Assessing the impacts of *Lantana camara* and opportunities for ecological restoration after its removal: does clearing facilitate both soil and native vegetation recovery?

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Abstract

Invasive alien plants (IAPs) are one of the major contributing factors to biodiversity loss, and *Lantana camara* is among the top ten alien invaders worldwide. *Lantana camara* threatens native biodiversity and human health, prevents natural succession, and has an economic and environmental impact globally. With current climate change and future predictions, these IAPs are anticipated to continue posing huge threats to ecosystem composition, structure, and function. Even though *L. camara* is a widespread IAP, there is still limited knowledge in South Africa on how it influences soil physicochemical properties at the species level, vegetation communities, and soil seed banks at the community level following its invasion. There is also minimal knowledge on the management and control (i.e., clearing for restoration purposes) of *L. camara* in South Africa, especially in the Eastern Cape province of South Africa. To address the knowledge gap, this thesis was structured into three main aspects: understanding *L. camara* invasion mechanisms, evaluating invasion impacts on both the aboveground and belowground communities, and invasion management. The main objectives of this thesis were (i) to examine how *L. camara* invasion (at a species level) affected soil physicochemical properties across different seasons, (ii) to assess how *L. camara* influences natural vegetation (at a community level), (iii) to examine the effects of *L. camara* invasion (at the community level) on belowground soil seed banks and also assess the availability of pioneer native species and IAPs in the soil seed banks, and (iv) to evaluate soil and vegetation responses following *L. camara* clearing in comparison to invaded and uninvaded conditions. To answer these objectives, different studies were carried out in the Eastern Cape province, South Africa, on various farms within the Albany Thicket Biome.

The results (Chapter 3) show that *L. camara* alters and modifies some soil physical properties, such as soil infiltration rate, repellency, and soil penetration resistance, in the communities it invades. A significant decrease in soil penetration under the *L. camara* canopy was observed compared to soils from the edge and out position. Moreover, significantly faster infiltration rates were observed in the canopy and edge positions than in the out position. The study also observed that these modifications in soil physical properties vary depending on the season. A seasonal comparison in soil penetration showed that soil was more compact in the dry season than the wet season, and significantly faster infiltration rates were observed in summer than in the other seasons. The soil collected under the invaded sampling positions was mostly wettable (80–100%), and not strongly, severely, or extremely repellent across all the seasons. The changes in soil properties caused by *L. camara* could create favourable conditions for its

growth and invasion. Seasonal changes in soil properties also highlight how environmental conditions, especially temperature and rainfall patterns, can affect soil physical properties.

The findings in Chapter 4 observed both the negative and positive impacts of *L. camara*, where the species did not have negative effects on species richness, diversity, or cover of some native species growth forms (i.e., graminoids and forbs). For all species, both species richness and Shannon-Wiener (*H*') were significantly higher in the *L. camara* invaded condition compared to the uninvaded condition. The Simpson's (*J*') and Pielou's evenness (*D*') indices, however, showed no differences between the invasion conditions. Furthermore, the effects of *L. camara* on vegetation cover were growth form-dependent, with differences being noted for trees and shrubs but not for graminoids and forbs. Changes in vegetation structure and composition were also noted where *L. camara* created favourable conditions for some species to co-occur with it, meaning that its known trait of changing soil physicochemical properties could benefit some species. Generally, the results of this study showed that the effects of *L. camara* on vegetation are varied and do not have a predictable pattern, so they should not be generalised.

The findings (Chapter 5) also indicate that the *L. camara* invasion had a negative impact on seedling abundance and composition but not species diversity and richness. This is evident through the decrease in seedling abundance of forbs and graminoids in the *L. camara* invaded condition. *Lantana camara* also acted as a refuge for some plant species, mostly native forbs and grasses, including *Aptenia cordifolia*, *Chamaesyce prostrata*, *Oxalis* spp., and *Setaria* spp., as well as alien forbs such as *Bidens pilosa*, *Plantago lanceolata*, and *Taraxacum officinale*, suggesting *L. camara* does not entirely eliminate less competitive plant species but can co-exist with them. *Lantana camara* also displaced some native species, and this could be associated with their displacement in the standing vegetation. Moreover, the species also displaced the seed banks of some alien species, thus showing its competitive ability. Overall, *L. camara* invasion negatively influenced soil seed bank seedling abundance and composition of some species, but not diversity and richness.

