vilà and Gimeno, 2007; Gioria and Osborne 2009), influences the structure and persistence of the standing vegetation (Bakker et al., 1996; Saatkamp et al., 2014). However, there is generally limited data on both the changes in SB communities brought about by IAPs (Brock, 2003; Krinke et al., 2005) and the seed longevity of these species within soil SBs (but see Saatkamp et al., 2009).

Soil SBs have been defined by Roberts (1981) as viable seeds stored in the soil and are correlated with standing vegetation (SV), seed production and seed persistence (van der Valk and Pederson 1989; Cox and Allen, 2008). As alluded to above, IAP SBs are important within plant communities and play an important role in vegetation dynamics but are easily and frequently overlooked (Holmes and Newton, 2004; Soriano et al., 2014). Seeds within the soil SB are either transient or persistent (Thompson and Grime, 1979), and the average lifespan of a seed is determined by genetic and morphophysiological characteristics and its relationship with biotic/abiotic factors (Blaney and Kotanen 2001; Soriano et al., 2014). Factors known to extend this lifespan *in situ* include small seed size, chemical and/or physical seed defenses (against soil invertebrates and microbes), dormancy, and persistence (Baskin and Baskin 1998; Gardarin et al., 2010).

Seed persistence refers to the survival of a seed post maturity on a parent plant (Long et al., 2015) or as seeds that survive in SBs for many years and germinate after disturbance (de Jong et al., 2013). Seed persistence allows for the dispersal of seeds away from the parent plant, through time allowing the seed to avoid germination in unfavourable conditions (Ooi, 2012). Seeds that persist in SBs undergo periods of dormancy, and there are two criteria in developing SB persistence: (1) immediate seed germination and (2) non-germinating seeds should survive within the SB and resist seed coat degradation (de Jong et al., 2013). Once seeds are mature, they persist in soil SBs until they reach one of two outcomes; germination or death (Long et al., 2014). However, within the SB, seeds can experience favourable and/or harsh conditions (including temperature, light and rain), leading to variability in persistence times (Long et al., 2014). The success of alien species as invaders is often increased by seed persistence in soil, and effective and sustainable management of IAPs is often challenged by persistent-seeded IAPs (Richardson and Kluge, 2008).

Based on the above, understanding SB persistence of alien species in relation to seed physico-chemical characteristics can be useful in predicting the invasion potential of specific species (Grewell et al., 2019) and inform the management strategies for established and emerging IAPs. Methods for assessing soil SB persistence include age determination ^{14}C dating (McGraw et al., 1991), seed burial experiments of seeds (Saatkamp et al., 2009), and the testing of germinability of artificially aged or control deteriorated seeds (Telewski and Zeevart, 2002). Seed burial experiments are accurate measures of soil SB survival. Seed persistence in the soil is an advantage in population persistence (Reed et al., 2002; Saatkamp et al., 2009), and seed burial is regarded as an essential prerequisite to persistence (Garner and Witkowski, 1997; Witkowski and Garner, 2008). The persistence of seeds in the soil is particularly important in habitats subject to disturbance and/or when environmental conditions are unfavourable for germination and subsequent seedling growth (Moles et al., 2003). Alien plant species produce large seed sets accommodating for high survival of seedlings after germination, decay, or predation of seeds within the soil (Marchante et al., 2010). The surviving seeds form persistent SBs that become a source of future generations, making it difficult to control and eradicate established invaders (Marchante et al., 2010), especially after the initial clearing of the SV. Therefore, alien seeded species have greater seed longevity within the soil due to their high seed sets. Weed seeds, on the other hand, have more difficulty entering undisturbed (via tillage) soil and remain on the surface, followed by germination. However, using rainfall and hygroscopic awns seeds, weedy species from families such as Poaceae are able to self-bury (Collins and Wein, 1997; Benvenuti, 2007). Weed seeds have poor emergence when sown on the soil surface due to increased vulnerability but tend to do better under controlled laboratory conditions where there is no drying out of the soil surface and reduced predation (Grundy et al., 2003).

Germination in many species frequently occurs below surface levels due to a moist environment surrounding seeds, which prevents them from drying out, as is often the case when they are unburied (Harper and Benton, 1966; Chen and Maun, 1999; Liu et al., 2011). While ageing within the soil, seeds undergo changes in terms of their quality which ultimately leads to death (Milošević and Malešević, 2004; Baskin and Baskin, 2014) if germination does not occur. However, seed ageing mechanisms in the SB and the similarity/dissimilarity of these mechanisms across species and seed types remain largely unknown, particularly for IAPs. Based on previous studies on the ageing of seeds stored in *ex situ* seed banks or subjected to artificial ageing (e.g. Walters et al., 2005a; Probert et al., 2009; Colville and Pritchard, 2019; Ballesteros et al., 2020), it can be expected that the rate at which ageing occurs in the soil is: (1) species-specific but with some families (e.g. Orchidaceae, Apiaceae, Poaceae, and Asteraceae) being typically shorter-lived than others, (2) dependent on the embryo/seed ratio (with seeds possessing small underdeveloped embryos tending to be shorter-lived), and (3) dependent on some structural (e.g. seed coat), biochemical (e.g. lipid peroxidation), and physico-chemical (e.g. lipid crystallization and melting) factors.

The persistence of seeds within soil SBs has been directly related to mass and shape (Thompson et al., 1993) as well as the thickness of the seed coat (Davis et al., 2008; Gardarin et al., 2010). Seeds that are small and spherical are able to penetrate through the soil more easily and are believed to exhibit higher persistence due to a greater burial depth. Furthermore, an increase in burial depth helps in the delay of germination, leading to a decrease in seed loss (Thompson et al., 1993). The seed coat can also serve as a physical and chemical barrier, which protects and conserves both the seed and the embryo from factors such as parasitic attacks, temperature and water oscillations (Mohamed-Yasseen et al., 1994). The seed coat can also assist with the nutrition and growth of the embryo, and it plays a role in seed dispersal, dormancy and germination (Salmeri et al., 2015). Due to these functions, it is also important to study the morphology, ultrastructure and anatomy of seed coat characteristics in order to understand and predict seed persistence (Salmeri et al., 2015). There are also reports that seed oil content and fatty acid composition can influence seed ageing based on the fast ageing (via water immersion in a water bath) of certain oily species, particularly those with unsaturated fatty acids (Priestley et al., 1983; Balešević-Tubić et al., 2010); however, no significant correlations between these parameters have been found for seeds stored dry in *ex situ* SBs (Walters et al., 2005b), aged artificially at high moisture and temperature (Probert et al., 2009), or within the soil SB (Gardarin et al., 2010). It must be mentioned that these studies focused on crop species and not IAPs.

When designing alien management and habitat restoration efforts within invaded areas, it is useful to characterize the status of the soil SB (Wearne and Morgan, 2006). For example, when a site is cleared of aliens, it is important to know which (alien) species may persist as propagules in the SB and for what duration (Holmes, 2002). Knowledge of seed persistence in SBs is limited for southern African (and for most vegetation types) (O'Connor and Bredenkamp, 1997; Wilson and Witkowski, 2003; Witkowski and Garner, 2008). This is worrying as South Africa (SA) has a major alien invasion problem with approximately 10 million ha of land having been invaded (Poona, 2008; Richardson et al., 2020a), and the control of alien plant species poses serious challenges to ecosystem managers in terms of manpower, finances, and time spent (Marais, 1998; Cilliers et al., 2004; van Wilgen et al., 2020b). According to Witkowski and Garner (2008), IAPs that form seed banks play an important role in re-invasion of newly cleared areas. However, as is the case for many of the IAPs found across SA, studies on seed persistence within soil SBs have yet to be conducted for *S. mauritianum* (Witkowski and Garner, 2008).

Seeds of alien species can accumulate within SBs, and long-lived seeds remain in the soil as “hidden legacies” for extended periods of time, ultimately negatively affecting the management and clearing of these species (Passos et al., 2017). The seeds of species that persist in the SB are able to remain dormant in the soil until favourable conditions, such as alternating temperatures, arise (Rodrıguez-Echeverrıa et al., 2013; Passos et al., 2017). Seed traits such as relative embryo size (i.e. ratio of embryo to seed), which typically differs across species and between endospermic and non-endospermic seeds, have been identified as correlates of seed longevity under artificial (warm/moist and cold/dry) storage conditions (Walters et al., 2005a; Probert et al., 2009; Merritt et al., 2014). Traits such as mass, shape, and seed coat thickness also have been identified as correlates of seed longevity in the SB (Thompson et al., 1993; Davis et al., 2008; Gardarin et al., 2010). Triacylglycerols have also be shown to be important in the storage physiology and germination of seeds, and changes in the physical (thermal) behaviour of lipids show triacylglycerols as a sink of protectants during the ageing process (Crane et al., 2006). The focus on lipid thermal profiles in the literature is based on suggestions in the literature that seeds with high lipid contents age rapidly (Priestley, 1986; Walters et al., 2005a). Changes in thermal behaviour, which can arise in seeds at high moisture levels, have been used to explain seed ageing (Ballesteros et al., 2017). However, very little is known about the relationships (if any) between physical and chemical seed traits (e.g. thermal behaviour) and seed longevity in wild species in general, and alien species in particular, within natural SBs.

This motivated the present study, which was designed to assess whether selected seed physical (seed size, shape, mass, and seed coat thickness) and/or chemical (specifically changes in lipid melting properties) traits can be used as potential indicators of IAP persistence in natural SBs. The seed longevity of five IAPs typical of subtropical urban green spaces in the eThekwini Municipal Area (South Africa) was investigated via a burial study that spanned two years. The species included were *Solanum mauritianum* Scop. (Solanaceae, shrub), *Ricinus communis* L. (Euphorbiaceae, shrub), *Melia azedarach* L. (Meliaceae, tree), *Senna didymobotrya* (Fresen.) H.S. Irwin & Barneby (Fabaceae, shrub or small tree) and *Canna indica* L. (Cannaceae, herb) and were selected based on the fact that they represent a variety of families, life forms and seed types. At the time of this study, only a few seed burial studies focussed on IAPs (Costea et al., 2005; Holmes et al., 2005; Marchante et al., 2010; Silva and Vieira, 2017). These studies showed that the number of seeds in the soil declined over time (months), and seeds that survived burial had high viability but low germinability (Costea et al., 2005; Holmes et al., 2005; Marchante et al., 2010). In addition, these studies report that viable seeds form persistent SBs, which act as a source of replenishment, making it difficult for IAP control.

5.2. MATERIALS AND METHODS

5.2.1. Plant material

Seeds of *S. mauritianum, R. communis, M. azedarach, S. didymobotrya* and *C. indica* were collected from wild populations in New Germany, Durban, South Africa (-29° 47' 37.11" S, 30° 52" 58.46" E). These species were selected on the basis of field surveys across the city which revealed these species to be widespread and frequently encountered in the EMA and presently invasive within all study sites (Appalasamy et al., 2020; Chapter 2). All five species recognised as category 1 invasives may not be grown and must be controlled (1a = *M. azedarach* and *S. didymobotrya*; and 1b = *S. mauritianum*, *R. communis* and *C. indica*), according to the National Environmental Management: Biodiversity Act ([NEMBA] Act no. 10 of 2004), and Alien and Invasive Species List 2020 (Department of Environment, Forestry and Fisheries, 2020). Mature seeds were collected from five randomly selected reproductively mature plants that were > 5 m apart from each other and conveyed to the laboratory immediately. Seeds were set out for burial as described below on the day of collection.

5.2.2. Seed burial experimental design

Following a randomized block design similar to that of Saatkamp et al. (2009), a burial experiment was set up. Seeds were buried in a state in which they are naturally shed from the parent plant into the environment and enters the seed bank via its dispersal mode. *Solanum mauritianum* and *M. azedarach* seeds were enclosed by fruit tissue, while seeds of *R. communis, S. didymobotrya* and *C. indica* were first removed from their fruits. Fruits/seeds were placed in nylon mesh bags (< 1 mm) and buried in soil at a depth of 5 cm (Mennan and Zandstra, 2006; Harrison et al., 2007), in an area (University of KwaZulu-Natal, -29° 49' 3.96" S, 30° 56' 22.85" E) covered with grass species typical of the site at which the parent plants occurred, for a period of 30 months. For the randomised block design, four pits (representing four blocks) were dug out 1 m apart, and seven large mesh bags were placed within each block. Within each large mesh bag, there were five smaller mesh bags, each containing 25 seeds of one of the five species. Each mesh bag within a block represented seven time intervals (T1 – T7), with one bag being retrieved from each block every three months for the first 12 months (since the rate ageing for seeds within the SB was unknown).

After it was established that the seeds had the ability to persist in the soil, sampling intervals were extended to six months. However, it should be mentioned that for some species, there were losses of whole seeds which were predated or disintegrated. Four batches of 25 seeds each that were not subjected to any burial were used to assess initial viability (T0) for all species. This meant that a total of 700 seeds per species were used for the entire seed burial experiment (T1 – T7). At each sampling time (every three/six months), mesh bags of individual species were excavated from the respective sampling block and brought back to the laboratory to assess seed germinability (non-predated or disintegrated) and mortality (predated or disintegrated as per Ter Heerdt et al., 1996). The number of intact, non-germinated seeds was also recorded, and these seeds were left to germinate in germination trays with potting mix for 30 days under greenhouse conditions as described below.

5.2.3. Germination assays

Fresh seeds (T0; 4 trials of n = 25 seeds each) and buried seeds that were intact and non-germinated at each sampling interval were placed within individual inserts in germination trays filled with commercial potting soil (Grovida, South Africa) and set out to germinate under greenhouse conditions for 30 days. Seeds were watered three times a week. After 30 days, non-germinated seeds were tested for viability using a tetrazolium (TTZ) test.

5.2.4. Tetrazolium test

Non-germinated seeds were cut in half along the length of the embryo and placed individually in 2 ml of 1% (w/v) 2,3,5-triphenyl tetrazolium chloride (TTC), prepared in 0.05 M phosphate buffer (pH 7.3) and left for 12 h in a dark at room temperature (after Perumal et al., 2014). Embryos were then placed in deionised water to stop the reaction. Embryos that stained pink-red (due to the formation of formazan) were considered viable.

5.2.5. Seed physical characteristics

Seed mass (n = 25) was determined according to Subbiah et al. (2019) for all five species. Seeds were weighed on a five-place balance, dried at 80 ºC for 48 h in an oven, and then re-weighed to determine their seed mass (g). Seed dimensions (width, length and diameter) were measured using digital callipers (TA 150 mm digital vernier).

5.2.6. Scanning electron microscopy (SEM)

Seeds of all five species (n = 3) were fractured, and seed coats were placed onto metal stubs using carbon tape. The samples were then sputter-coated with gold (deposition of c. 30 nm) using a Quorum Q150R ES sputter coater. Seed coat thickness of each species was observed using a Zeiss Ultra Plus Field Emission Gun SEM (FEG SEM) and a Zeiss LEO 1450 SEM, and photomicrographs were captured. Seed coat thickness (µm) was measured at five points per sample using ImageJ software (version 1.45; NIH, Bethesda, MD, USA) (Woodenberg et al., 2019).

5.2.7. Differential scanning calorimetry (DSC)

Thermal behaviour of freshly harvested and buried seeds from all five species researched was measured using a differential scanning calorimetry (DSC). This experiment was conducted to predict the predominant fatty acid of the seed storage lipids (i.e. triacylglycerol's [TAGs]), estimate the lipid content for the diverse species (after Ballesteros and Walters, 2007), and investigate the change in the melting properties of the TAGs of seeds or seed tissues over burial time. Seed deterioration has been shown to affect the physical properties of lipids by decreasing the energy of the melting transition of TAGs (Vertucci, 1992; Porteous et al., 2019), and this measurement enables further characterisation of the physical and structural status of the seeds.

As mentioned earlier, for some species, there were losses of whole seeds due to predation and disintegration. The seeds that remained at each sampling interval were directed towards the germination assays as a priority which meant that while the seeds of all five species were scanned after zero and three months of burial, only three species (viz. *S. didymobotrya*, *R. communis* and *C. indica*) were scanned after six months and only two species (*R. communis* and *C. indica*) were scanned after nine months. Seeds were analysed when intact (non-germinated, non-predated, and not necrotic), although some degraded seeds of *R. communis* and *S. didymobotrya* were scanned for comparative purposes. Five seeds per species/burial time were analysed by DSC. All seeds, immediately after excavation, were dried at 15% RH and 25 °C for seven days and shipped to the UK. Seeds arrived within five days after shipment and were further dried at 15% RH and 15 ºC for 5 – 7 more days before scanned. Seeds were dried to slow down deteriorative reactions until scanned and to homogenise seed moisture content for comparison across species and storage times. For some species, the whole seed was scanned in the DSC (e.g. *S. mauritianum*, *M. azedarach*, and *S. didymobotrya*). For *R. communis* and *C. indica*, the embryo and endosperm were scanned separately. Seeds or seed tissues were scanned at the moisture content reached by drying at the conditions indicated above, which averaged 0.040 ± 0.007 g H_2O/g DW for *S. mauritianum* seeds, 0.037 ± 0.002 g H_2O/g DW for *M. azedarach* seeds, 0.045 ± 0.018 g

H_2O/g DW (freshly harvested) and 0.097 ± 0.006 g H_2O/g DW (buried) for *S. didymobotrya* seeds, 0.028 ± 0.003 g H_2O/g DW for *R. communis* endosperm, 0.076 ± 0.005 g H_2O/g DW for *C. indica* endosperm, and 0.097 ± 0.006 g H_2O/g DW (freshly harvested) and 0.126 ± 0.014 g H_2O/g DW (buried) for *C. indica* embryos.

Phase transitions in seeds and seed tissues were determined using a Mettler-Toledo DSC-1 (Greifensee, Switzerland), calibrated for temperature with indium (156.6 °C) standards and energy with indium (28.54 J g^{-1}) standards. The presence of phase transitions was determined from heating thermograms recorded between -150 ºC and +90 ºC while scanning at a rate of 10 °C min^{-1}. The onset temperature of the melting transitions was determined from the intersection between the baseline and a line drawn from the steepest portion of the transition peak. The enthalpy (ΔH) of the transition was determined from the area encompassed by the peak and the baseline. The size and temperature of the triacylglycerol's (TAG) melting transitions allowed for the prediction of predominant fatty acid of the TAG and estimated the lipid content for the diverse species (after Ballesteros and Walters, 2007). Second-order transitions in heating scans were identified as glass melting events, and the Tg was assigned as the midpoint in the displacement of power during the scan (e.g. Ballesteros et al., 2017). All analyses were performed using Mettler-Toledo Stare software version 12.0 (Mettler-Toledo, Switzerland). Enthalpies of exothermic and endothermic events are expressed on a per g DW basis.