The results in Chapter 6 indicated that clearing *L. camara* is an effective method for reducing its population. However, our findings suggest that clearing alone may not be enough to re-establish these communities with native species. This is because the results of this study showed varied changes in soil properties and native vegetation (species richness, species diversity, percentage cover, and composition) after *L. camara* clearing. For example, soil moisture and soil penetration resistance showed no significant differences among the invasion conditions; only monthly variations were observed. This is an indication that seasonality influenced these properties. Significantly lower soil infiltration rates were observed in the

cleared condition compared to the other conditions and were influenced by the months and the interaction of the clearing conditions and months. The water droplet penetration time showed no significant difference among the clearing conditions over the three months, and all the soil collected from the three clearing conditions was mostly wettable. Soil chemical properties showed that the *L. camara* invaded and cleared conditions had significantly lower soil pH compared to the uninvaded condition, and an increase in soil pH was observed after clearing *L. camara.* Vegetation characteristics showed that both the Shannon-Wiener index (H') and the Simpson's index (D') were lower in the invaded and cleared conditions compared to the uninvaded condition, and significant differences were observed. A slight increase in the H' and D' indices was also observed after clearing *L. camara.* The mean percentage cover for trees and shrubs was significantly higher in the invaded condition than in the cleared and uninvaded conditions. However, the mean percentage cover of forbs and graminoids was similar among the invaded, cleared, and uninvaded conditions, and no significant differences were observed. When *L. camara* was cleared, native species recovery was observed and was more notable in the understory species. Overall, some signs of vegetation recovery were observed, although challenges such as secondary invaders and re-invasion by *L. camara* were noted in the cleared areas. This chapter then concluded that active restoration interventions should be incorporated during restoration to fast-track soil and vegetation recovery.

The findings of this thesis will make several significant contributions to the field of biological invasions and provide baseline information that can be used in future studies. These are discussed in the various research chapters. Overall, the thesis concludes that *L. camara* invasion has varied impacts on native vegetation and soil, and its clearance, should be prioritised to reduce the negative impacts. However, *L. camara* cleared areas (by WfW in South Africa) require follow-up and monitoring at an early stage to assess vegetation and soil restoration success. In addition, active management measures after *L. camara*'s removal should be considered for clearing programmes to yield positive ecosystem recovery.

Keywords: active restoration; disturbance; ecological impacts; ecosystem restoration; invasion drivers; invasive plants; passive management; physicochemical properties; recovery; seed banks

Declaration

I, Uviwe Bolosha, hereby declare that the entire work found within this document titled “Assessing the impacts of *Lantana camara* and opportunities for ecological restoration after its removal: does clearing facilitate both soil and native vegetation recovery?” is my original work and that all the sources used or quoted have been appropriately acknowledged within the text and list of references. The thesis is submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in Environmental Science at Rhodes University and has not been submitted for any degree nor examination at any other university.

Uviwe Bolosha		25/05/2024
………………………..	…………………………….	…………………
Name	**Signature**	**Date**

Dedication

To my amazing children, Lilo & Itha_landa Bolosha

and

late sister Zukiswa Kitsili

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List of abbreviations

ANOVA	Analysis of variance
DBH	Diameter at Breast Height
DEA	Department of Environmental Affairs
DEFF	Department of Environment, Forestry, and Environment
IAPs	Invasive Alien Plants
IAS	Invasive Alien Species
NEMBA	National Environment Management Biodiversity Act
NISC	National Invasive Species Council
PCA	Principal Component Analysis
WDPT	Water Droplet Penetration Time
WfW	Working for Water

Chapter 1: General introduction

1.1. Introduction

The intensification of global development has been associated with increased human mobility, which in turn has led to many species being introduced outside of their natural ranges (Lockwood et al. 2005; Simberloff et al. 2013; IPBES, 2019; IPBES, 2023). Biological invasions are a global anthropogenic problem that alter ecosystem composition, structure, and function (Ricciardi et al. 2017). Globally, Invasive Alien Species (IAS) threaten native environments (e.g., causing biodiversity loss) and socio-economic systems (e.g., human health) (Mack et al. 2000; Taylor et al. 2012). Apart from climate change and habitat loss, invasion by IAS is globally regarded as a key driver of biodiversity loss (Lowe et al. 2000). Estimates suggest that approximately 16% of the world’s biodiversity hotspots are vulnerable to invasion by IAS (Ealry et al. 2016). Andreu et al. (2009) elaborated on the direct economic costs caused by biological invasions and how they cause damage to infrastructure, resulting in the loss of production of natural resources and natural capital. Pimentel et al. (2005) estimated the economic damage caused by biological invasions in the United States to exceed US $120 billion per year, while Sinden et al. (2004) estimated that approximately US $13 million is spent each year on managing invasive weeds in Australia. Recent estimates by Diagne et al. (2021) and Fantle-Lepczyk et al. (2022) reported an increase in these costs per decade, and the current total costs associated with invasions were reported to be about US $1.29 trillion. According to current estimates, South Africa invests around ZAR 2 billion (or roughly US $111 million at the current exchange rate) annually in the management of IAS (Le Maitre et al. 2020; van Wilgen et al. 2020).

According to Keam et al. (2009), biological invasions usually follow a sequence that starts with introduction, progresses to establishment, and culminating in spread and invasion. A modified framework of IAS invasion by Blackburn et al. (2011) showed that an introduced species passes through four invasion stages, namely transport, introduction, establishment, and spread. Hulme et al. (2008) suggest that biological invasion occurs through several pathways that are related to transport and trade. This means that developments in the transport systems and current trade networks may result in species being distributed outside their natural range. Invasive Alien Plants (IAPs) are among some of the species that have been intentionally or unintentionally introduced into different regions outside their natural range (Keller et al. 2011; Wardle et al. 2011). According to Keller et al. (2011), the most common pathways for introducing IAPs are intentional introductions for ornamental and horticultural purposes, whereas unintentional introductions are mainly through contaminants and ship movement for agricultural trade. For example, most invasive *Acacia* and *Eucalyptus* species were intentionally introduced in South Africa by the forestry plantation industry for wood and tannin during the colonial period (Richardson et al. 2020).

Once IAPs have been introduced into a new area, several species-specific traits have been associated with their expansion, e.g., prolific seeding, widely dispersed seeds, fast reproduction rates, a long flowering season, the ability to regenerate from seeds, stems, and roots, unpalatability, and having multiple dispersal vectors (Pysek and Richardson, 2008; Pysek et al. 2009; van Kleunen et al. 2010). These traits give IAPs an advantage and make them effective competitors. Lonsdale (1999) also reported on how plant invasion can be facilitated by factors such as (1) the number of seeds being recruited into a new environment; (2) the basic characteristics of the species; and (3) the susceptibility of the habitat to new invasions where habitats become vulnerable due to a variety of factors such as disturbance, lack of native competitors, absence of natural predators or diseases, altered environmental conditions, human activities, and climate change (Ibanez et al. 2021). Thus, IAPs have been observed to be more competitive than most native species (Zengeya et al. 2020). Invasive alien plants compete with native plant species for space, light, nutrients, and water (Levine et al. 2003). In South Africa, approximately 383 plant species have been listed as IAPs under the National Environmental Management: Biodiversity Act (NEM:BA A&IS Regulations of 2020), with plants such as *Acacia* spp., *Chromolaena odorata*, *Eucalyptus* spp., *Hakea* spp., *Lantana camara*, *Pinus* spp., and *Solanum mauritianum* listed as major invaders with substantial effects on biodiversity and ecosystem services (Clusella-Trullas and Garcia, 2017; van Wilgen et al. 2020).

Besides the above-mentioned invasion traits, several ecosystem-based traits facilitate the spread of IAPs, i.e., climate change, fire, agricultural practices, land abandonment, and habitat disturbance (Bellingham et al. 2005; Hulme, 2009). For example, agricultural areas, grazing lands, and different land use types in urban areas provide conducive environments and become source pools for new infestations and their spread (Lundgren et al. 2004; Ruwanza, 2016; Wang et al. 2016). Additionally, riparian zones, roadways, railway tracks, and canals serve as corridors for the establishment and spread of IAPs (Sharma et al. 2005). For example, Ruwanza and Mhlongo (2020) showed that river and road intersections facilitate *L. camara* invasions in Limpopo province, South Africa. Invasive alien plants have significant impacts on a diverse range of habitat types and communities (terrestrial and aquatic habitats) (Mack et al. 2015; Pathak et al. 2021; Erckie et al. 2022), and Cronk and Fuller (2015) acknowledge how IAPs can pose significant threats to many of Africa's conservation areas. Evans (2003) outlined the six types of impacts caused by invasive species: (1) production impacts; (2) price and market impacts; (3) trade impacts; (4) food security and nutrition impacts; (5) human health impacts; and (6) environmental and economic impacts. The standardised impacts of invasive species by the IUCN include posing risks to human health; they are the major drivers of biodiversity loss and species extinctions; and they negatively affect food security and livelihoods. Fundamentally, IAS have impacts on native species, on the economy, and on the quality of life (IPBES, 2023).