5.2.8. Data analysis

Data for individual species (across time intervals) were carried out in SPSS (Version 2). All continuous data (e.g. seed size, seed coat thickness, enthalpy of melting, etc.) were tested for normality using the Shapiro Wilks/Kolmogorov-Smirnov test. Non-parametric data were log-transformed where necessary. An independent t-test or ANOVA was run (one way) for all parameters across all species. A non-parametric correlation test (Spearman rank) was used to test for relationships between seed coat thickness and viability of seeds post-burial for all species. The potential relationship between burial time and enthalpy of melting or lipid melting peaks and between moisture content and Tg were analysed by the Pearson's correlation coefficient.

As explained above, seeds were assessed for viability in two ways: 1) germination and 2) positive staining following a TTZ test. Data for both percentage germination and positive staining are presented here, but all inter-specific comparisons of SB longevity were based on 'seed viability': the sum of percentage germination and percentage positive staining. Viability data were treated as proportion data according to Crawley (2007). Genstat software 14.2 (VSN International Ltd. 2011) was used to fit germination/burial time data to logistic functions using binomial error distributions and to calculate P50 (time at which 50% of initial germination is lost). This approach enabled the provision of error estimates and statistical comparison on the effects of species on longevity (Ballesteros et al., 2019). Three types of logistic functions were tested (probit, logit, and complementary log-log, e.g. Ellis et al., 1986 [viability equations, probit]; Ballesteros et al., 2019 [logit]; Faria et al., 2020 [probit vs logit]), all of which produced comparable results. Significance of burial time and species on seed viability were tested using GLMs and a binomial error distribution available in Genstat software 14.2.

5.3. RESULTS

5.3.1. Seed morphological and anatomical traits

Seeds of *R. communis* are encased in a spiny seed capsule with brown-black colouration, a light brown caruncle at the tip, has a large embryo in the endosperm, and has foliaceous cotyledons (dicotyledonous). Seeds are shed when the capsule dehisces (Fig. 5.1A). *Solanum mauritianum* has small seeds encased in a berry. The berries are yellow when mature and contain hundreds of seeds that are round and flat in shape. Seeds of *S. mauritianum* have a reticulate testa, and cotyledons are ovate (dicot) and are shed with the berry intact (Fig. 5.1B). Seeds of *C. indica* are round and black and are enclosed within a soft capsule. *Canna indica* is monocotyledonous, and the cotyledons remain in close contact with the endosperm. Seeds of this species are shed when the pericarp opens (Fig. 5.1C). *Melia azedarach* small seeds are in a berry that is elongated in shape with a hard outer casing (surrounded by a pericarp) with approximately five compartments for each seed. *Melia azedarach* is dicotyledonous, have linear cotyledons, and seeds are shed with an intact pericarp (Fig. 5.1D). Seeds of *S. didymobotrya* are flat, grey and located within legumes (pods) that are brown when seeds are mature. This species is dicotyledonous and is shed upon dehiscence (Fig. 5.1E).

Seed (dry) mass varied widely and significantly across species: *C. indica* > *R. communis* > *S. didymobotrya* > *M. azedarach* > *S. mauritianum* (Table 5.1). Species were significantly different in terms of seed mass, and there was slight seed mass variation within a species.

Seed length and width also differed significantly across species: *R. communis* had the greatest seed length > *S. didymobotrya* > *M. azedarach* > *C. indica* > *S. mauritianum*, and *C. indica* had the greatest seed width > *R. communis* > *S. didymobotrya* > *M. azedarach* > *S. mauritianum* (Table 5.1).

Figure 5.1: Seed morphology of the five species of interest; *Ricinus communis* (A), *Solanum mauritianum* (B), *Canna indica* (C), *Melia azedarach* (D) and *Senna didymobotrya* (E). Scale bar = 1 mm. Seeds of two species are shown in red boxes next to the fruit (B and D). A close-up image of seeds (B) are represented in the blue box.

Table 5.1: Seed mass, size, and coat thickness of the five species investigated.

Species	Seed dry mass (g)	Seed size		Seed coat thickness (µm)
		Length (mm)	Width (mm)	
Ricinus communis	0.28±0.03 ^{b}	9.32±0.42 ^{a}	4.96±0.22 ^{b}	183.83±17.19 ^{b}
Solanum mauritianum	0.001±0.0002 ^{e}	1.95±0.14 ^{e}	0.62±0.05 ^{e}	61.03±5.91 ^{e}
Canna indica	0.34±0.01 ^{a}	5.81±0.30 ^{d}	5.57±0.27 ^{a}	1532.78±197.08 ^{a}
Melia azedarach	0.03±0.002 ^{d}	7.30±0.46 ^{c}	2.33±0.28 ^{d}	79.80±7.74 ^{d}
Senna didymobotrya	0.25±0.01 ^{c}	8.42±0.43 ^{b}	3.71±0.35 ^{c}	174.75±12.20 ^{c}

Values represent mean ± SD (n = 25 for all parameters, except for seed coat thickness [n = 3]) and superscript lettering indicates significant differences (P < 0.05, t-test) within parameters, across species.

Seed coat thickness measured using scanning electron micrographs of fractured seeds (Fig. 5.2) followed a similar trend (in species rank) to seed mass and width and differed significantly across species: *C. indica* > *R. communis* > *S. didymobotrya* > *M. azedarach* > *S. mauritianum* (Table 5.1). Interestingly, *S. mauritianum* had the lowest values for all traits measured.

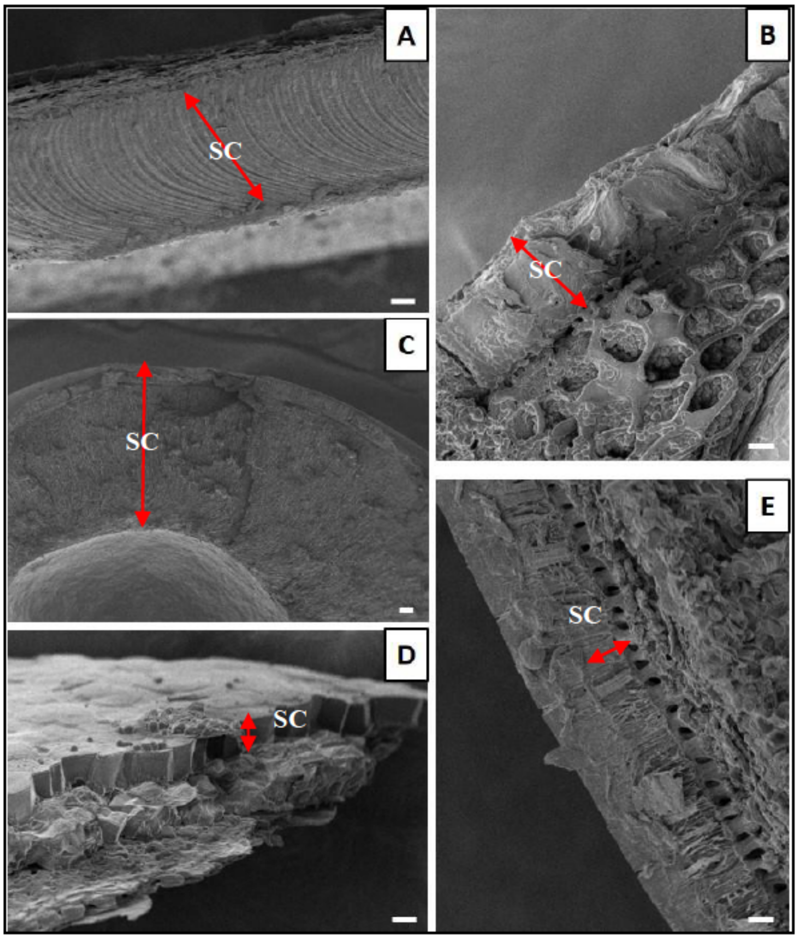

Figure 5.2: Seed coat thickness (µm) for the species investigated: *Ricinus communis* (A), *Solanum mauritianum* (B), *Canna indica* (C), *Melia azedarach* (D) and *Senna didymobotrya* (E). Scale bar = 1 µm. Red arrows indicate the thickness of representative seed coats (SC) for each species.

5.3.2. Seed viability during burial

Seed viability (germinated and non-germinated positively stained seeds) was looked at within species across burial times (Fig. 5.3). Except for *S. mauritianum* (Fig. 5.3 E), which remained 100% germinable over time, germination for all species changed significantly ($P < 0.05$) over time. Percentage non-germinated seeds which stained positively changed significantly ($P < 0.05$) over time in *C. indica* (Fig. 5.3A) and *S. didymobotrya* only (Fig. D); this was not true for *M. azedarach* and *R. communis* ($P = 0.065$ and 0.108, respectively). In *C. indica*, *R. communis* and *S. didymobotrya,* viability was dominated by germinable seeds before burial, but as viability declined with an increase in burial time, viability was dominated by seeds that were not germinable but stained positively. In the relatively shorter-lived *M. azedarach* seeds, the pattern was slightly different: viability declined with burial time, but the majority of the seeds that were viable remained germinable (Fig. 5.3B). All subsequent analyses were based on viability data (germination and positive staining percentages combined).

In terms of fresh seeds, *S. mauritianum* and *C. indica* had comparably high initial viability, 100% and 96%, respectively (Fig. 5.4). Viability values for fresh seeds of these two species were significantly higher than those for *R. communis* (53%), *S. didymobotrya* (47%) and *M. azedarach* (38%) (Fig. 5.4). When seeds were buried for 2.5 years and retrieved every six months to assess viability, only *S. mauritianum* maintained 100% germination (Fig. 5.4). Seeds of the remaining species exhibited a decline in viability over time, with all species exhibiting the lowest viability at the end of the burial period (T5: 30 months in Fig. 5.4). *Ricinus communis* had a slight increase at between 12 and 18 months, with a decline thereafter. Except for *S. mauritianum*, there were significant differences between initial and final viability in all species.

Additionally, the GLM applied to model germination vs. burial time indicated that viability decreased significantly ($P < 0.001$) over time for all species except for *S. mauritianum*, independently of the three types of logistic link functions used to fit the sigmoidal trends that are characteristic of seed longevity. However, the rate of this decline differed across the four species in which viability was lost over time. In terms of ageing rates (based on slopes of the GLM, see Table 5.2 for probit link function), there were no significant differences between *S. didymobotrya* and *C. indica* (P = 0.23); however, there were significant differences (P < 0.001) in ageing rates between *R. communis* and *M. azedarach*, and other species (*C, indica* and *S. didymobotrya*). Interestingly, while *R. communis* ageing rates (slopes) were significantly different to other species, the trends observed for this species were inconsistent: viability increased from 0 to three months, dropped rapidly from three to six months, increased in month 18, and then dropped again. Ageing rates based on P50 (Table 5.2) indicated that, among the species that showed viability decline over time, *C. indica* had the highest longevity (11.96 months), while *M. azedarach* had the lowest (4.71 months). Longevity was similar for *R. communis* (9.56 months) and *S. didymobotrya* (9.29 months).

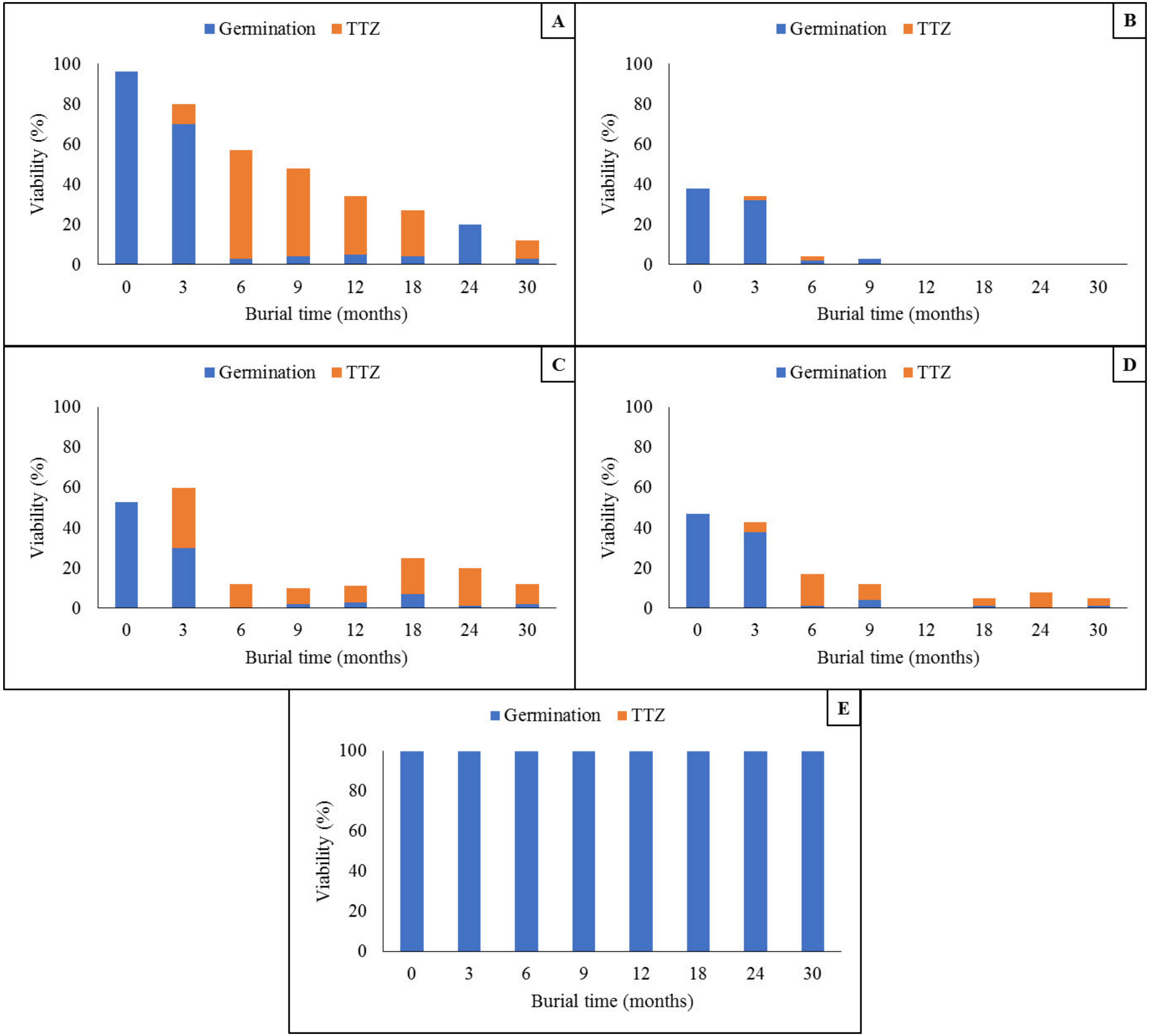
A
B
C
D
E
Germination
TTZ
Viability (%)
Burial time (months)
0
20
40
60
80
100
0
3
6
9
12
18
24
30

Figure 5.3: Stacked bars depicting the change in seed viability: germinated and non-germinated seeds that stained positively (TTZ) over burial time (months). A – E represent the five study species: A = *Canna indica*, B = *Melia azedarach*, C = *Ricinus communis*, D = *Senna didymobotrya*, E = *Solanum mauritianum.* Significant differences ($P < 0.05$, Kruskal Wallis) within species across time were identified.

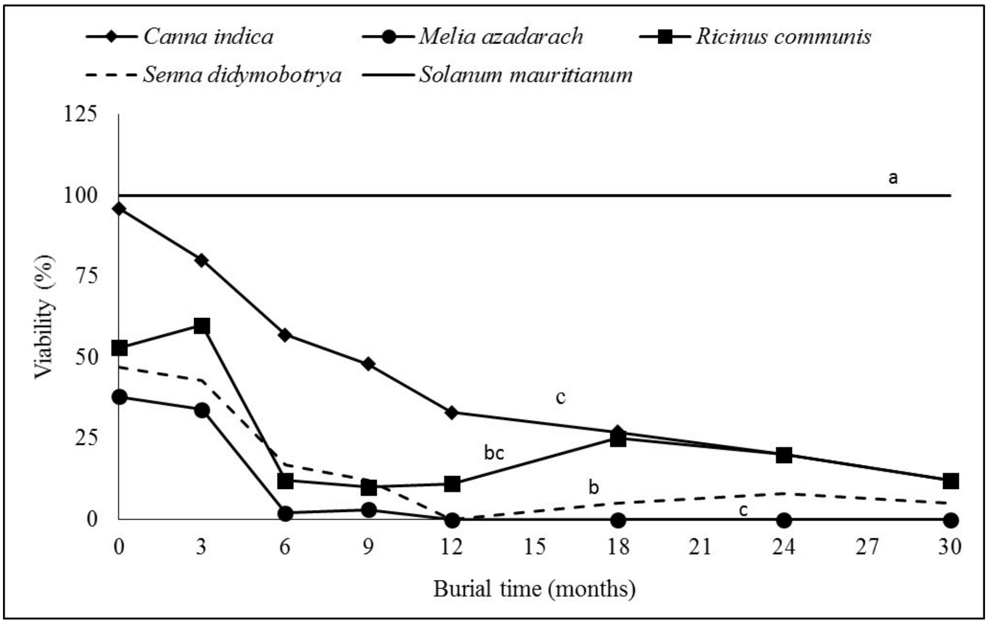

Figure 5.4: Viability percentage for buried seeds of the species investigated, assessed at 3/6 months intervals. Values represent the mean ± SD of four trials of 25 seeds each. Standard deviations ranged from 0 – 26.11. $P < 0.05$ for all species (excluding *S. mauritianum*) when initial and final germination values were compared within species.

Table 5.2: Slopes and P50 values calculated from GLM using probit as a link function.

Species	Slope	P50 (months)	Lower 95%	Upper 95%
Solanum mauritianum	*	*	*	*
Ricinus communis	-0.055 ± 0.005[a]	9.56 ± 0.89	7.75	11.22
Canna indica	-0.083 ± 0.006[b]	11.96 ± 0.61	10.79	13.15
Senna didymobotrya	-0.089 ± 0.006[b]	9.29 ± 0.63	8.05	10.50
Melia azedarach	-0.526 ± 0.05[c]	4.71 ± 0.18	4.36	5.07

*Slope was zero and P50 was not calculated as there was no significant decrease over time. Different letters indicate that slopes are significantly different at the 0.05 level in the GLM.

5.3.3. Changes in seed lipid thermal profiles during seed burial

Estimated lipid contents were obtained from the enthalpy of melting of the DSC scans run on freshly harvested seeds. *Melia azedarach*, *R. communis* and *S. mauritianum* had relatively high oil contents compared with *C. indica* and *S. didymobotrya*, as estimated by the enthalpy of lipid meting from the DSC scans (Table 5.3). Among the species with high oil contents, values were significantly highest for *M. azedarach*, followed by *S. mauritianum* and *R. communis*, while *S. didymobotrya* and *C. indica* had significantly lower oil contents (Table 5.3). The DSC melting scans and the onset of the lipid melting specifically suggested that the predominant fatty acids (Table 5.3) as reported in literature were linolenic in *M. azedarach* (Bachheti et al., 2012), *C. indica* and *S. didymobotrya* (Ballesteros and Walters, 2007), oleic in *S. mauritianum* (Jarret et al., 2016), and ricinoleic in *R. communis* (Huang et al., 2015).

Burial time not only affected seed viability, but also changed their physico-chemical properties. In terms of the thermal fingerprint of the storage lipids, all species (excluding *S. mauritianum*) showed decreases in germination over time accompanied by changes in the enthalpy of melting of the lipid, the temperature of the lipid melt, or both. For example, *M. azedarach* showed a change in the thermal fingerprint and the temperature of the lipid melting transitions, moving from one single peak with the onset at about -35 ºC in the non-buried seeds to two distinctive peaks, one with onset at -36.0±0.2 ºC a second with onset at -12.7±0.5 ºC. However, the total melting enthalpy of the lipid signal did not change over time, suggesting that while total lipid content did not change, the composition of the lipid TAG changed, most likely from predominantly linolenic (Table 5.3) to a mixture of linolenic and oleic based on the onset temperatures of the double peak signatures (estimations made after Ballesteros and Walters, 2007). The lipid melting signal of *R. communis* seeds changed over the storage time with the main peak detected at -47.8±0.3 ºC in unaged seeds with a progressive move to -51.5±0.6°C in seeds buried for nine months. The small change detected in the melting peak temperature of *R. communis* could not be related to any different fatty acids. *Senna didymobotrya* and *C. indica* seeds had very low lipid contents and no significant changes were observed in their enthalpy of melting or melting temperature.

Table 5.3: Estimated initial lipid content and predominant fatty acid of fresh seeds.

Species	Initial estimated lipid content (%)	Initial predominant fatty acid
Ricinus communis	17.0±1.0 [c]	ricinoleic
Solanum mauritianum	23.0±2.0 [b]	oleic
Canna indica	6.0±1.0 [d]	linolenic
Melia azedarach	35.0±1.0 [a]	linolenic
Senna didymobotrya	1.0±0.4 [e]	linolenic

Values represent mean ± SD (n = 5) and superscript lettering represents significant differences (*P* < 0.05, t-test) within parameters, across species. See Table D1, Appendix D for additional data.

The change in the lipid thermal fingerprint was particularly evident in seeds that were necrotic, as in *S. didymobotrya* and *R. communis* seeds, in which the lipid peak was barely detectable except for a small peak at about -80 ºC in *R. communis* that cannot be related to any known fatty acid. The changes in the lipid melting were also observed in the enthalpy of the lipid melting peak for some species. For example, in *R. communis*, the enthalpy of the lipid melting peak significantly decreased from 15.3±0.3 mJ g^{-1} DW to 10.6±0.8 mJ g^{-1} DW over the whole burial time ($P < 0.05$), indicating that the lipid content decreased from 17% to about 12%. Similarly, enthalpy of melting and temperature of the lipid signal decreased (although not significantly) over burial time for *C. indica* embryos. Along with a lack of viability over time, *S. mauritianum* melting signal did not change over the burial time, which was considered short (i.e. three months).

5.4. DISCUSSION

5.4.1. Seed longevity patterns (ageing) during burial

Freshly harvested seeds of *S. mauritianum* and *C. indica* seeds ranked highest (statistically comparable) in terms of viability, with viability in the remaining species being significantly lower. Perhaps one of the most important findings of the study was that whilst *S. mauritianum* retained a 100% viability throughout the two-year burial period, the other four species lost viability over time but at differential rates. Viability in *C. indica*, *R. communis* and *S. didymobotrya* viability was dominated by germinable seeds before burial, but as viability declined with an increase in burial time, viability was dominated by seeds that were not germinable but stained positively. These results are similar to studies that showed the retention of viability but a decline in germinability in seeds of invasive alien species within soil SBs (Costea et al., 2005; Holmes et al., 2005; Marchante et al., 2010). The extreme ends of this continuum of SB longevity were occupied by *C. indica* (11 months) and *M. azedarach* (4 months). The current study found that P50 values and seed mass had the same species ranking order (viz. *C. indica, R. communis, S. didymobotrya, M. azedarach,* and *S. mauritianum*- seed mass only), suggesting that seed mass is linked with the ageing rate of seeds, while other studies have reported a weak, but significant positive correlation between seed mass and P50 (Merritt et al., 2014). Interestingly, *C. indica* had the highest seed mass and the thickest seed coat, while *M. azedarach* had the second-lowest seed mass and seed coat thickness. Even though this is a comparative study, it examined a very limited number of species, with *S. mauritianum* being an exception as it is the smallest seed in size, the lightest in weight, and has the thinnest seed coat. The small number of species used does not allow for the confirmation of whether or not endospermic seeds across IAPs have lower seed longevity compared with non-endospermic seeds (Probert et al., 2009).

Results also suggested that estimated lipid content is not related to ageing rate, as it occurred with other comparative seed longevity studies based on 195 (Probert et al., 2009) and 276 (Walters et al., 2005a) species. Some studies have suggested that the high oil content of seeds of species such as *R. communis* makes them more prone to deterioration (Drumond et al., 2019). However, the current study cannot establish any relation between oil content and ageing rates, as species with the highest oil contents in this paper (>15%) showed both the highest (*S. mauritianum*) and the lowest (*M. azedarach*) P50. The relation of the TAG composition in ageing rate is not completely clear due to the small number of species used. Still, apparently, the species with the higher longevity (*S. mauritianum*) presented a monounsaturated fatty acid predominantly with the highest melting temperature (oleic). In contrast, the other species showed polyunsaturated fatty acids (linolenic) or monounsaturated fatty acids with very low melting temperatures (ricinoleic).

5.4.2. Morphological and anatomical traits aiding in IAPs seed longevity

Typical seed traits of IAPs are greater seed size, rapid germination rates, and the ability to germinate and grow faster than their indigenous (and non-native) counterparts (Graebner et al., 2012). Seeds of some species in the study are produced in high numbers and are generally small in size aiding in dispersal and seed burial. Seeds of these species do not need to be physically removed from their exocarp in order for them to be buried for germination. The current study found similar results where seeds of *M. azedarach* and *S. mauritianum* germinated during the burial period even though they were still enclosed within the fruit upon burial. *Melia azedarach* seeds are encased in fruit containing a hard endocarp and are known to germinate whether in or out of the fruit (Voigt et al., 2011). *Solanum mauritianum* seeds are found within soft fleshy fruit, and even though seeds are dispersed by frugivores, germination success in this species does not depend on frugivorous digestion, and it does not require the fruit pulp to be removed (Jordaan and Downs, 2012). The remaining three species required seeds to be removed from their fruits (capsules/pods/legumes) for germination; however, germination can be difficult because of impermeable seed coats (Souza Filho et al., 2011). *Ricinus communis* capsules dehisce and release seeds from within (Perdomo et al., 2013), making the process of seeds detaching from the parent plant and falling into the soil easier. Seeds of *Canna indica* are round and small and require scarification prior to germination due to impermeable seed coats (Souza Filho et al., 2011). *Senna didymobotrya* contain 9 – 16 seeds per pod/legume and are flattened oblongoid seeds (Orwa et al., 2009; Jeruto et al., 2017), which are easy to bury beneath the soil due to their lightweight (third lightest seed in the current study).

Seed bank persistent seeds have been positively correlated with seed mass and seed coat thickness (Davis et al., 2008; Gardarin et al., 2010). Persistence has also been found to be influenced by seed shape (Thompson et al., 1993; Honda, 2008); small and spherical seeds enter the soil easier and have a higher persistence than other seeds (Thompson et al., 1993). This is supported in the current study by the results obtained for *C. indica,* which is rounded in shape, had a high seed mass, a thick seed coat, and had the highest seed longevity compared with the four other species (except *S. mauritianum*). While the results for *S. mauritianum* appear to be contradictory (smallest in size and lightest in weight) to the relationship between seed mass and longevity in the current study. However, seeds of the remaining study species decreased in viability and had higher seed size and mass compared with *S. mauritianum*. Small-seed species being more likely to bury deep within the soil (> 3 cm), allowing them to escape being cleared (alien clearing programmes) from top-layer soils or other land disturbances, and they are insulated from germination initiation (Brits, 1986; Pierce and Moll, 1994). Studies report that small seeds survive deep within the soil as there are insufficient resources at those depths, and under dense alien stands, there is a higher chance of finding viable seeds deeper in the soil than close to the surface (Baskin and Baskin, 1988; Bond et al., 1999; Cheib and Garcia, 2011). However, it is worth noting that even though *R. communis* and *C. indica* had decreasing viability over time, *C. indica* seeds were still intact after each burial period, and this could be due to persistent seed traits mentioned above.

The seed coat of *C. indica* is impermeable to water due to silica, callose, lignin and lipids in the upper and lower seed coat layers, respectively (Graven et al., 1997). However, *R. communis* seeds have fairly thick seed coats permeable to water allowing some seeds to germinate within the soil, while other seeds became necrotic or were eaten during burial periods. Apart from the author's unpublished observations of mucilage around *S. mauritianum* seeds in the current study, there are no such reports in the literature making it difficult to confirm whether or not the seed coat and its associated mucilage is a protective mechanism against predation and/or seed mortality. However, seeds of a close relative of the species, *S. indicum* L., have a mucilaginous coating that protects the seed from desiccation and promotes germination by acting as a source of moisture (Ahmed et al., 2017). Similarly, the mucilage layer of *S. mauritianum* seeds, if present, could offer protection from seed coat desiccation and predators. Seed coat thickness, like mass and size across species, showed significant differences across species. Most of *M. azedarach* seed coats were found empty (no endosperm or embryo present) upon excavation, while some of *S. didymobotrya* seeds were found to have germinated within the SB during the burial experiment. However, *S. mauritianum* seeds were found intact across all excavation periods with no visible signs of seed coat deterioration or germination. Several studies have found a negative relationship between seed coat thickness and seed mortality (e.g. Gardarin et al., 2010), which is opposite to results in the current study. These results suggest that seed persistence in the SB may not strictly be linked to morphological traits such as size and shape, as well as seed coat thickness, particularly when different soil types and climates are studied. Different soil types and from different climatic regions will have different moisture contents within the soil, and wetter soil with warmer temperatures will most likely soften the seed coat and allow for predation to occur. High temperature, humidity and moisture in storage speeds up the deterioration of seeds which reduces their longevity (Marcos Filho; 2015; Drumond et al., 2019). Therefore, seed coat exclusively may not be related to seed longevity in the soil.

Empty seed coats (without the endosperm and embryo) for *R. communis* and *M. azedarach* can be due to germination (author personally observed roots upon exhumation) or predation; however, this was beyond the scope of the study to explore this in detail. In *R. communis*, viability declined dramatically beyond 3 months; however, there was a slight increase in germination between 12 and 18 months. Studies report that the elaiosome of these seeds have inhibitory substances for germination, which imposes dormancy (Lagoa and Pereira, 1987; Martins et al., 2009). When seeds fall onto the soil, the elaiosome is said to rot away and separates from the seed, which ends the dormancy period of the seed (Martins et al., 2009). The slight significant increase in viability (germination + positively stained seeds) for month 18 appears to have been associated with a relatively greater proportion of germinable seeds than the burial time preceding and following it. Therefore, all we can assume is that differences in wetting and drying events across the burial sites could have led to slight differences across samples in the rate at which the elaiosome rotted away.

5.4.3. Changes in seed lipid thermal profiles in the soil seed bank

Estimated lipid content from DSC scans was highest for fresh seeds of *M. azedarach* and lowest for fresh seeds of *S. didymobotrya*. The predominant fatty acids for all study species were consistent with those fatty acids reported in the literature, with a predominant composition of unsaturated fatty acids (e.g. Bachheti et al., 2012; Yusuf et al., 2015; Huang et al., 2015; Jarret et al., 2016; Okonwu and Ariaga, 2016). Unsaturated fatty acids, although a great source of energy for germination, are more prone to deterioration through lipid peroxidation than saturated fatty acids (Drumond et al., 2019). All unsaturated fatty acids found in fresh seeds of the current study are prone to deterioration, especially for species with high lipid contents mainly formed of polyunsaturated fatty acids (linolenic), such as *M. azedarach* and *R. communis*, which had the lowest P50 values. Therefore, even though these species can have the ability to be invasive in new environments, their lipid contents still deteriorated over time, causing a decrease in their longevity, e.g. *M. azedarach*. With decreases in germination over time for *C. indica*, *R. communis*, *M. azedarach*, and *S. didymobotrya* there were also changes in either/both enthalpy of melting of the lipid, and the temperature of the lipid melt, suggesting different deterioration patterns are species-specific. For example, for *M. azedarach* seeds, DSC scans show changes in linoleic and oleic fatty acids content when buried seeds are compared with freshly harvested seeds, with no changes in enthalpy of melting.

This increase in oleic and decrease of linoleic over time suggest a chemical transformation of the fatty acid as the seed is ageing, which is possible through the oxidation cycle (Scarth and McVetty, 1999). Linoleic acid may have decreased, showing an increase in oleic acid due to increases in soil temperature (Canvin, 1965) during summer periods. On the other hand, DSC scans for *R. communis* show a significant decrease in the enthalpy of melting while the changes in the melting temperature are not very large, suggesting a decrease in oil content or a change in the freezing/melting characteristics due to ageing (Vertucci, 1992). For *S. mauritianum*, its retention of 100% viability over burial time could be related to the limited change in the melting signal over the first three months of burial, but this species will have to be subjected to DSC analysis for much longer periods in order to confirm this. What is clear though, is that invasive species such as *S. mauritianum* and *C. indica* will pose a great threat to indigenous vegetation given their ability to persist within the soil.

5.5. CONCLUSION

Invasiveness of plant species is frequently associated with rapid spread and the high production of seeds that can persist in the soil for long periods, and seed traits are linked to SB persistence. In the current study, the number of intact buried seeds decreased over time, and intact seeds showed low viability after two and a half years of being buried. The decline in viability over time in *C. indica*, *R. communis*, and *S. didymobotrya* was associated with a decline in germinability. While the decline in viability was most rapid in *M. azedarach*, the majority of seeds that remained viable were germinable. However, seeds of *S. mauritianum* retained 100% viability in the soil throughout the burial period, though some seeds were lost entirely to predation/disintegration (for DSC analyses). The results suggest that variable combinations (species-specific to an extent) of morphological and anatomical (viz. seed mass, shape and seed coat thickness) and chemical (lipid thermal profiles) traits do appear to influence SB longevity in IAPs. The total number of species studied was also low, but this represents what is believed to be the first comparative study on the relationship between seed physico-chemical traits of IAPs and natural SB longevity. The low number of species and traits studied and/or the phenotypic plasticity associated with seed post-harvest physiology in wild species may explain the absence of significant relationships between the seed physical and/or chemical traits and seed bank longevity using the traits investigated. Nevertheless, the results suggest of the five IAPs investigated, all of which produce large numbers of seeds (R-strategy species), all except *S. mauritianum* formed persistent short-lived seedbanks (viability approximately one year). This is concerning since *S. mauritianum* is an established invasive or emerging as an invasive at a global scale. The results suggest that IAP clearing programmes need to consider seed traits, such as seed bank persistence, when prioritising species for control, timing alien clearing efforts and deciding on the frequency of monitoring for secondary invasions at cleared sites. The study has yielded the beginnings of a conceptual continuum of SB longevity for IAPs, with *S. mauritianum* representing longest-lived and *M. azedarach* the shortest-lived. A continuum of seed behaviour is a means of placing a number of species in a sequential order to show the progression in the expression of a trait (e.g.

desiccation tolerance [see Berjak and Pammenter, 1994]). The range of the continuum is defined by the extremes, i.e. the highest and lowest level of expression of the trait. However, the value of the continuum as a tool increases as the number of species that it is populated with increases. A continuum such as the one proposed here, once populated with more species, could help practitioners involved in IAP control by serving as an additional criterion for categorising species in terms of invasiveness.

CHAPTER 6

Synthesis of findings, limitations, recommendations and overall conclusions

6.1. Introduction

Biological invasion is a major influence in the Anthropocene's biodiversity crises (Rai, 2015), i.e. the era in which anthropogenic activity drives climate and environmental change (van Wilgen et al., 2020a). This activity and, to a certain extent, climate change has affected plant invasions (Rodriguez-Merino et al., 2018). Limited implementation of ecological restoration programmes (well documented in the literature [Gaertner et al., 2012; Holmes et al., 2020]), in light of limited resources such as funding (Holmes et al., 2020) have exacerbated the threats posed by alien plants. Although numerous efforts to clear alien plants and/or to mitigate their effects have been initiated globally, these invasions remain largely unabated. At a global scale, the increases in the number of alien species have not shown any indication of reaching a saturation point, with some invasive taxa showing higher rates for alien species in recent times compared with earlier recordings (Seebens et al., 2017). It should be noted, though, that were it not for the implementation of legislation to reduce the threat to biodiversity posed by alien invasion, the number and impact of alien species would have been much worse over the past century (Seebens et al., 2017).

Invasion biology has therefore emerged as a discipline of global importance over the last few decades with many studies investigating this problem at temporal (Müllerová et al., 2017) and spatial (Vaz et al., 2018) scales, and in a range of habitat conditions (e.g. pristine [Nxele, 2012; Janion-Scheepers and Griffiths, 2020] to highly transformed [Potgieter et al., 2020] and types (e.g. forest [Dyderski et al., 2019], grassland [Czarniecka-Wiera et al., 2020]). This research has shown that alien plant species enter non-native habitats where they can become naturalised and, in some cases, invasive, which is when they affect indigenous species, transform habitats and affect ecosystem functioning (Didham et al., 2005; Le Maitre et al., 2020; Zengeya et al., 2020).

South Africa, harbouring three global hotspots, is particularly susceptible to the problem of IAPs entering natural vegetation (Zengeya et al., 2020). As levels of urbanisation increase across the country, the increasing prevalence of aliens in rapidly developing cities (Boon et al., 2016) is becoming an increasingly concerning phenomenon. The present study characterised the prevalence of alien plant species in one such area (viz. eThekwini Municipal Area [EMA]) in South Africa. Most importantly, the study area is located within the Maputaland-Pondoland Albany (MPA) hotspot, which allowed for useful comparative analyses between indigenous and alien species within urban green spaces.