It is well recognised that agriculture contributes significantly to economic growth and food security (Meijerink and Roza, 2007; Wu et al. 2014); however, it may also facilitate plant invasions. Several studies have recorded a positive correlation between agricultural practices and invasion and how the intensity of agricultural practices plays a major role (Dostalek et al. 2014; O'Connor and van Wilgen, 2020). By 2030, as per the National Development Plan of South Africa, the government plans to improve national food security for smallholders and subsistence farmers through increased agriculture (National Development Plan, 2011). However, if associated with increased plant invasion, this would be difficult to achieve as they have adverse impacts on grazing lands (O'Connor and van Wilgen, 2020). The perceived impacts may therefore precipitate a crisis within the agricultural sector, which will then affect many large- and small-scale farmers. An important and critical issue thus relates to how to manage and control IAPs because if they are not managed and controlled, they will spread and invade other communities, resulting in a significant decline in ecosystem services and altering many benefits that humans receive from the environment, disrupting their livelihoods (Turpie et al. 2008). Approaches and initiatives such as clearing, chemical use, and prescribed fire have been implemented to manage, control, and counter the adverse effects of IAPs (Lorenzo and Morais, 2023). However, these have their own challenges; e.g., the use of chemicals to control IAPs can result in adverse effects on the environment, and the timing of prescribed fires may limit the effectiveness of managing IAPs. Other IAP management challenges, such as secondary invasion, re-invasion, and the influence of environmental factors such as climate change and fire, have been documented (van Rensberg et al. 2017; Torres et al. 2018; Finch et al. 2021). In some cases, challenges are associated with factors such as the type of invader, the extent of the invasion, and land use. Financial limitations and a lack of human capital have also contributed to the failure of IAP management programmes (van Wilgen et al. 2020). Although these challenges may constrain the management of IAPs (Day et al. 2003; Love et al. 2009; Ruwanza et al. 2013; van Rensberg et al. 2017), some studies have reported that the control of IAPs through clearing can yield positive results through both suppressing the invader and facilitating native plant recovery (van Wilgen et al. 2012; Ruwanza et al. 2013). Given that management of IAPs is necessary to reduce negative impacts, more research is needed to generate scientific knowledge and provide evidence-based information that can be used to manage biological invasions.

1.2. Theoretical background

1.2.1. Invasive alien plant invasion theories and frameworks

Biological invasions are one of the major drivers of biodiversity loss globally (IPBES, 2019; van Wilgen et al. 2020), and IAPs are characterised by traits that facilitate their spread and invasion (Mathakutha et al. 2019). Plant invasions are a repercussion of globalisation (Mack et al. 2000), and disturbance tends to promote plant invasions (Rahlao et al. 2010; O'Connor and van Wilgen, 2020). There is no doubt that IAPs thrive and successfully invade disturbed habitats. But the questions are how do they invade? Which traits are associated with invasiveness? And which habitats are prone to invasion by IAPs? A systematic study of biological invasions under the SCOPE program was formulated in the 1980s to answer the above questions, particularly to identify which species are successful invaders, which habitats are prone to invasion, and which management approach best reduces invasion (Richardson and Pysek, 2006).

To understand invasion success, it is necessary to first understand the first stage of the invasion process (introduction), which requires IAPs to overcome several barriers that can constrain their establishment and spread, thus preventing them from being invasive. During the introduction stage, a key barrier to overcome is the geographic barrier, where humans play a key role in moving IAPs from one area to another. It is believed that increased human movement has facilitated species movement from one place to another, thus overcoming many geographic barriers (Richardson et al. 2000). Although humans are the main drivers of moving IAPs, natural processes such as river flooding and wind have also resulted in the movement of IAPs from one geographic area to another (Richardson et al. 2000). Once an IAP has overcome the geographic barrier and arrived in a new area, it passes through several stages (colonisation, naturalisation, and invasion) until it becomes invasive with some noticeable impacts. A species may be classified as an alien (has arrived in an area and overcomes geographic barriers), a casual alien (has overcome environmental and reproduction barriers), naturalised (has overcome dispersal barriers), or invasive (has overcome all barriers and causes impacts) (Richardson et al. 2000). Some of these barriers are documented by Richardson et al. (2000), Henderson et al. (2006), and Foxcroft et al. (2008) and include geographic barriers (oceans), environmental barriers (abiotic and biotic) such as temperature, deficient levels of soil nutrients, parasites, herbivores, and competitors, and dispersal barriers (ability to reproduce and spread).

Several hypotheses have been put forward to explain plant invasions and discuss how these species become successful invaders (Hierro et al. 2005; Inderjit et al. 2005; Cadotte et al. 2021). Understanding the factors associated with IAP growth and spread is fundamental to minimising the negative impacts and developing effective management measures (Levine et al. 2003).

The first hypothesis discussed is the enemy release hypothesis, which focuses on the biotic interactions where IAPs in a new range lack natural enemies (i.e., pathogens and herbivores) that usually influence or limit their population size and density in their native range (Joshi and Vrieling, 2005). Keane and Crawley (2002) report on three main arguments associated with this hypothesis: (1) natural enemies play a crucial role in controlling plant populations; (2) plant enemies have huge impacts on native vegetation as compared to invasives; and (3) a decrease in enemy regulation may benefit certain species, thus resulting in higher plant population growth and density. Studies by Torchin and Mitchell (2004) on pathogens, Eschtruth and Battles (2009) on herbivores, and Lucero et al. (2019) on rodents reported how the absence, decrease, or release of natural enemies leads to successful invasion. This theory then builds understanding of the invasion success of *L. camara* in South Africa (which is further discussed in detail in the upcoming chapters) and how the apparent lack or limitation of natural enemies can aid in making *L. camara* a widespread and noxious IAP despite intense management and control efforts (Baars and Neser, 1991; Vardien et al. 2012). *Lantana camara*, a highly invasive plant, thrives in disturbed habitats such as river banks, roadsides, abandoned agricultural lands, and forest margins (Vardien et al. 2012). It has become of significant concern in South Africa due to its ecological and economic impacts (Vardien et al. 2012; Ruwanza et al. 2020). In South Africa, it is classified as a category 1b invasive plant under the Alien and Invasive Species Regulations, National Environmental Management: Biodiversity Act of 2004. This designation requires land occupiers to control or remove it, with no trade or planting allowed. The plant was introduced into South Africa in 1858 at Cape Town, Western Cape province (Stirton, 1977), and it was declared a noxious weed in 1946 in KwaZulu Natal (Oosthuizen, 1946; Wells and Stirton, 1988).

The second hypothesis is the resource availability hypothesis (Kuebbing et al. 2013). Plant species require resources to colonise and establish new areas, and resource availability benefits both native and IAPs. However, an increase in resource availability increases the probability that species such as IAPs that have high phenotypic plasticity will successfully invade and spread (Richardson and Pysek, 2006; Liu et al. 2017). Davis et al. (2000) discussed how resources (water, nutrients, light, and oxygen) and competitive ability are the key factors driving the invasion success of IAPs. Ruwanza and Shackleton (2016), Gibbons et al. (2017), and Liu et al. (2017) also demonstrate how soil physicochemical properties such as soil moisture and soil nutrients can facilitate the invasion of various IAPs. This study embraces this theory to enhance understanding of *L. camara*. In most disturbed areas (i.e., roadsides, farmland, degraded land, grazing areas, riparian areas, etc.), *L. camara* uses the available resources, which in turn promotes its invasiveness. For example, in most agricultural areas where disturbance frequencies are higher, *L. camara* generally successfully invades and spreads.

The third commonly considered hypothesis is the niche hypothesis, which considers how IAPs can take advantage of unfilled niches (space) or underutilised resources, hence becoming successful invaders (Hierro et al. 2005). For instance, *L. camara* may invade and recruit in disturbed or empty niches (bare soil, reduced vegetation cover, and cleared areas) and use available resources, specifically excess nutrients in the soil. This can occur through *L. camara* influencing soil properties in ways that favour its growth over natives. The opportunity windows hypothesis discussed by Johnstone (1986) and Rai (2013) links the invasion success of IAPs with the availability of empty niches, and this availability fluctuates spatio-temporally. This theory emphasises the significance of the temporal availability of resources in influencing IAPs.