In recent years there has been a growing interest in understanding plant invasions within urban environments in South Africa (Mavimbela et al., 2018; van Wilgen et al., 2020b; Appalasamy et al., 2020) and globally (Kühn et al., 2017; Cadotte et al., 2017). This research has collectively highlighted the need to assess the prevalence of alien invasive species in relation to anthropogenic disturbance and climate change and develop methods to quantify the risk they pose to indigenous species systematically. This was the rationale behind the current study, which using a subtropical urban matrix in South Africa as a case study aimed to contribute to the design of an evidence-based framework (Figure 6.1) for prioritising urban green spaces and alien species within them for monitoring and control by:

- Developing a spatial approach to identifying non-indigenous floristic hotspots by integrating data on floristics and levels of non-natural disturbance;
- Comparing alien and indigenous floristic ordering, plant diversity (alpha and functional), and co-occurrence patterns in relation to levels of non-natural disturbance;
- Assessing the effects of non-natural disturbance on alien and indigenous seed bank (SB) floristics;
- Try to identify potential seed physical and/or chemical indicators of SB persistence in five IAPs.

There are various policies and frameworks in place in the EMA, such as Legislative ad Policy Framework governing IAP Control (Conservation of Agricultural Resources Act No. 43 of 1983 [CARA], National Environmental Management: Biodiversity Act No. 10 of 2020 [NEMBA], eThekwini Municipality Framework Strategy and Action Plan for the control of Invasive Alien Species). The eThekwini Municipality framework was put together by the Environmental Planning and Climate Protection Department (EPCPD) in 2011 in response to Chapter 5, Section 76(2)(a) of NEMBA (Terblanche et al., 2013). The strategy and action plan aims to direct invasive alien species control in the EMA towards achieving quick and more efficient outcomes and sets targets that can be measured and assessed. The guideline for IAP control includes planning and preparation.

Planning around IAP control focusses on areas that are surveyed to be cleared and are based on the following guiding principles in terms of implementation (Terblanche et al., 2013):

(1) Areas of IAPs posing fire risks to houses or infrastructure should be targeted as priority;

(2) Riparian areas are a priority for IAP clearing projects;

(3) Moderate to low IAP infestation in wetland areas are treated by implementing controlled burning and is followed by mechanical removal;

(4) Indigenous vegetation located amongst IAPs must be protected during the clearing process;

(5) Large alien trees used for aesthetic or functional purposes must be removed in a phased approach;

(6) Invasive trees away from structures can be ring-barked or poisoned and left;

(7) To prevent soil erosion on steep slopes, horizontal contours must be applied;

(8) On gentle gradients, clearing should start from the outside of an area inwards;

(9) Disposal of IAP material must be dealt with carefully.

Preparation involves determining whether the land is municipal-owned or not, the procurement and safe storage of herbicides, equipment, personal protective equipment (PPE), the setting up of camps for workers, and necessary training for all workers. Planning and preparation are followed by budgeting, control methods, post-removal, follow-up, rehabilitation and monitoring.

While the guiding principles for operationalising IAP control are relatively well established, frameworks for monitoring and prioritising sites and alien species for control are not as refined, and there are challenges of them not being equally effective at different geographic scales and across different habitats. Furthermore, these frameworks often also suffer the weakness of not capturing the multi-dimensionality of plant invasiveness, the direct and indirect effects of anthropogenic activities, the natural and imposed heterogeneity of landscapes, the potentiality for alien-indigenous plant interactions and the relationship between the standing vegetation (SV) and natural SBs. Evidence-based frameworks for prioritising sites and species for alien plant control, particularly within urban areas, can, therefore, supplement and aid existing EMA policies/guidelines for alien plant by preceding their planning and preparation phases, or it may help in developing new approaches to monitoring alien plant species in urban spaces.

6.2. Findings, limitations, recommendations

The methods, findings and recommendations that emerged from the investigations conducted as part of this study were synthesised to produce an evidence-based framework (Fig. 6.1) for prioritising urban green spaces and IAPs within them for alien monitoring and control. The most important findings from the study were brought together with current thinking (e.g. Foxcroft et al., 2011; Gaertner et al., 2016) around IAP monitoring and control to produce a collection of steps that, if attempted using a logical progression approach, can assist practitioners, land managers and researchers in prioritising sites and species for alien plant control. The spatial and relational arrangement of the various areas of investigation and methodological approaches incorporated in the framework (and the current study) show how these can be brought together to generate a holistic understanding of how to approach the monitoring of alien plant prevalence, indicators and drivers, and the impacts and risks they pose (Gaertner et al., 2016). The combination of status, impacts, and indicators most applicable to a particular city or region will be dependent on the human, financial and scientific resources available but should in all cases form the basis of management interventions focused on IAP control and biodiversity conservation.

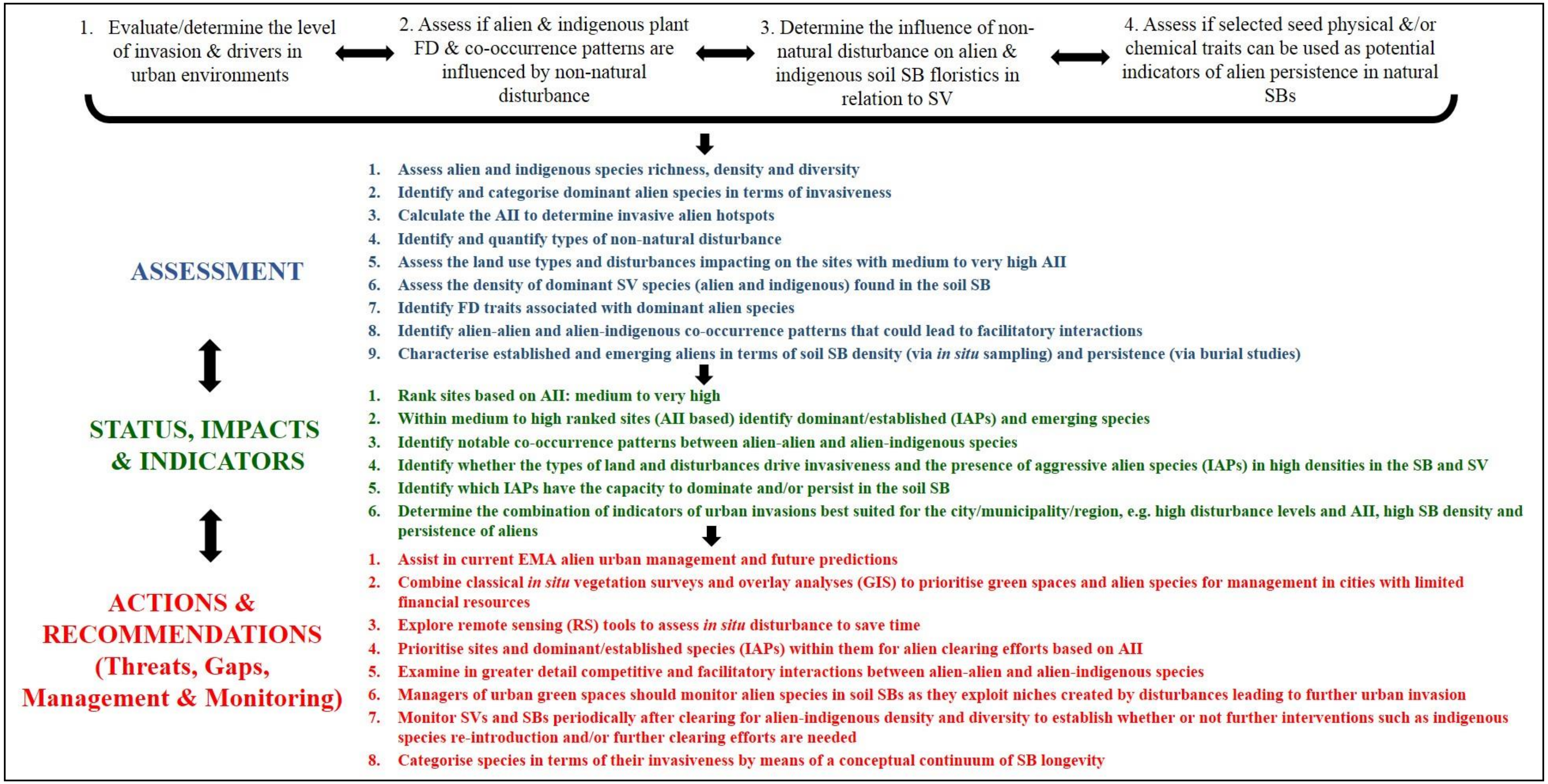

Figure 6.1: A proposed framework for prioritising urban green spaces and alien species within them for monitoring and control interventions. FD = functional diversity, SB = seed bank, SV = standing vegetation, AII = alien invasive index, IAP, invasive alien plant, EMA = eThekwini Municipality, GIS = geographic information systems, RS = remote sensing.

In terms of the specific findings of the current study, non-natural disturbance related to anthropogenic activity influenced species richness and density (Fig. 6.1). More specifically, levels of disturbance were positively related to invasive alien species richness **(Chapter 2)**. This disturbance was mainly in the form of illegal solid-waste dumping, footpaths, grazing, resource abstraction, and unplanned fires. These activities may explain why invasive alien species richness was higher closer to informal settlements in the urban matrix studied.

Perhaps one of the most important and novel outputs of the study was the development of an Alien Invasive Index (AII), which in integrating alien species richness and plant density, allows for the identification of invasive alien hotspots. Furthermore, the AII has the potential to identify emerging hotspots and has practical uses and implications for assisting alien control and management programmes. Importantly, levels of disturbance were significantly positively correlated with the AII developed **(Chapter 2),** which validates its use in areas exposed to anthropogenic disturbance.

However, there were several limitations to this aspect of the study. The urban green spaces investigated in this study represented a number of vegetation types and though an attempt was made to capture this diversity, sampling intensity across these vegetation types was unfortunately not comparable. This prevented rigorous comparisons among vegetation types and more robust conclusions about the potential relationships between IAPs and vegetation type within an urban matrix. Furthermore, disturbance levels could have been assessed multiple times during the study. However, the *in situ* assessment of disturbance is extremely time-consuming, and there may be a need to explore the use of remote sensing tools for this purpose. There is also room to further develop and refine the disturbance classification and measurement instrument developed in the present study (see Table A2, Appendix A).

The investigation described in **Chapter 3** explored how alien species could be potentially interacting with indigenous species in an urban matrix and patterns between their diversity and co-occurrence. Alpha diversity differed between alien and indigenous species; alpha diversity was significantly positively related to indigenous species richness and significantly negatively related to alien species richness. Functional diversity was strongly related to disturbance (caused by anthropogenic activity). Alien plant species were more functionally diverse than indigenous plant species, and alien plants co-existed with indigenous species at all sites. This co-occurrence could be attributed to facilitatory and/or increased susceptibility to invasion based on habitat- or species-specific characteristics. High alien-indigenous pairing frequencies suggest that certain indigenous species (e.g. *Centella asiatica*) could be facilitating the presence of IAPs (e.g. *Solanum mauritianum*); these observations are significant as they provide support for further research into how alien control programmes can reduce the potential for alien-indigenous facilitatory interactions. Overall, FD proved to be a valuable index to understand alien and indigenous functional interactions in urban green spaces exposed to environmental change and anthropogenic disturbances. Under a changing climate, interactions between alien and indigenous species will become an increasingly important consideration. The limitations in this aspect of the study included not examining the competitive and facilitatory interactions of alien and indigenous species inferred from the co-occurrence patterns observed. Future studies focussing on invasions in urban green spaces that examine these interactions are needed. A focused investigation on competitive and facilitatory interactions (or neutral interactions) amongst alien and indigenous species would have provided more insight into the floristic patterns that were observed at these sites and the role of species traits in shaping these. On this note, the number and categories of traits investigated were limited (most especially those related to reproduction), and this needs to be significantly increased in futures studies that aim to assess the utility of using changes in functional diversity to understand the relationship between disturbance and IAPs. One example of a species trait to consider is resource requirements, as other studies have found that alien and indigenous species are more likely to co-occur due to resource availability for growing conditions (Daehler, 2003).

The SB investigation featured in **Chapter 4** revealed higher alien species densities compared with indigenous species. This greater presence of alien species (including invasive) seeds within the SB could be based on the high reproductive outputs of alien species and seed morphological and anatomical traits that allow them to persist in the soil until a disturbance activity or event (e.g. clearing, grazing, footpaths) occurs. While level of disturbance was found to influence alien and indigenous floristic patterns in the SV (**Chapters 2** and **3)**, this has rarely been shown at the soil SB level, particularly in urban settings. Species identified within SBs of the EMA sites sampled were largely reflective of the SV. Results also indicated a higher richness of indigenous species than alien species and many herb and grass species as opposed to trees. There was high similarity between SBs and SV, and this occurred at sites with high and medium levels of disturbance as found in other studies in the general region (Bhugeloo, 2020). In the present study disturbance levels were strongly related to SB species richness and density. This suggests non-natural disturbance is likely to affect the SB mainly through its effects on the SV. In this regard, disturbance is likely to compromise the regeneration of indigenous flora within urban green spaces as high disturbance levels will promote the emergence and persistence of alien species. The study's limitations include – the limited time for which the soil SBs were left to germinate (one year only). Other studies have suggested longer germination periods, to factor in dormancy in some species, as well as sampling the persistent SB (Bhugeloo, 2020). A better understanding on SBs in undisturbed sites and more intensive and comparable levels of sampling across all vegetation types is required, and would serve as a benchmark for more robust comparisons with SBs from disturbed sites. Nevertheless, the results highlight the importance of considering the regeneration potential of a site and the potential for secondary invasions when urban green spaces are subjected to alien clearing. Importantly, the findings featured in **Chapter 4** highlight that disturbance not only influences SV but the SB as well. The findings of **Chapters 3 and 4** also highlight the need to consider both alien and indigenous floristics when surveying urban green spaces, as there are likely to be past, present and future interactions between these species sub-sets.

Finally, the seed longevity of five IAPs found to occur in the SV within the study area was investigated using burial studies **(Chapter 5)**. Seed longevity was related to selected morphological, anatomical and chemical traits. One of the species with small seeds and a thin seed coat (viz. *Solanum mauritianum*) exhibited 100% germination pre-burial, a high estimated lipid content, and 100% viability throughout the burial period. The high viability for *S. mauritianum* was most likely due to the presence of a protective mucilage layer surrounding the seed coat. While viability decline significantly with burial time in the other four species, there were inter-specific differences in terms of the rate of this decline. Also, while the viability of *C. indica*, *R. communis*, and *S. didymobotrya* was dominated by germinable seeds before burial, as viability declined with an increase in burial time, viability was dominated by seeds that were not germinable but remained viable. Interestingly, *Melia azedarach* differed slightly where viability declined with burial time, but the majority of the seeds that were viable remained germinable. As the viability potential of the seeds of four species decreased over time, the lipid composition of seeds of the respective species also changed, but this was not the case again with the relatively long-lived seeds of *S.*

mauritianum. *Solanum mauritianum* was the longest-lived species in the conceptual continuum developed, while *M. azedarach* was the shortest-lived species. This proposed continuum could help practitioners involved in IAP control by serving as an additional criterion for categorising species in terms of invasiveness. The low number of species and traits studied and/or the phenotypic plasticity associated with seed post-harvest physiology in wild species may explain the absence of significant relationships between the seed physical and/or chemical traits and seed bank longevity using the traits investigated. A major limitation of the current study was that the presence and type of dormancy associated with these species were not characterised. Secondly, germination rate of study species should have been recorded to assess whether the burial period affected seed vigour (i.e. the sum total of those properties of the seed which determine the level of activity and performance of the seed or seed lot during germination and seedling emergence). Finally, based on the lack of basic seed biology information for a number of important IAPs in SA and globally, these studies need to be extended to other IAPs that are found at high densities in the SV (**Chapters 2** and **3**) and the SB (**Chapter 4**). Seed germination experiments under different simulated climate change scenarios would also be beneficial as this can inform predictive models for plant invasion.

6.3. General recommendations

This study showed non-natural disturbance as one of the major drivers of IAPs in urban green spaces, and the results of **Chapters 2 and 3** collectively support those of other studies that have shown alien plant establishment to be promoted by disturbance related to anthropogenic activity (Hobbs and Huenneke, 1992; Celesti-Grapow et al., 2006). This highlights the need to assess and monitor non-natural disturbances across urban green spaces at regular intervals as changes (e.g. increased illegal solid-waste dumping, unplanned burning, resource abstraction and animal grazing) are common within urban areas but are also spatially heterogeneous. A quick and effective first step in reducing the impacts of non-natural disturbance would be the implementation of more controlled access to natural urban green spaces and more effective policing of illegal dumping and excessive resource abstraction. This should be accompanied by more systematic monitoring of IAP prevalence, as described in the framework (Fig. 6.1) presented here. This will, however, be challenging given the increasing prevalence of informal settlements and demand for grey infrastructure (human-engineered infrastructure) in urban areas throughout South Africa (McConnachie et al., 2008). South Africa is a signatory to numerous international biodiversity and climate change conventions, but the prioritisation of biodiversity conservation and control of invasions will prove even more challenging as the government tries to overcome the short- to medium-term fiscal strain of the COVID-19 pandemic (Ataguba et al., 2020).

In this regard, economically strained and resource-limited municipalities alien plant control efforts informed by the AII developed here could increase the efficacy of IAP management strategies. Increased knowledge of plant invasions in urban green spaces will also be beneficial when it comes to releasing biological agents into these areas. This, combined with remote sensing monitoring technology (Vaz et al., 2018) and community involvement (e.g. community based or citizen science clearing programmes [Atchison et al., 2017]), will contribute to more effective monitoring and control of IAPs. However, a factor to consider is that these approaches require substantial human capacity investment given the size and number of urban green spaces within municipalities such as the EMA. At present, the formal sector is understaffed and the informal community based/ citizen science sectors are under-represented.

The results of the present and a number of recent studies conducted within cities (e.g. Cape Town) argue for guidelines and policy development around plant invasions to focus at local, provincial and national levels to focus on urban green spaces since transformation and degradation within urban matrices promote biological invasions. In this regard, a national set of proposed indicators for biological invasions and their management was described by Wilson et al. (2018). A total of 20 indicators were proposed, and results from the current study speak to several of these: species (number and status of alien species, extent of alien species, abundance of alien species, and impact of alien species), and site: (alien species richness, relative invasive abundance, and impact of invasions) based indicators. The current study has also demonstrated how to practically use these indicators to assess plant invasiveness in urban contexts.

The current study admittedly focussed on a single localised urban scenario, and the local management of urban green spaces varies greatly in SA, ranging from municipalities that formulate their tailor-made management and monitoring guidelines and policies to those that largely lack this capability. The EMA is quite proactive in this context when compared to other local governments. However, their challenge is implementation and monitoring. Although this study has proposed a framework for prioritising sites and species for alien plant control in urban green spaces, other elements also need to be considered (e.g. role of fire, clearance programmes, social aspects etc.). However, the framework proposed will hopefully prompt local governments to review their existing alien invasion plant management strategies and use the framework as a basis for the development of more refined and/or context-specific versions thereof. The framework presented could also benefit from the addition of other dimensions of invasion biology (e.g. exploration of reproductive traits). Investigations on competitive and facilitatory behavioural patterns amongst alien and indigenous species could also be very informative and useful. Knowledge on these interactions will allow monitoring and clearing programmes to be proactive at sites in which facilitatory relationships are detected.

On this note, the National Status Report call for information on biological invasions, the extent and impacts, and the efficiency of current interventions to inform policy responses (Wilson et al., 2017). However, reporting is not standardised at the local level and furthermore does not discriminate among land-use types (e.g. urban green spaces versus rural green spaces). Standardised and more specific reporting would provide a more useful picture of the levels and impacts of invasion in urban green spaces at local scales.

This study also highlighted the need for more focused studies on soil SBs (**Chapter 4**) and the persistence of invasive alien seeds within the soil (**Chapter 5**). Due to time constraints of the current study, soil SBs were only left to germinate for one year; however, according to Walck et al. (2005), in order to factor in seed dormancy, longer germination periods are required for burial studies. In terms of how morphological, anatomical, and chemical traits influence alien plant seed longevity, the findings of the present study are novel, but future data on a much larger variety of species and life forms are needed for concrete conclusions. Apart from investigating the presence and mechanism of seed dormancy that exist in alien species, their susceptibility to seed rotting (necrosis) should also be considered before these burial studies are initiated. Lastly, due to time constraints, the current study could not visualise the lipids in the seeds studied (Mendiondo et al., 2014) using light microscopy. Staining of lipids and viewing via light microscopy will allow for the visualisation of lipid distribution in seeds, giving insight into the structural changes of lipids during the burial of these seeds, which can then be used to further understand the differential scanning calorimetry (DSC) results.

6.4. Concluding remarks

The current study set out to understand alien floristics, invasion hotspots, co-occurrence, seed banks and aspects of seed biology within an urban matrix in SA. It is becoming increasingly concerning that natural urban green spaces within rapidly developing parts of the country, such as the EMA, are being transformed at an alarming rate. These urban green spaces often harbour high numbers of alien species, with some identified as invasive alien hotspots in this study. While no estimates exist on the spatial cover of alien vegetation in the EMA, the extent and intensity of invasions are abundantly manifested in indirect ways – the cost and energy of alien clearance activities and the visual displays of alien prevalence when some species such as *Melia azedarach* and *Tithonia diversifolia* are in flower in the EMA. The hotspot areas need to be prioritised for alien control and restoration initiatives. The results suggest that if urban green spaces within the EMA do not have adequate control and restoration programmes in place, informed by systematic monitoring, alien species (particularly IAPs) will increasingly out-compete indigenous species. This threat cannot be ignored in rapidly developing municipalities since the data presented here and in a number of studies across the world suggest that IAPs are promoted by non-natural disturbances and are well represented across different vegetation types in both the SV and SBs. It is hoped that the evidence-based framework presented in this chapter can be used by the local and national government, service providers and practitioners to prioritise urban green spaces and species within them for alien monitoring and control. Tangible gains in controlling alien plant invasions are usually only evident after years of effort, but a multi-disciplinary research approach and multi-stakeholder buy-in (government agencies, scientists, industry and civil society) can fast-track the realisation of these gains.

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APPENDIX A – Chapter 2

Table A1. Durban Metropolitan Open Space System (D'MOSS) sampling sites in the EMA (n = 30).

Site	Coordinates	D'MOSS site size (m^2)	Altitude (m)	Vegetation	Disturbance (%)
1 [N]	29.775833˚S 30.982016˚E	162 052.98	70	forest	21
2 [N]	29.633137˚S 31.041872˚E	10 720.10	50	forest	34
3 [N]	29.674654˚S 31.041173˚E	94 712.95	41	thicket	30
4 [N]	29.601318˚S 31.162881˚E	47 966.80	82	forest	27
5 [N]	29.63739˚S 30.997569˚E	130 406.83	154	grassland	27
6 [N]	29.709505˚S 31.022083˚E	158 591.90	65	savanna	27
7 [E]	29.854141˚S 30.92904˚E	357 478.23	190	grassland	33
8 [E]	29.878098˚S 30.96719˚E	445 788.52	73	savanna	28
9 [E]	29.813038˚S 30.983766˚E	795 627.93	39	thicket	33
10 [E]	29.83509˚S 30.9659˚E	55 616.54	151	savanna	30
11 [E]	29.803127˚S 30.95092˚E	51 151.34	67	savanna	39
12 [E]	29.87892˚S 30.93368˚E	25 650.68	134	grassland	33
13 [S]	29.981046˚S 30.952393˚E	226 978.15	5	forest	33
14 [S]	30.072797˚S 30.861594˚E	330 889.92	52	forest	27
15 [S]	30.205156˚S 30.767718˚E	22 830.62	107	forest	33

16 [S]	29.9157˚S 30.96122˚E	1 008 501.00	90	savanna	30
17 [S]	29.93304˚S 30.88544˚E	257 774.69	145	savanna	24
18 [S]	30.03519˚S 30.81505˚E	92 753.56	156	thicket	30
19 [W]	29.72477˚S 30.657159˚E	549 339.94	721	savanna	26
20 [W]	29.755938˚S 30.749491˚E	533 740.73	700	savanna	30
21 [W]	29.713804˚S 30.626794˚E	759 656.32	792	grassland	27
22 [W]	29.827809˚S 30.761357˚E	974 340.30	540	forest	36
23 [W]	29.805633˚S 30.63534˚E	263 678.94	620	savanna	26
24 [W]	29.653431˚S 30.809158˚E	415 771.10	160	thicket	22
25 [C]	29.794028˚S 30.883552˚E	46 655.27	316	savanna	47
26 [C]	29.887731˚S 30.852797˚E	558 127.09	276	forest	28
27 [C]	29.773802˚S 30.80375˚E	27 626.27	527	grassland	23
28 [C]	29.89303˚S 30.84582˚E	144 156.95	273	savanna	27
29 [C]	29.816769˚S 30.817688˚E	43 122.11	406	grassland	27
30 [C]	29.86421˚S 30.83587˚E	724 784.92	214	savanna	22

Superscript lettering ([N, E, S, W, C]) represents the five sectors of the EMA.

Table A2. Scoring matrix used to quantify the level of disturbance at each site.

Type of disturbance		1	2	3	4	5
	Replicate 1					
Footpaths and trampling	Replicate 2					
	Replicate 3					
	Replicate 1					
Livestock browsing (browse line or damage to foliage)	Replicate 2					
	Replicate 3					
	Replicate 1					
Wood harvesting (stumps left behind)	Replicate 2					
	Replicate 3					
	Replicate 1					
Agriculture (presence of planted/harvested fields)	Replicate 2					
	Replicate 3					
	Replicate 1					
Resource abstraction (soil, water, stones)	Replicate 2					
	Replicate 3					
	Replicate 1					
Solid waste (dumping)	Replicate 2					
	Replicate 3					
Effluent (storm water, urban, industrial)	Replicate 1					

	Replicate 2
	Replicate 3
	Replicate 1
Recent burning (planned, unplanned)	Replicate 2
	Replicate 3

43

44 **Table A3.** Alien taxa found in D'MOSS sites of the EMA surveyed in this study.

Invasive category	**Family**	**Species**	**Invasive* (X)**	**Life cycle: Annual/Perennial**	**Life form**
Category 1b	Anacardiaceae	*Schinus terebinthifolius* Raddi.	X	P	Tree
	Apocynaceae	*Catharanthus roseus* (L.) G.Don	-	P	Herb
	Asteraceae	*Ageratum conyzoides* L.	X	A	Herb
	Asteraceae	*Chromolaena odorata* (L.) R.M.King & H.Rob	X	P	Shrub
	Asteraceae	*Montanoa hibiscifolia* Benth.	X	P	Shrub
	Asteraceae	*Parthenium hysterophorus* L.	X	A	Herb
	Asteraceae	*Sphagneticola trilobata* (L.) Pruski	X	P	Herb
	Asteraceae	*Tithonia diversifolia* (Hemsl.) A.Gray	X	A/P	Shrub
	Asteraceae	*Xanthium strumarium* L.	-	A/P	Herb
	Bignoniaceae	*Tecoma stans* (L.) Juss. Ex Kunth	X	P	Shrub
	Cactaceae	*Opuntia stricta* (Haw.) Haw.	X	P	Shrub
	Cactaceae	*Pereskia aculeata* Mill.	X	P	Shrub/Climber
	Cannaceae	*Canna indica* L.	X	P	Herb
	Commelinaceae	*Tradescantia fluminensis* Vell.	X	P	Creeping herb
	Convolvulaceae	*Ipomoea alba* L.	X	A	Herbaceous climber
	Convolvulaceae	*Ipomoea indica* (Burm.f.) Merr.	X	P	Climber

Convolvulaceae	*Ipomoea purpurea* (L.) Roth	-	P	Climber
Fabaceae	*Albizia lebbeck* (L.) Benth.	X	P	Tree
Fabaceae	*Mimosa pigra* L.	-	A	Shrub
Fabaceae	*Senna didymobotrya* (Fressin.) H.S.Irwin & Bameby	X	A/P	Shrub/Tree
Fabaceae	*Senna hirsuta* (L.) H.S.Irwin & Bameby	-	A/P	Shrub
Fabaceae	*Senna septemtrionalis* (Viv.) H.S.Irwin & Barneby	X	P	Shrub/Tree
Lamiaceae	*Plectranthus barbatus* Andrews	X	P	Herb
Lauraceae	*Litsea glutinosa* (Lour.) C.B.Rob.	X	P	Tree
Malvaceae	*Malvastrum coromandelianum* (L.) Garcke	-	A	Shrub
Meliaceae	*Melia azedarach* L.	X	P	Tree
Myrtaceae	*Psidium guineense* Sw.	X	A	Shrub/Small tree
Nephrolepidaceae	*Nephrolepis cordifolia* (L.) C.Presl var. *cordifolia*	X	A/P	Fern
Passifloraceae	*Passiflora suberosa* L.	X	P	Climber
Passifloraceae	*Passiflora subpeltata* Ortega	-	P	Climber
Phytolaccaceae	*Rivina humilis* L.	X	P	Herb
Rosaceae	*Rubus cuneifolius* Pursh	X	P	Shrub
Sapindaceae	*Cardiospermum grandiflorum* Sw.	X	A	Herb
Solanaceae	*Datura stramonium* L.	X	A	Herb

	Solanaceae	*Solanum mauritianum* Scop.	X	A	Small shrub/Tree
	Verbenaceae	*Lantana camara* L.	X	P	Shrub
	Verbenaceae	*Verbena bonariensis* L.	-	A/P	Herb
	Verbenaceae	*Verbena brasiliensis* Vell.	-	A/P	Herb
	Verbenaceae	*Verbena officinalis* L.	-	P	Herb
Category 2	Euphorbiaceae	*Ricinus communis* L.	X	P	Shrub
	Fabaceae	*Acacia mearnsii* De Wild.	X	P	Tree
	Fabaceae	*Leucaena leucocephala* (Lam.) de Wit	X	P	Shrub/Tree
	Salicaceae	*Populus* x *canescens* (Aiton) Sm.	X	P	Tree
Category 2/3	Myrtaceae	*Psidium guajava* L.	X	P	Shrub/Small tree
Category 3	Verbenaceae	*Duranta erecta* L.	X	P	Shrub/Tree
Naturalised exotic	Euphorbiaceae	*Euphorbia cyathophora* Murray	-	A	Herb
	Euphorbiaceae	*Euphorbia hirta* L.	-	A	Herb
	Fabaceae	*Desmodium incanum* DC.	-	P	Scrambler/Herb
	Fabaceae	*Tephrosia purpurea* (L.) Pers. subsp. *purpurea*	-	A/P	Herb
	Rubiaceae	*Richardia brasiliensis* Gomes	-	A/P	Herb
	Rubiaceae	*Richardia scabra* L.	-	A/P	Herb
Not declared	Amaranthaceae	*Amaranthus dubius* Mart. ex Thell.	-	A/P	Herb
	Amaranthaceae	*Amaranthu hybridus* L.	-	A/P	Herb
	Amaranthaceae	*Gomphrena celosioides* Mart.	-	P	Herb
	Anacardiaceae	*Mangifera indica* L.	-	P	Shrub/Tree

Araceae	*Monstera deliciosa* Liebm.	-	P	Shrub
Asteraceae	*Ambrosia artemisiifolia* L.	-	A	Herb
Asteraceae	*Bidens pilosa* L.	-	A	Herb
Asteraceae	*Conyza bonariensi*s (L.) Cronquist	-	A	Herb
Asteraceae	*Conyza sumatrensis* (Retz.) E.Walker	-	A	Herb
Asteraceae	*Eclipta prostrata* (L.) L.	-	A	Herb
Asteraceae	*Galinsoga parviflora* Cav.	-	A	Herb
Asteraceae	*Hypochaeris radicata* L.	-	P	Herb
Asteraceae	*Lactuca serriola* L.	-	A	Herb
Asteraceae	*Sonchus oleraceus* L.	-	A	Herb
Asteraceae	*Tagetes minuta* L.	-	A	Herb
Asteraceae	*Taraxacum officinale* Weber	-	P	Herb
Cactaceae	*Trichocereus macrogonus* (Salm-Dyck) Riccob.	-	P	Shrub
Fabaceae	*Albizia julibrissin* (Willd.) Durazz.	-	P	Tree
Fabaceae	*Mimosa pudica* L.	-	A/P	Herbaceous creeper
Malvaceae	*Abutilon theophrasti* Medik.	-	A	Shrub
Malvaceae	*Hibiscus trionum* L.	-	P	Herb
Oxalidaceae	*Oxalis corniculata* L.	-	A/P	Herb
Oxalidaceae	*Oxalis latifolia* Kunth	-	A/P	Herb
Passifloraceae	*Passiflora foetida* L.	-	A/P	Herbaceous vine
Plantaginaceae	*Plantago major* L.	-	P	Herb

	Polygonaceae	*Rumex crispus* L.	-	A/P	Herb
	Solanaceae	*Physalis angulata* L.	-	A	Herb
	Solanaceae	*Solanum nigrum* L.	-	A/P	Herb
	Tropaeolaceae	*Tropaeolum majus* L.	-	P	Herb

Invasive* (X): Invasive according to NEMBA and specifically to the eThekwini Metropolitan Area.

Table A4. Alien species and the total number of sites (frequency) they occur in across the EMA.

Species	**Site frequency**[#]
***Lantana camara**	25
***Chromolaena odorata**	23
Conyza sumatrensis	23
Bidens pilosa	22
Tagetes minuta	21
***Solanum mauritianum**	20
***Ipomoea indica**	19
Desmodium incanum	19
Malvastrum coromandelianum	18
***Melia azedarach**	17
***Ageratum conyzoides**	15

Taraxacum officinale	15
Oxalis corniculata	14
****Ricinus communis***	13
Mimosa pudica	12
****Rubus cuneifolius***	11
****Cardiospermum grandiflorum***	11
****Nephrolepis cordifolia* var. *cordifolia***	10
***Conyza bonariensi*s**	9
****Tithonia diversifolia***	8
****Leucaena leucocephala***	8
****Senna didymobotrya***	8
****Litsea glutinosa***	8
****Psidium guajava***	8
****Parthenium hysterophorus***	7
Gomphrena celosioides	6
****Tecoma stans***	6
Rumex crispus	6
Solanum nigrum	6
****Schinus terebinthifolius***	5
Lactuca serriola	5
****Sphagneticola trilobata***	5

***Canna indica**	5
Tephrosia purpurea* subsp. *purpurea	5
***Passiflora suberosa**	5
Verbena bonariensis	5
Ambrosia artemisiifolia	4
Eclipta prostrata	4
***Montanoa hibiscifolia**	4
***Ipomoea alba**	4
Oxalis latifolia	4
Richardia scabra	4
Galinsoga parviflora	3
***Tradescantia fluminensis**	3
Plantago major	3
Amaranthus hybridus	2
Mangifera indica	2
***Opuntia stricta**	2
Mimosa pigra	2
***Senna hirsuta**	2
Passiflora foetida	2
***Rivina humilis**	2
Amaranthus dubius	1

Catharanthus roseus	1
Monstera deliciosa	1
Hypochaeris radicata	1
Sonchus oleraceus	1
Xanthium strumarium	1
****Pereskia aculeata***	1
Trichocereus macrogonus	1
Euphorbia cyathophora	1
Euphorbia hirta	1
****Acacia mearnsii***	1
Albizia julibrissin	1
Albizia lebbeck	1
****Senna septemtrionalis***	1
****Plectranthus barbatus***	1
Hibiscus trionum	1
****Psidium guineense***	1
Passiflora subpeltata	1
****Populus*** **x** ***canescens***	1
****Datura stramonium***	1
Tropaeolum majus	1
****Duranta erecta***	1

Verbena brasiliensis	1
Abutilon theophrasti	1
Physalis angulata	1

*Invasive Alien Plants (IAPs)
Site frequency# (total number of sites in which species occur)

Table A5. Significant relationships between AII and level of disturbance (n = 240).

		Level of disturbance
Alien invasive index (AII)	R^2	0.401
	P	0.028

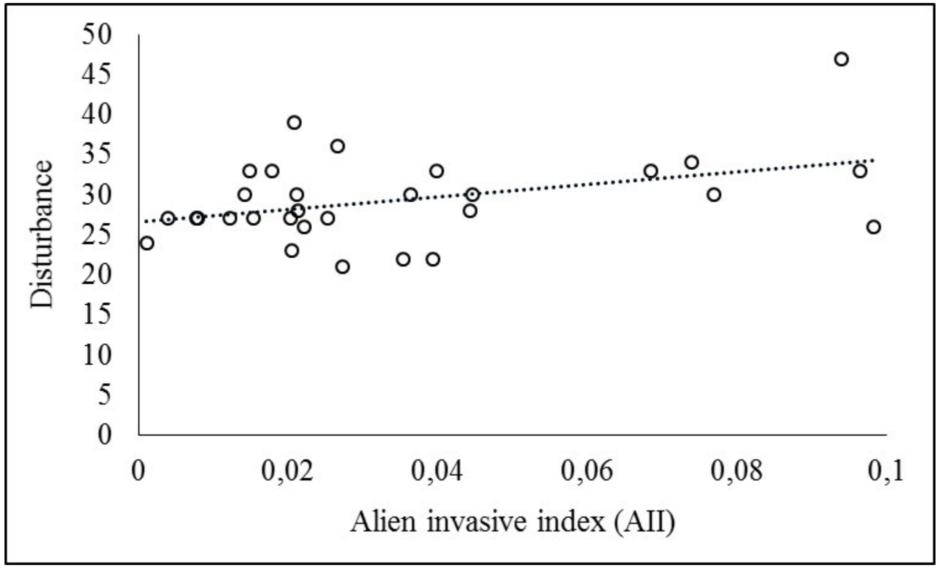

Figure A1: Scatterplot showing the relationship between disturbance level and the Alien Invasive Index (AII)

Table A6. Component matrix of alien floristics, levels of disturbance, proximity to roads, settlement, and industry (n = 240).

	Component			
	PC 1	PC 2	PC 3	PC 4
Total plant density	0.859	-	0.359	-
Non-invasive alien plant density	0.743	-	0.561	-
Invasive alien plant density	0.650	0.312	-	0.303
Distance to roads	0.601	-	-	-

Total species richness	-	0.933	-	-
Invasive alien species richness	-	0.902	-0.325	-
Alien species richness	-	-	0.842	-
Distance to industry	-	-	0.632	-
Distance to informal settlements	-	-	-	-0.783
Disturbance	-	-	-	0.778

APPENDIX B – Chapter 3

Table B1. Sampling sites across D'MOSS in the eThekwini Municipal Area (n= 30). Sectors within the EMA for each site is given as well as the values used to determine disturbance class (≤ 24 = very low; 25 – 28 = low; 29 – 30 = medium; 31 – 39 = high; and ≥ 40 = very high).

Sector*	**Site**	**D'MOSS site size (m^2)**	**Coordinates**	**Vegetation**	**Level of disturbance**
North	1	162 052.98	29.775833°S, 30.982016°E	forest	21: very low
	2	10 720.10	29.633137°S, 31.041872°E	forest	34: high
	3	94 712.95	29.674654°S, 31.041173°E	thicket	30: medium
	4	47 966.80	29.601318°S, 31.162881°E	forest	27: low
	5	130 406.83	29.63739°S, 30.997569°E	grassland	27: low
	6	158 591.90	29.709505°S, 31.022083°E	savanna	27: low
East	7	357 478.23	29.854141°S, 30.92904°E	grassland	33: high
	8	445 788.52	29.878098°S, 30.96719°E	savanna	28: low
	9	795 627.93	29.813038°S, 30.983766°E	thicket	33: high
	10	55 616.54	29.83509°S, 30.9659°E	savanna	30: medium
	11	51 151.34	29.803127°S, 30.95092°E	savanna	39: high
	12	25 650.68	29.87892°S, 30.93368°E	grassland	33: high
South	13	226 978.15	29.981046°S, 30.952393°E	forest	33: high
	14	330 889.92	30.072797°S, 30.861594°E	forest	27: low
	15	22 830.62	30.205156°S, 30.767718°E	forest	33: high
	16	1 008 501.00	29.9157°S, 30.96122°E	savanna	30: medium

	17	257 774.69	29.93304°S, 30.88544°E	savanna	24: very low
	18	92 753.56	30.03519°S, 30.81505°E	thicket	30: medium
	19	549 339.94	29.72477°S, 30.657159°E	savanna	26: low
	20	533 740.73	29.755938°S, 30.749491°E	savanna	30: medium
West	21	759 656.32	29.713804°S, 30.626794°E	grassland	27: low
	22	974 340.30	29.827809°S, 30.761357°E	forest	36: high
	23	263 678.94	29.805633°S, 30.63534°E	savanna	26: low
	24	415 771.10	29.653431°S, 30.809158°E	thicket	22: very low
	25	46 655.27	29.794028°S, 30.883552°E	savanna	47: very high
	26	558 127.09	29.887731°S, 30.852797°E	forest	28: low
Central	27	27 626.27	29.773802°S, 30.80375°E	grassland	23: very low
	28	144 156.95	29.83903°S, 30.84582°E	savanna	27: low
	29	43 122.11	29.816769°S, 30.817688°E	grassland	27: low
	30	724 784.92	29.86421°S, 30.83587°E	savanna	22: very low

*North (n = 6): 1= Newlands East, 2= Verulam, 3= Ottawa, 4= Tongaat, 5= Redcliffe, 6= Phoenix;
*East (n = 6): 7= Westville, 8= Berea, 9= Clare Hills, 10= Sherwood, 11= Reservoir Hills, 12= Hillary;
*South (n = 6): 13= Prospecton, 14= Kingsburgh (n=6): 15= Craigieburn, 16= Montclair, 17= Chatsworth, 18= Amanzimtoti;
*West (n = 6): 19= Inchanga, 20= Outer west Durban, 21= Cato Ridge, 22= KwaNdengezi, 23= Mpumalanga, 24= Qiniselani Manyuswa;
*Central (n = 6): 25= New Germany, 26= Savanna Park - Pinetown, 27= Everton, 28= Caversham Glen - Pinetown, 29= Mahogany Ridge, 30= Mariannheights - Pinetown

Table B2. ***Alien and indigenous species found across the 30 study sites in the EMA.**

Family	Species	Life form	[1]Life cycle/[2]Origin	Reproductive mode	[3]Dispersal syndrome
Acanthaceae	*Asystasia gangetica* (L.) T.Anderson	Herb	A/1,2	Seed Achene	Explosive capsule
Acanthaceae	*Barleria obtusa* Nees	Shrub	P/1	Seed Achene	Explosive capsule
Acanthaceae	*Phaulopsis imbricata* (Forssk.) Sweet	Herb, climber	P/1	Seed	Unknown
Acanthaceae	*Ruellia cordata* Thunb.	Herb, shrub	P/1	Seed	Water
Acanthaceae	*Thunbergia alata* Bojer ex Sims	Herb	P/1	Seed	Water
Acanthaceae	*Thunbergia atriplicifolia* E.Mey. ex Nees	Herb	P/1	Seed	Water
Amaranthaceae	**Amaranthus dubius* Mart. ex Thell.	Shrub	P/3,4	Seed	Wind, water, B/H/A
Amaranthaceae	**Amaranthus hybridus* L.	Herb	P/1	Seed	Wind
Amaranthaceae	**Gomphrena celosioides* Mart.	Herb	P/4	Seed	B/H/A
Anacardiaceae	**Mangifera indica* L.	Herb	P/2	Seed	B/H/A
Anacardiaceae	**Schinus terebinthifolius* Raddi.	Herb, shrub	P/1	Seed	Wind, B/H/A
Anacardiaceae	*Searsia crenata* (Thunb.) Moffett	Herb, shrub	P/4	Seed	B/H/A
Apiaceae	*Centella asiatica* (L.) Urb.	Herb	P/2	Seed	B/H/A
Apocynaceae	**Catharanthus roseus* (L.) G.Don	Herb	A/1	Seed	Wind, water, B/H/A
Apocynaceae	*Xysmalobium undulatum* (L.) Aiton f. var.	Herb	P/1	Seed	Wind

	undulatum				
Araceae	**Monstera delicious* Liebm.	Herb	P/3	Seed Achene	B/H/A
Asparagaceae	*Asparagus asparagoides* (L.) Druce	Herb	A/1	Seed	Water, B/H/A
Asphodelaceae	*Aloe maculata*	Herb	P/1	Seed	Wind
Asphodelaceae	*Kniphofia linearifolia*	Herb	P/1	Seed	Wind, water
Asteraceae	**Ageratum conyzoides* Mill.	Herb	A/4	Seed	Wind, water
Asteraceae	*Afroaster hispidus* (Thunb.) J.C.Manning & Goldblatt Burtt Davy ex C.A.Sm.	Herb	A/1	Seed	Unknown
Asteraceae	**Ambrosia artemisiifolia* L.	Herb	P/3	Seed	Wind, water
Asteraceae	*Arctotis arctotoides* (L.f.) O.Hoffm.	Herb	A/1	Seed	Wind
Asteraceae	*Berkheya bipinnatifida* (Harv.) Roessler	Herb, climber	P/1	Seed	Wind
Asteraceae	*Berkheya speciosa* (DC.) O.Hoffm.	Herb	P/1	Seed	Wind
Asteraceae	**Bidens pilosa* L.	Herb	P/3,4	Seed	Wind, water, B/H/A
Asteraceae	*Brachylaena discolor* DC.	Tree	A/1	Seed	Wind
Asteraceae	**Chromolaena odorata* (L.) R.M.King & H.Rob	Herb	A/3,4	Seed	Wind, B/H/A
Asteraceae	*Chrysanthemoides monilifera* (L.) Norl.	Herb, shrub	A/1	Seed	Wind, water, B/H/A
Asteraceae	**Conyza bonariensis* (L.) Cronquist	Herb	P/3,4	Seed	Wind
Asteraceae	**Conyza sumatrensis* (Retz.) E.Walker	Herb	P/4	Seed	Wind
Asteraceae	*Dicoma speciosa* DC.	Herb	P/1,2	Seed	Wind
Asteraceae	**Eclipta prostrata* (L.) L.	Herb	A/2	Achene	Wind

Asteraceae	**Galinsoga parviflora* Cav.	Herb	P/4	Seed	Wind, B/H/A
Asteraceae	*Helichrysum appendiculatum* (L.f.) Less.	Herb, climber	P/1	Seed Rhizome	Wind
Asteraceae	*Helichrysum pallidum* DC.	Herb	P/1	Seed	Wind
Asteraceae	*Helichrysum panduratum* O.Hoffm. var. *panduratum*	Herb, shrub	P/	Seed	Wind
Asteraceae	*Helichrysum petiolare* Hilliard & B.L.Burtt	Herb	P/1	Seed	Wind
Asteraceae	*Helichrysum splendidum* (Thunb.) Less.	Herb, shrub	P/1	Seed	Wind
Asteraceae	*Hilliardiella aristata* (DC.) H.Rob	Herb	P/1	Seed	Wind
Asteraceae	**Hypochaeris radicata* L.	Tree	P/2,5	Seed	Wind, B/H/A
Asteraceae	**Lactuca serriola* L.	Shrub	P/2,3,5	Seed	Wind
Asteraceae	**Lactuca tysonii* (E.Phillips) C.Jeffrey	Tree	P/1	Seed	Water, B/H/A
Asteraceae	**Montanoa hibiscifolia* Benth.	Herb	P/3	Seed Achene	Wind, water, B/H/A
Asteraceae	*Nidorella undulata* (Thunb.) Sond. ex Harv.	Herb	P/1	Seed Achene	Wind
Asteraceae	**Parthenium hysterophorus* L.	Herb	P/3,4	Seed	Wind, B/H/A
Asteraceae	*Senecio deltoideus* Less.	Herb	P/1	Seed	Wind
Asteraceae	*Senecio madagascariensis* Poir.	Herb	P/1	Seed	Wind
Asteraceae	*Senecio tamoides* DC.	Herb	P/1	Seed	Wind
Asteraceae	**Sonchus oleraceus* L.	Herb, shrub	P/2,5	Seed	Wind, water, B/H/A
Asteraceae	**Sphagneticola trilobata* (L.) Pruski	Climber	P/3	Seed	Gravity,

					B/H/A
Asteraceae	**Tagetes minuta* L.	Herb	A/4	Seed	Wind, water, B/H/A
Asteraceae	**Taraxacum officinale* Weber	Herb	A/5	Seed	Wind
Asteraceae	**Tithonia diversifolia* (Hemsl.) A. Gray	Herb, shrub	A/3	Seed	Wind, water
Asteraceae	**Xanthium strumarium* L.	Herb	A/3	Seed Achene	B/H/A
Bignoniaceae	**Tecoma stans* (L.) Juss. Ex Kunth	Herb	P/3,4	Seed	Wind, water
Brassicaceae	*Lepidium africanum* (Burm.f.) DC. subsp. *africanum*	Herb	P/1	Seed	Wind, B/H/A
Cactaceae	**Opuntia stricta* (Haw.) Haw.	Shrub, tree	A/3,4	Seed	Gravity, B/H/A
Cactaceae	**Pereskia aculeata* Mill.	Herb	P/3,4	Seed Rhizome	B/H/A
Cactaceae	**Trichocereus macrogonus* (Salm-Dyck) Riccob.	Shrub, tree	P/4	Seed	Gravity, B/H/A
Cannabaceae	*Celtis africana* Burm.f.	Shrub	P/1,2	Seed	B/H/A
Cannabaceae	*Trema orientalis* (L.) Blume	Tree	P/1,2,6	Seed	B/H/A
Cannaceae	**Canna indica* L.	Herb	P/3,4	Seed	B/H/A
Commelinaceae	*Commelina africana* L.	Herb, climber	P/1	Seed	B/H/A
Commelinaceae	*Commelina erecta* L.	Herb	A/1,2,3,4	Seed	B/H/A
Commelinaceae	**Tradescantia fluminensis* Vell.	Herb	P/4	Seed Rhizome	Water

Convolvulaceae	*Hewittia malabarica* (L.) Suresh	Tree	P/1,2	Seed	Wind
Convolvulaceae	**Ipomoea purpurea* (L.) Roth	Herb	P/3,4	Seed	Wind, B/H/A
Convolvulaceae	**Ipomoea alba* L.	Herb	P/1,2	Seed	Water, B/H/A
Convolvulaceae	**Ipomoea indica* (Burm.f.) Merr.	Herb	A/2,3,4	Spores	Water, B/H/A
Convolvulaceae	*Ipomoea cairica* (L.) Sweet var. *cairica*	Climber	P/3	Seed	B/H/A
Crassulaceae	*Crassula perforata* Thunb.	Herb	P/1	Seed	Unknown
Crassulaceae	*Kalanchoe neglecta* Toelken	Herb	P/1	Seed	Unknown
Cucurbitaceae	*Coccinia palmata* (Sond.) Cogn.	Herb	P/1	Seed	B/H/A
Cyperaceae	*Cyperus compressus* L.	Graminoid	A/1,2,3,4	Seed	Wind
Cyperaceae	*Cyperus cyperoides* (L.) Kuntze	Graminoid	P/1	Seed	Wind
Cyperaceae	*Cyperus esculentus* L.	Graminoid	P/1	Seed	Wind
Cyperaceae	*Cyperus obtusiflorus* Vahl	Graminoid	P/1	Seed	Wind
Cyperaceae	*Cyperus rotundus* L.	Graminoid	P/1,2,5	Seed	Wind
Cyperaceae	*Fimbristylis complanata* (Retz.) Link	Graminoid	P/1,2,4	Seed	Wind
Cyperaceae	*Kyllinga alba* Nees	Graminoid	P/1	Seed	Wind
Cyperaceae	*Pycreus polystachyos* (Rottb.) P.Beauv.	Graminoid	P/1	Seed	Wind
Dipsacaceae	*Scabiosa columbaria* L.	Herb, shrub	P/1,2,5	Seed	B/H/A
Ebenaceae	*Diospyros lycioides* Desf.	Herb	A/1	Achene	B/H/A
Euphorbiaceae	*Acalypha villicaulis* Hochst.	Herb	P/1	Seed	Unknown
Euphorbiaceae	*Dalechampia capensis* A.Spreng.	Shrub	P/1	Seed	Explosive
Euphorbiaceae	**Euphorbia cyathophora* Murray	Shrub, tree	P/3,4	Seed	Water, explosive capsule

Euphorbiaceae	**Euphorbia hirta* L.	Herb, shrub	P/3,4	Seed	Gravity, B/H/A
Euphorbiaceae	*Euphorbia tirucalli* L.	Tree	P/1	Seed	B/H/A
Euphorbiaceae	**Ricinus communis* L.	Shrub	P/1	Seed	B/H/A
Fabaceae	**Acacia mearnsii* De Wild.	Tree	A/6	Seed	Water, B/H/A
Fabaceae	*Acacia robusta* Burch. subsp. *clavigera* (E.Mey.) Brenan	Tree	P/1	Seed Rhizome	B/H/A
Fabaceae	*Albizia adianthefolia* (Schumach.) W.Wight var. *adianthifolia*	Tree	P/1	Seed Rhizome	Wind
Fabaceae	**Albizia julibrissin* (Willd.) Durazz.	Tree	P/2	Seed	Water
Fabaceae	**Albizia lebbeck* (L.) Benth.	Tree	P/2,6	Seed	Wind
Fabaceae	*Chamaecrista mimosoides* (L.) Greene	Shrub, tree	P/1,2	Seed	Gravity
Fabaceae	*Crotalaria lanceolata* E.Mey.	Shrub, tree	P/1,2,5	Seed	Unknown
Fabaceae	**Desmodium incanum* DC.	Shrub, tree	P/4	Seed	B/H/A
Fabaceae	*Eriosema cordatum* E.Mey.	Herb	P/1	Seed	B/H/A
Fabaceae	*Eriosema preptum* C.H.Stirt.	Herb	P/1	Seed	B/H/A
Fabaceae	*Erythrina caffra* Thunb.	Herb	A/1	Seed	B/H/A
Fabaceae	*Indigofera hilaris* Eckl. & Zeyh. var. *hilaris*	Shrub	A/1	Seed	Gravity
Fabaceae	**Leucaena leucocephala* (Lam.) de Wit	Herb	P/3	Seed	Gravity
Fabaceae	**Mimosa pigra* L.	Shrub	P/4	Seed	B/H/A
Fabaceae	**Mimosa pudica* L.	Shrub	P/4	Seed	B/H/A
Fabaceae	*Neonotonia wightii* (Wight ex Arn.) J.A.Lackey	Herb	P/1,2	Seed Achene	Water, gravity

Fabaceae	*Pseudarthria hookeri* Wight & Arn. var. *hookeri*	Herb	P/1	Spores	Unknown
Fabaceae	**Senna didymobotrya* (Fressin.) H.S Irwin & Bameby	Shrub, tree	P/1	Seed	Wind, water
Fabaceae	**Senna hirsuta* (L.) H.S. Irwin & Bameby	Herb	P/3,4	Seed	Water
Fabaceae	**Senna septemtrionalis* (Viv.) H.S.Irwin & Barneby	Shrub	P/3	Seed	Water, B/H/A
Fabaceae	*Tephrosia capensis* (Jacq.) Pers. var. *capensis*	Herb	P/1	Seed	Explosive capsule
Fabaceae	**Tephrosia purpurea* (L.) Pers. subsp. *purpurea*	Herb	P/2	Seed	Explosive capsule
Fabaceae	*Tephrosia villosa* (L.) Pers.	Tree	P/1,2	Seed	Explosive capsule
Fabaceae	*Trifolium burchellianum* Ser. subsp. *burchellianum*	Herb	P/1	Seed	Unknown
Gentianales	*Gomphocarpus physocarpus* E.Mey.	Herb	A/1	Seed	Wind, water
Geraniaceae	*Geranium flanaganii* R.Knuth	Herb	P/1	Seed	Explosive capsule, B/H/A
Geraniaceae	*Geranium wakkerstroomianum* R.Knuth	Herb	P/1	Seed	Explosive capsule
Hyacinthaceae	*Drimiopsis maxima* Baker	Shrub, tree	P/1	Seed	Unknown
Hypoxidaceae	*Hypoxis hemerocallidea* Fisch. C.A.Mey. & Ave-Lall	Herb	A/1	Seed	Explosive capsule
Lamiaceae	*Clerodendrum glabrum* E.Mey.	Herb	P/1	Seed	B/H/A
Lamiaceae	*Leonotis leonurus* (L.) R.Br.	Shrub	P/1	Seed	Water, B/H/A

Lamiaceae	*Plectranthus amboinicus* (Lour.) Spreng.	Herb, shrub	A/1	Seed	B/H/A
Lamiaceae	**Plectranthus barbatus* Andrews	Herb, shrub	P/1,2	Seed	B/H/A
Lamiaceae	*Plectranthus ciliatus* E.Mey. ex Benth.	Herb	P/1	Seed	B/H/A
Lauraceae	**Litsea glutinosa* (Lour.) C.B.Rob.	Tree	P/2,5	Seed	B/H/A
Lobeliaceae	*Lobelia flaccida* (C.Presl) A.DC. subsp. *flaccida*	Herb	A/1	Seed	Unknown
Lobeliaceae	*Monopsis decipiens* (Sond.) Thulin	Herb	P/1	Seed	Explosive capsule
Malvaceae	**Abutilon theophrasti* Medik.	Herb	A/2	Seed	Gravity
Malvaceae	*Hibiscus cannabinus* L.	Tree	P/2	Seed	Water
Malvaceae	*Hibiscus diversifolius* Jacq. subsp. *diversifolius*	Herb	A/7	Seed	Explosive capsule
Malvaceae	*Hibiscus lunarifolius* Willd.	Herb, shrub	P/1,2	Seed Achene	Water
Malvaceae	*Hibiscus surattensis* L.	Climber	P/1,2	Seed	Explosive capsule
Malvaceae	**Hibiscus trionum* L.	Shrub	P/1,2,5	Seed	Water
Malvaceae	**Malvastrum coromandelianum* (L.) Garcke	Herb	A/3	Seed	Wind
Malvaceae	*Pavonia burchellii* (DC.) R.A.Dyer	Shrub	P/1	Seed	Wind, explosive capsule
Malvaceae	*Sida cordifolia* L. subsp. *cordifolia*	Shrub	P/2,6	Seed	Water, B/H/A
Malvaceae	*Triumfetta pilosa* Roth var. *pilosa*	Shrub	P/1	Seed	B/H/A
Melastomataceae	*Dissotis canescens* (E.Mey. ex R.A.Graham)	Shrub	P/1	Seed	Unknown

	Hook.f.				
Meliaceae	*Ekebergia capensis* Sparrm.	Herb	P/1	Seed	B/H/A
Meliaceae	**Melia azedarach* L.	Tree	P/2,6	Seed	Wind, B/H/A
Melianthaceae	*Bersama tysoniana* Oliv.	Shrub	A/1	Seed	B/H/A
Menispermaceae	*Cissampelos torulosa* E.Mey. ex Harv.	Shrub, tree	P/1	Seed	B/H/A
Myrtaceae	**Psidium guajava* L.	Tree	P/3,4	Seed	B/H/A
Myrtaceae	**Psidium guineense* Sw.	Tree	P/3,4	Seed	B/H/A
Nephrolepidaceae	**Nephrolepis cordifolia* (L.) C.Presl var. *cordifolia*	Herb	P/2,6	Seed Achene	Wind
Onagraceae	*Ludwigia octovalvis* (Jacq.) P.H.Raven	Tree	P/3,4	Seed	Water
Oxalidaceae	**Oxalis corniculata* L.	Herb	A/3,4	Seed	Explosive capsule
Oxalidaceae	**Oxalis latifolia* Kunth	Herb	A/3,4	Seed	Explosive capsule
Passifloraceae	**Passiflora foetida* L.	Herb	P/3,4	Seed Achene	B/H/A
Passifloraceae	**Passiflora suberosa* L.	Climber	P/3,4	Seed	B/H/A
Passifloraceae	**Passiflora subpeltata* Ortega	Climber	P/3,4	Seed	B/H/A
Phyllanthaceae	*Phyllanthus polygonoides* Nutt. ex Spreng.	Shrub	P/1	Seed	Wind
Phyllanthaceae	*Phyllanthus myrtaceus* Sond.	Herb	P/3	Seed	Wind
Phytolaccaceae	**Rivina humilis* L.	Climber	P/3,4	Seed	Water, B/H/A
Plantaginaceae	*Plantago lanceolata* L.	Herb	P/1,2,5	Seed	Wind, B/H/A
Plantaginaceae	**Plantago major* L.	Herb, shrub	P/2,5	Seed	Wind, B/H/A

Poaceae	*Aristida adscensionis* L.	Graminoid	A/3,4	Seed	Wind
Poaceae	*Cyambopogon excavates* (Hochst.) Stapf ex Burtt Davy	Graminoid	A/1,2	Seed	Wind
Poaceae	*Cynodon dactylon* (L.) Pers.	Graminoid	A/1	Seed	Wind
Poaceae	*Digitaria ciliaris* (Retz.) Koeler	Graminoid	A/2	Seed	Wind
Poaceae	*Digitaria eriantha* Steud.	Graminoid	A/1	Seed	Wind
Poaceae	*Digitaria longifolia* (Retz.) Pers.	Graminoid	A/1,2,6	Seed	Wind
Poaceae	*Digitaria ternate* (A.Rich.) Stapf	Graminoid	A/2	Seed	Wind
Poaceae	*Panicum coloratum* L.	Graminoid	A/1	Seed	Wind
Poaceae	*Panicum maximum* Jacq.	Graminoid	A/1	Seed	Wind
Poaceae	*Rendlia altera* (Rendle) Chiov.	Graminoid	A/1	Seed	Wind
Poaceae	*Setaria lindenbergiana* (Nees) Stapf	Graminoid	A/1	Seed	Wind
Poaceae	*Setaria megaphylla* (Steud.) T.Durand & Schinz	Graminoid	A/1	Seed	Wind
Poaceae	*Setaria pallide-fusca* (Schumach.) Stapf & C.E.Hubb.	Graminoid	A/1	Seed	Wind
Poaceae	*Setaria sagittifolia* (A.Rich.) Walp.	Graminoid	A/1	Seed	Wind
Poaceae	*Sorghum halepense* (L.) Pers.	Graminoid	A/5	Seed	Wind
Poaceae	*Tragus berteronianus* Schult.	Graminoid	A/1,2	Seed	Wind
Poaceae	*Urochloa oligotricha* (Fig. & De Not.) Henrard	Graminoid	A/1	Seed	Wind
Polygonaceae	**Rumex crispus* L.	Herb	P/2,5	Seed	Wind, water, B/H/A
Pteridaceae	*Cheilanthes viridis* (Forssk.) Sw.	Herb	P/1	Seed	Wind
Ranunculaceae	*Clematis brachiata* Thunb.	Climber	P/1	Seed	Wind

Rosaceae	**Rubus cuneifolius* Pursh	Shrub	P/3	Seed	B/H/A
Rosaceae	*Rubus rigidus* Sm.	Herb	P/1	Seed	B/H/A
Rubiaceae	**Richardia brasiliensis* Gomes	Herb	P/3,4	Seed	B/H/A
Rubiaceae	**Richardia scabra* L.	Herb, climber	P/4	Seed	B/H/A
Ruscaceae	*Dracaena aletriformis* (Haw.) Bos	Herb	P/1	Seed	Unknown
Salicaceae	**Populus canescens* (Aiton) Sm.	Tree	P/2,3,5	Seed	Wind
Sapindaceae	**Cardiospermum grandiflorum* Sw.	Climber	P/4	Seed	Wind, water
Sapindaceae	*Hippobromus pauciflorus* (L.f.) Radlk.	Tree, shrub	P/1	Seed	Unknown
Smilacaceae	*Smilax anceps* Willd.	Shrub	P/1	Seed	Unknown
Solanaceae	**Datura stramonium* L.	Herb	P/3	Achene	Explosive capsule
Solanaceae	**Physalis angulata* L.	Herb	P/3,4	Seed	Water
Solanaceae	*Solanum aculeastrum* Dunal	Herb	P/1	Seed	B/H/A
Solanaceae	*Solanum incanum* L. var. *lichtensteinii* Bitter	Herb, shrub	P/1,2	Seed	B/H/A
Solanaceae	**Solanum mauritianum* Scop.	Shrub	P/4	Seed	Water
Solanaceae	**Solanum nigrum* L.	Shrub	P/2,5	Seed	B/H/A
Strelitziaceae	*Strelitzia nicolai* Regel & Korn.	Tree	P/1	Seed	B/H/A
Thymeleaceae	*Gnidia cuneata* Meisn.	Herb	P/1	Seed	Unknown
Thymeleaceae	*Gnidia kraussiana* Meisn.	Herb	A/1	Seed	Unknown
Tropaeolaceae	**Tropaeolum majus* L.	Climber	P/4	Seed	Water, B/H/A
Verbenaceae	**Duranta erecta* L.	Shrub	A/3,4	Seed	B/H/A
Verbenaceae	**Lantana camara* L.	Shrub	P/4	Seed	B/H/A
Verbenaceae	*Lantana rugosa* Thunb.	Shrub	P/1	Seed	B/H/A

Verbenaceae	**Verbena bonariensis* L.	Herb	P/4	Seed	B/H/A
Verbenaceae	**Verbena brasiliensis* Vell.	Herb	P/4	Seed	Wind, water, B/H/A
Verbenaceae	**Verbena officinalis* L.	Herb	P/5	Seed	B/H/A

[1]P = perennial, A = annual
[2]1 = Africa, 2 = Asia, 3 = North America, 4 = South America, 5 = Europe, 6 = Australia, 7 = Pantropical
[3]B/H/A = bird/human/animal dispersal

Table B3. Species richness and density for alien and indigenous species across all study sites**.**

Site	**Richness**			**Density (individuals/m^2)**			**Vegetation**
	Alien	**Indigenous**	**Total**	**Alien**	**Indigenous**	**Total**	
1	21	16	37	0.67	0.21	0.88	forest
2	25	10	35	1.06	0.30	1.35	forest
3	22	12	34	1.54	0.20	1.73	thicket
4	16	9	25	0.33	0.12	0.44	forest
5	21	22	43	0.56	1.55	2.11	grassland
6	24	10	34	0.51	0.34	0.845	savanna
7	20	20	40	3.76	1.08	4.83	grassland
8	20	13	33	0.53	0.23	0.755	thicket
9	17	2	19	1.06	0.01	1.065	savanna

10	17	15	32	1.80	0.40	2.195	savanna
11	14	10	24	0.95	0.33	1.275	savanna
12	17	13	30	0.45	0.68	1.12	grassland
13	21	18	39	0.50	0.91	1.4	forest
14	20	13	33	0.35	0.21	0.56	forest
15	14	13	27	1.47	1.04	2.5	forest
16	17	15	32	0.31	0.18	0.485	savanna
17	12	22	34	0.07	1.19	1.255	savanna
18	23	25	48	0.75	0.49	1.235	thicket
19	18	12	30	0.73	0.41	1.135	savanna
20	18	13	31	2.53	0.60	3.13	savanna
21	12	12	24	0.76	0.90	1.66	grassland
22	22	9	31	0.88	0.24	1.115	forest
23	19	8	27	1.68	0.10	1.775	savanna
24	22	13	35	0.85	0.38	1.22	thicket
25	19	11	30	1.03	0.21	1.235	savanna
26	17	11	28	0.85	0.33	1.17	forest
27	9	7	16	0.77	0.37	1.135	grassland
28	9	15	24	0.29	0.37	0.66	savanna
29	12	14	26	0.44	0.68	1.11	grassland
30	19	13	32	0.78	0.26	1.035	savanna

Table B4. Alpha diversity (Shannon's exponential index and Simpson's inverse index) for alien and indigenous species across all study sites.

Site	Shannon's exponential index	Simpson's inverse index	Site	Shannon's exponential index	Simpson's inverse index
1	19.14	14.38	**16**	18.47	13.71
2	15.37	10.68	**17**	12.07	7.00
3	15.45	9.48	**18**	24.86	17.58
4	13.33	10.57	**19**	17.59	11.74
5	13.83	7.59	**20**	16.12	8.32
6	17.98	10.87	**21**	14.52	9.47
7	15.84	9.87	**22**	17.27	10.46
8	15.99	9.98	**23**	7.13	3.97
9	9.93	6.99	**24**	19.68	13.04
10	9.47	5.29	**25**	16.01	9.69
11	9.70	6.04	**26**	14.69	8.54
12	12.26	6.60	**27**	20.03	14.28
13	12.39	6.89	**28**	11.73	6.16
14	20.41	14.18	**29**	22.98	16.39
15	12.87	7.83	**30**	18.74	11.51

Diversity scores for each site are based on quadrat data

Table B5. Functional diversity (FD) of four categorical traits for alien, indigenous and combined species across all study sites.

Trait	Alien species	Indigenous species	All species
Dispersal syndrome FD	5.50 ± 1.40 [b]	3.54 ± 1.16 [c]	8.55 ± 1.84 [a]
Life form FD	4.87 ± 1.36 [b]	3.72 ± 1.33 [c]	7.66 ± 1.77 [a]
Reproductive mode FD	1.58 ± 0.49 [b]	1.39 ± 0.42 [b]	1.93 ± 0.55 [a]
Life cycle FD	5.23 ± 1.49 [b]	3.41 ± 1.47 [c]	7.47 ± 2.26 [a]
Combined trait FD	4.91 ± 1.20 [b]	3.36 ± 1.06 [c]	7.47 ± 1.59 [a]

Values represent means ± SD across all sites (n = 30). Superscript lettering represents significance across taxa for each categorical trait ($P > 0.05$, ANOVA)

Table B6. Component matrix of FD, non-natural disturbance, and land use (n = 240).

	Component	
	PC1	PC2
Level of disturbance	0.800	-
Distance to informal settlements	-0.804	0.303
Distance to roads	-	-0.510
FD	-	0.831

Table B7. Component matrix of FD and plant floristics (n = 240).

	Component	
	PC1	PC2
Alien species richness	0.809	-
Alien plant density	0.676	-
Indigenous species richness	-	0.846
Indigenous plant density	-	0.853
FD	0.690	-

Table B8. Positive alien-alien (non-invasive/invasive*) species co-occurrences across study sites.

Species 1 (sp. 1)	Species 2 (sp. 2)	No. of sites (sp. 1)	No. of sites (sp. 2)	Observed co-occurrence	Expected co-occurrence	Probability of co-occurrence
*Lantana camara**	*Solanum mauritianum**	25	20	19	16.7	0.556
Conyza sumatrensis	*Tagetes minuta*	23	21	19	16.1	0.537
*Cardiospermum grandiflorum**	*Ricinus communis**	11	13	8	4.8	0.159
*Malvastrum coromandelianum**	*Parthenium hysterophorus**	18	7	7	4.2	0.14
*Malvastrum coromandelianum**	*Tecoma stans**	18	6	6	3.6	0.12
*Ipomoea indica**	*Tecoma stans**	19	6	6	3.8	0.127
*Oxalis corniculata**	*Passiflora suberosa*	14	5	5	2.3	0.078
*Ricinus communis**	*Tecoma stans**	13	6	5	2.6	0.087
*Leucaena leucocephala**	*Passiflora suberosa*	8	5	4	1.3	0.044
*Ipomoea purpurea**	*Mimosa pudica*	4	12	4	1.6	0.053
*Oxalis latifolia**	*Ricinus communis**	4	13	4	1.7	0.058
*Canna indica**	*Cardiospermum grandiflorum**	5	11	4	1.8	0.061
*Rubus cuneifolius**	*Tephrosia purpurea*	11	5	4	1.8	0.061
*Ageratum conyzoides**	*Ambrosia artemisiifolia*	15	4	4	2	0.067
*Ageratum conyzoides**	*Eclipta prostrata*	15	4	4	2	0.067
*Ageratum conyzoides**	*Montanoa hibiscifolia**	15	4	4	2	0.067

Ageratum conyzoides*	Richardia scabra	15	4	4	2	0.067
Schinus terebinthifolius*	Solanum nigrum	5	6	3	1	0.033
Ambrosia artemisiifolia	Senna didymobotrya*	4	8	3	1.1	0.036
Ipomoea purpurea	Litsea glutinosa*	4	8	3	1.1	0.036

Table B9. Positive alien-indigenous (non-invasive* and invasive**) species co-occurrences across study sites

Species 1 (sp1)	**Species 2 (sp2)**	**No. of sites (sp1)**	**No. of sites (sp2)**	**Observed co-occurrence**	**Expected co-occurrence**	**Probability of co-occurrence**
Centella asiatica	_Conyza sumatrensis_*	15	23	14	11.5	0.383
Centella asiatica	_Solanum mauritianum_**	15	20	13	10	0.333
_Bidens pilosa_*	_Commelina erecta_	22	13	12	9.5	0.318
Commelina erecta	_Ipomoea purpurea_**	13	19	11	8.2	0.274
Berkheya speciosa	_Conyza sumatrensis_*	10	23	10	7.7	0.256
Cardiospermum grandiflorum**	_Commelina erecta_	11	13	8	4.8	0.159
Commelina africana	_Litsea glutinosa_**	20	8	8	5.3	0.178
Litsea glutinosa**	_Neonotonia wightii_	8	16	7	4.3	0.142
Cheilanthes viridis	_Rubus cuneifolius_**	8	11	6	2.9	0.098
Chrysanthemoides monilifera	_Leucaena leucocephala_**	11	8	6	2.9	0.098
Gomphocarpus physocarpus	_Malvastrum coromandelianum_**	6	18	6	3.6	0.12
Hewittia malabarica	_Passiflora suberosa_**	10	5	5	1.7	0.056
Hewittia malabarica	_Parthenium hysterophorus_**	10	7	5	2.3	0.078
Canna indica**	_Coccinia palmata_	5	9	4	1.5	0.05

Coccinia palmata	*Lactuca serriola**	9	5	4	1.5	0.05
Berkheya speciosa	*Tephrosia purpurea**	10	5	4	1.7	0.056
Chrysanthemoides monilifera	*Passiflora suberosa***	11	5	4	1.8	0.061
*Ambrosia artemisiifolia**	*Centella asiatica*	4	15	4	2	0.067
Centella asiatica	*Eclipta prostrata**	15	4	4	2	0.067
Centella asiatica	*Richardia scabra**	15	4	4	2	0.067
Hypoxis hemerocallidea	*Taraxacum officinale**	4	15	4	2	0.067
Berkheya speciosa	*Galinsoga parviflora**	10	3	3	1	0.033
Berkheya speciosa	*Plantago major**	10	3	3	1	0.033
Gomphocarpus physocarpus	*Schinus terebinthifolius***	6	5	3	1	0.033
Ipomoea cairica	*Passiflora suberosa***	6	5	3	1	0.033
Phyllanthus polygonoides	*Rumex crispus**	5	6	3	1	0.033
*Senna didymobotrya***	*Sida cordifolia*	8	4	3	1.1	0.036

Table B10. Co-occurring species (**invasive, *alien, indigenous) and their functional traits (B = bird, H = human, A = air)

Trait	Species					
	***Solanum mauritianum*	***Lantana camara*	**Conyza sumatrensis*	**Bidens pilosa*	**Tagetes minuta*	*Centella asiatica*	*Commelina erecta*
Life form	Shrub	Shrub	Herb	Herb	Herb	Herb	Herb
Life cycle	Perennial	Perennial	Perennial	Perennial	Annual	Perennial	Annual
Reproductive mode	Seed	Seed	Seed	Seed	Seed	Seed	Seed
Dispersal syndrome	Water	B/H/A	Wind	Wind, water, B/H/A	Wind, water, B/H/A	B/H/A	B/H/A

APPENDIX C – Chapter 4

Table C1. Soil seed bank species (alien and indigenous), life form and total density across all sites.

Family	Species	Life form	Alien (X)	Total density (Germinants/m^2)
Amaranthaceae	*Amaranthus dubius* Mart. ex Thell.	Shrub	X	18.20
Apiaceae	*Centella asiatica* (L.) Urb.	Herb	-	133.47
Asparagaceae	*Asparagus asparagoides* (L.) Druce	Herb	-	7.28
Asteraceae	*Ageratum conyzoides* Mill.	Herb	X*	36.40
Asteraceae	*Ambrosia artemisiifolia* L.	Herb	X	45.50
Asteraceae	*Arctotis arctotoides* (L.f.) O.Hoffm.	Herb	-	36.40
Asteraceae	*Bidens pilosa* L.	Herb	X	6.07
Asteraceae	*Chromolaena odorata* (L.) R.M.King & H.Rob	Herb	X*	145.16
Asteraceae	*Chrysanthemoides monilifera* (L.) Norl.	Herb	-	36.40
Asteraceae	*Conyza bonariensis* (L.) Cronquist	Herb	X	138.46
Asteraceae	*Conyza sumatrensis* (Retz.) E.Walker	Herb	X	303.50
Asteraceae	*Eclipta prostrata* (L.) L.	Herb	X	36.40
Asteraceae	*Galinsoga parviflora* Cav.	Herb	X	158.62
Asteraceae	*Helichrysum appendiculatum* (L.f.) Less.	Herb	-	72.80
Asteraceae	*Helichrysum petiolare* Hilliard & B.L.Burtt	Herb	-	72.80
Asteraceae	*Helichrysum splendidum* (Thunb.) Less.	Herb	-	145.60

Asteraceae	*Hilliardiella aristata* (DC.) H.Rob	Herb	-	18.20
Asteraceae	*Lactuca serriola* L.	Shrub	X	36.40
Asteraceae	*Parthenium hysterophorus* L.	Herb	X	148.14
Asteraceae	*Tagetes minuta* L.	Herb	X	102.38
Asteraceae	*Taraxacum officinale* Weber	Herb	X	109.20
Commelinaceae	*Commelina africana* L.	Herb	-	48.53
Commelinaceae	*Commelina erecta* L.	Herb	-	72.84
Convolvulaceae	*Ipomoea indica* (Burm.f.) Merr.	Herb	X*	18.20
Cyperaceae	*Cyperus compressus* L.	Graminoid	-	25.70
Cyperaceae	*Cyperus crassipes* Vahl	Graminoid	-	24.33
Cyperaceae	*Cyperus cyperoides* (L.) Kuntze	Graminoid	-	1.30
Cyperaceae	*Cyperus esculentus* L.	Graminoid	-	42.57
Cyperaceae	*Cyperus obtusiflorus* Vahl	Graminoid	-	52.93
Cyperaceae	*Cyperus rotundus* L.	Graminoid	-	42.61
Cyperaceae	*Fimbristylis complanata* (Retz.) Link	Graminoid	-	58.92
Cyperaceae	*Kyllinga alba* Nees.	Graminoid	-	23.89
Cyperaceae	*Pycreus polystachyos* (Rottb.) P.Beauv.	Graminoid	-	31.31
Ebenaceae	*Diospyros lycioides* Desf.	Herb	-	5.20
Euphorbiaceae	*Acalypha villicaulis* Hochst.	Herb	-	36.40
Euphorbiaceae	*Ricinus communis* L.	Shrub	X*	36.40
Fabaceae	*Acacia mearnsii* De Wild.	Tree	X	54.60

Fabaceae	*Albizia adianthefolia* (Schumach.) W.Wight var. *adianthifolia*	Tree	-	18.20
Fabaceae	*Chamaecrista mimosoides* (L.) Greene	Shrub	-	175.93
Fabaceae	*Crotalaria lanceolata* E.Mey.	Shrub	-	36.40
Fabaceae	*Desmodium incanum* DC.	Shrub	X	84.02
Fabaceae	*Indigofera hilaris* Eckl. & Zeyh. var. *hilaris*	Shrub	-	30.33
Fabaceae	*Mimosa pudica* L.	Shrub	X	163.8
Fabaceae	*Neonotonia wightii* (Wight ex Arn.) J.A.Lackey	Herb	-	105.56
Fabaceae	*Tephrosia purpurea* (L.) Pers. subsp. *purpurea*	Herb	X	103.13
Fabaceae	*Trifolium burchellianum* Ser. subsp. Burchellianum	Herb	-	12.13
Lauraceae	*Litsea glutinosa* (Lour.) C.B.Rob.	Tree	X*	36.40
Malvaceae	*Malvastrum coromandelianum* (L.) Garcke	Herb	X	14.12
Malvaceae	*Sida cordifolia* L. subsp. *cordifolia*	Shrub	-	9.10
Malvaceae	*Triumfetta pilosa* Roth var. *pilosa*	Shrub	-	27.30
Melastomataceae	*Dissotis canescens* (E.Mey. ex R.A.Graham) Hook.f.	Shrub	-	18.20
Oxalidaceae	*Oxalis corniculata* L.	Herb	X	39.89
Phyllanthaceae	*Phyllanthus polygonoides* Nutt. ex Spreng.	Shrub	-	61.90

Poaceae	*Cynodon dactylon* (L.) Pers.	Graminoid	-	19.37
Poaceae	*Digitaria ciliaris* (Retz.) Koeler	Graminoid	-	49.75
Poaceae	*Digitaria eriantha* Steud.	Graminoid	-	20.95
Poaceae	*Digitaria longifolia* (Retz.) Pers.	Graminoid	-	0.70
Poaceae	*Digitaria ternata* (A.Rich.) Stapf	Graminoid	-	6.34
Poaceae	*Panicum maximum* Jacq.	Graminoid	-	60.78
Poaceae	*Rendlia altera* (Rendle) Chiov.	Graminoid	-	20.40
Poaceae	*Tragus berteronianus* Schult.	Graminoid	-	1.82
Poaceae	*Urochloa oligotricha* (Fig. & De Not.) Henrard	Graminoid	-	18.20
Pteridaceae	*Cheilanthes viridis* (Forssk.) Sw.	Herb	-	51.57
Rubiaceae	*Richardia brasiliensis* Gomes	Herb	X	36.40
Rubiaceae	*Rubus cuneifolius* Pursh	Shrub	X*	48.53
Solanaceae	*Solanum nigrum* L.	Shrub	X	48.53
Verbenaceae	*Lantana camara* L.	Shrub	X*	135.69
Verbenaceae	*Lantana rugosa* L.	Shrub	-	18.20
Verbenaceae	*Verbena bonariensis* L.	Herb	X	36.40
Verbenaceae	*Verbena brasiliensis* Vell.	Herb	X	190.80

Values represent the total density of species found within the sampling area (n = 960 pots [4 reps x 8 quadrats x 30 sites]).
X* = Invasive alien plant

Table C2. Total species richness and density across all sampling sites.

Site*	**Total richness**			**Total density (Germinants/m²)**			**Site***	**Total richness**			**Total density (Germinants/m²)**		
	Indigenous species	Alien species	Total species	Indigenous species	Alien species	Total species		Indigenous species	Alien species	Total species	Indigenous species	Alien species	Total species
1[VL]	9	4	13	66.84	14.45	81.29	**16**[M]	3	5	8	38.91	51.06	89.97
2[H]	10	6	16	73.76	29.12	102.88	**17**[VL]	7	1	8	114.73	151.13	163.26
3[M]	7	10	17	58.91	180.99	239.9	**18**[M]	9	4	13	122.77	127.4	250.17
4[L]	12	6	18	160.85	140.36	301.21	**19**[L]	6	6	12	26.79	68.25	95.04
5[L]	6	1	7	31.19	18.2	49.39	**20**[M]	5	4	9	18.39	41.77	60.16
6[L]	5	4	9	86.23	45.99	132.22	**21**[L]	4	8	12	17.73	118.22	135.95
7[H]	6	3	9	45.35	16.45	61.80	**22**[H]	4	6	10	41.69	121.33	163.02
8[L]	6	7	13	66.75	101.33	168.08	**23**[L]	5	4	9	30.1	37.92	68.02
9[H]	6	4	10	38.14	74.01	112.15	**24**[VL]	6	8	14	52.12	101.11	153.23
10[M]	7	2	9	63.77	54.6	118.37	**25**[VH]	5	5	10	22.32	82.11	104.43
11[H]	3	6	9	6.66	123.36	130.01	**26**[L]	8	4	12	54.09	47.15	101.24
12[H]	7	5	12	77.11	150.15	227.26	**27**[VL]	6	6	12	43.39	85.94	129.33
13[H]	8	9	17	78.79	139.09	217.88	**28**[L]	6	4	10	78.84	84.93	163.77
14[L]	7	7	14	69.27	112.42	181.69	**29**[L]	6	4	10	86.2	81.9	168.10
15[H]	5	6	11	63.7	62.12	125.82	**30**[VL]	4	5	9	24.36	99.49	123.85

Values represent total species richness and density at each site (n = 960 pots [4 replicates x 8 quadrats x 30 sites]).

Table C3. Species richness and diversity indices for seed banks at sampling sites.

Site	Total species richness	Shannon's index (H)	Shannon's exponential index (H')	Simpsons's inverse index (1/D)
1^{VL}	13	2.22	8.54	6.81
2^{H}	16	2.23	7.54	5.04
3^{M}	17	2.17	7.68	5.21
4^{L}	18	2.22	7.94	5.60
5^{L}	7	1.67	4.93	4.30
6^{L}	9	1.66	4.74	3.90
7^{H}	9	2.03	6.94	6.23
8^{L}	13	2.27	8.05	7.02
9^{H}	9	1.95	6.87	6.03
10^{M}	9	1.79	5.25	4.32
11^{H}	9	1.57	4.43	3.41
12^{H}	12	2.05	6.62	5.40
13^{H}	15	2.18	10.10	7.98
14^{L}	14	2.20	8.32	6.97
15^{H}	11	2.08	7.17	5.96

16^{M}	6	1.25	4.00	2.97
17^{VL}	8	1.26	3.30	2.59
18^{M}	13	1.70	4.96	3.58
19^{L}	12	2.19	8.04	6.61
20^{M}	9	1.88	6.34	5.52
21^{L}	12	2.01	7.05	5.83
22^{H}	10	1.43	3.31	2.19
23^{L}	9	1.84	5.81	4.68
24^{VL}	14	2.40	10.21	9.09
25^{VH}	10	1.82	5.98	4.55
26^{L}	12	2.24	8.92	7.76
27^{VL}	12	2.29	8.22	7.43
28^{L}	10	1.66	4.71	3.81
29^{L}	10	1.84	5.71	4.79
30^{VL}	9	1.68	5.06	4.06

Values represent species richness and diversity indices at each site (n = 960 pots [4 replicates x 8 quadrats x 30 sites]).

Table C4. Sørenson and Jaccard similarity indices between soil seed banks (SBs) and standing vegetation (SV) within each site.

Site	**Sørenson similarity index (SSB vs SV)**	**Jaccard similarity index (SSB vs SV)**	**Disturbance**	**Vegetation**
1^{VL}	0.160	0.086	21	forest
2^{H}	0.163	0.088	34	forest
3^{M}	0.196	0.108	30	thicket
4^{L}	0.421	0.266	27	forest
5^{L}	0.125	0.066	27	grassland
6^{L}	0.333	0.200	27	savanna
7^{H}	0.226	0.127	33	grassland
8^{L}	0.227	0.128	28	thicket
9^{H}	0.074	0.038	33	savanna
10^{M}	0.200	0.111	30	savanna
11^{H}	0.344	0.208	39	savanna
12^{H}	0.368	0.225	33	grassland
13^{H}	0.352	0.214	33	forest
14^{L}	0.217	0.121	27	forest
15^{H}	0.228	0.129	33	forest
16^{M}	0.285	0.166	30	savanna

17^{VL}	0.157	0.085	24	savanna
18^{M}	0.222	0.125	30	thicket
19^{L}	0.256	0.146	26	savanna
20^{M}	0.270	0.156	30	savanna
21^{L}	0.235	0.133	27	grassland
22^{H}	0.238	0.135	36	forest
23^{L}	0.216	0.121	26	savanna
24^{VL}	0.340	0.205	22	thicket
25^{VH}	0.139	0.075	47	savanna
26^{L}	0.205	0.114	28	forest
27^{VL}	0.296	0.173	23	grassland
28 ^{L}	0.270	0.156	27	savanna
29 ^{L}	0.303	0.178	27	grassland
30 ^{VL}	0.333	0.200	22	savanna

Values represent similarity indices between soil seed bank vegetation and standing vegetation at each site (n = 960 pots [4 replicates x 8 quadrats x 30 sites]).

Table C5: Principle Component Analysis showing relationships between level of disturbance and soil seed bank floristics (alien and indigenous richness and density [germinants/m^2]) across all sites.

	Component	
	PC1	PC2
Total species density	0.913	-
Total species richness	0.903	-
Indigenous species density	0.749	0.545
Alien species richness	0.641	-0.625
Alien species density	0.593	-0.700
Indigenous species richness	0.636	0.651
Level of disturbance	-	0.515

Values represent relationships (R^2) between variables (n = 960 pots [4 replicates x 8 quadrats x 30 sites]).

APPENDIX D – Chapter 5

Table D1. Summary of the lipid melting profiles of freshly harvested and buried seeds for diverse periods of time measured by DSC. Values indicate the average of 2 – 4 values ± standard deviation. Same letters within each species indicate that values are not significantly different at a 0.05 level. Onset/peak1 indicates the main (larger) melting peak of the DSC scan.

Species	**Part of the seed**	**Burial time (months)**	**WC (gH_2O/gDW)**	**ΔH lipid (mJ/gdw)**	**onset1**	**peak1**	**Predicted FA**	**onset2**	**peak2**	**Predicted FA**
Solanum mauritianum	whole	0	0.046 ± 0.006	22.3 ± 1.7[a]	-12.1 ± 0.3[a]	-7.0 ± 0.3[a]	Oleic	-36.3 ± 0.1[a]	-31.9 ± 0.2[a]	Linolenic
	whole	3	0.036 ± 0.004	23.4 ± 2.5[a]	-12.4 ± 0.3[a]	-6.9 ± 0.2[a]	Oleic	-36.4 ± 0.2[a]	-31.9 ± 0.1[a]	Linolenic
Melia azedarach	whole	0	0.038 ± 0.002	31.9 ± 1.7[a]	-35.0 ± 0.9[a]	-22.9 ± 2.7[a]	Linolenic	-	-	-
	whole	3	0.035 ± 0.002	31.3 ± 1.9[a]	-36.0 ± 0.2[b]	-27.8 ± 0.7[b]	Linolenic	-12.7 ± 0.5	-4.3 ± 0.7	Oleic
Ricinus communis	cotyledon	0	0.024 ± 0.001	15.1 ± 4.5[ab]	-55.6 ± 0.2[a]	-47.8 ± 0.3[a]	Ricinoleic	-	-	-
	cotyledon	3	0.032 ± 0.0003	15.3 ± 0.6[a]	-55.9 ± 0.1[a]	-48.0 ± 0.1[a]	Ricinoleic	-	-	-
	cotyledon (rotten)	3	0.071 ± 0.011	3.0 ± 0.3[d]	-79.5 ± 1.3[c]	-70.2 ± 0.7[d]	Ricinoleic	-	-	-
	cotyledon	6	0.028 ± 0.001	10.8 ± 1.0[bc]	-59.0 ± 0.2[b]	-50.5 ± 0.6[b]	Ricinoleic	-	-	-
	cotyledon	9	0.026 ± 0.003	10.6 ± 0.8[c]	-59.1 ± 0.5[b]	-51.5 ± 0.6[c]	Ricinoleic	-	-	-
Canna indica	embryo	0	0.097 ± 0.006	3.7 ± 2.0[a]	-33.3 ± 2.9[a]	-21.1 ± 2.8[a]	Linolenic	9.4 ± 1.8[a]	13.8 ± 1.6[a]	Capric
	embryo	3	0.132 ± 0.003	4.3 ± 0.8[a]	-32.4 ± 1.4[a]	-21.1 ± 1.0[a]	Linolenic	8.8 ± 1.0[a]	12.2 ± 1.1[a]	Capric

	embryo	6	0.134 ± 0.013	3.0 ± 0.2^{a}	-34.6 ± 2.8^{a}	-28.1 ± 0.8^{c}	Linolenic	3.4 ± 0.2^{b}	8.4 ± 0.1^{b}	Capric
	embryo	9	0.112 ± 0.011	2.9 ± 0.6^{a}	-32.5 ± 3.2^{a}	-24.7 ± 1.9^{b}	Linolenic	2.1 ± 1.0^{b}	6.9 ± 0.9^{c}	Capric
Senna didymobotrya	whole	0	0.045 ± 0.018	< 0.1*	nd	nd	-	nd	nd	-
	whole	3	0.084 ± 0.003	0.8 ± 0.4	-36.3 ± 1.5	-19.1 ± 1.4	Linolenic	4.0 ± 1.8	9.0 ± 1.6	Capric
	whole (rotten)	6	0.090 ± 0.007	-	-	-	-	-	-	-

**Senna didmobotrya* (time 0) did not show apparent lipid melting transitions because baseline was very bumpy, but it showed a small lipid crystallization peak, indicting the presence of a lipid; nd: non-determined.