The fourth common theory is the invasion meltdown theory, which, like others, is acknowledged for being applicable across different habitat types (Simberloff and von Holle, 1999). This theory highlights how the presence of IAPs in an ecosystem promotes the invasion of additional plant species, thus increasing their probability of survival or ecological impact (Simberloff and von Holle, 1999). This theory has two assumptions: (1) positive interactions where an IAP can facilitate invasion by other IAPs; and (2) negative interactions where an IAP acts as a barrier for native species to arrive in new habitats.

The novel weapon hypothesis and the propagule pressure hypothesis are the fifth and sixth hypotheses that are also related to the success of IAPs (Cadotte et al. 2021). Inderjit et al. (2005) pointed out how some of the invasion hypotheses share similarities or overlap. Furthermore, Blumenthal et al. (2009) have reported on the synergy associated with the above-mentioned hypotheses and explained how these individual hypotheses cannot explain the success of every IAP. They then conclude that the interaction of these hypotheses is required to explain the success of IAP growth and spread. Thus, Jeschke and Heger (2018) recently formulated an integrated framework of hypotheses to better understand the dynamics of invasion theories, and Dai et al. (2020) discussed how the various hypotheses play a part in explaining plant invasions over time. This thesis presents and discusses several ecological characteristics related to *L. camara*'s success, effects, and management. The significant research done on understanding IAPs suggests that plant invasions are complex and context-dependent. The goal of studying plant invasions is to develop management strategies or models that will eliminate IAPs, reduce their abundance and seed supply, and, in turn, promote vegetation and soil recovery.

1.2.2. Models of restoring invaded ecosystems

Given that millions of hectares of land have been invaded by IAPs in South Africa (Zengeya and Wilson, 2020), their threat to biodiversity and how they lead to alterations in ecosystem composition, structure, and function have been recognised and documented (Pimentel et al. 2005). Clearing and restoration strategies are therefore fundamental and imperative. Ecological restoration is a growing field that is considered a way of conserving biological diversity and mitigating the loss of ecosystems (Choi, 2004). Its goal is to optimise ecosystem recovery; hence, Gann and Lamb (2006) documented that it must address four critical factors: increase biodiversity, improve human livelihoods, empower local people, and increase ecosystem productivity.

Richardson et al. (2007) and Holmes et al. (2020) noted how ecological restoration is a protracted, complicated process, and all the tasks involved in the restoration process need to be considered and planned. Depending on the IAP being cleared and the extent of the invasion, various ecological restoration initiatives after IAP clearing have been discussed, and some have shown that they may not always result in the expected outcomes. Norton (2009) noted that to conduct effective restoration of an IAP infested area, long-term investments are required. Nonetheless, Hall et al. (2021) reported on how restoration initiatives are mostly assessed in the short-term and how they mostly focus on vegetation. Research has also shown that in some areas, recovery can occur without intervention (passive), whereas in others, additional interventions are required (active) (Blanchard and Holmes, 2008; Ruwanza et al. 2013; Lamb et al. 2022).

Passive restoration is a strategy that relies only on the natural recovery of an ecosystem after clearing IAPs (Mostert et al. 2015; Holmes et al. 2020). Le Maitre et al. (2011) documented how the majority of restoration programs often use this approach since it is regarded as being cost-effective. However, this restoration strategy is often constrained by the unavailability of native seed banks or seedlings (Vosse et al. 2008; Ruwanza et al. 2013), secondary invaders or re-invasion by the same IAP that was cleared (Holmes et al. 2000; Nsikani et al. 2019), and legacy effects, which refer to the long-lasting impacts of IAPs on soil properties and ecosystem function (Nsikani et al. 2018, 2020). This then means that it is crucial to properly plan restoration and apply the correct clearing techniques. Studies such as Cuevas and Zalba

(2010) and Ruwanza et al. (2013) evaluated the ecological responses of passive restoration after clearing IAPs, and in cases where there were limited chances of ecosystem recovery, active restoration was recommended.

In circumstances where ecosystems do not fully recover after clearing of IAPs, active restoration is often recommended and includes additional restoration interventions (Holl and Aide, 2011). The active restoration strategy requires a lot of resources: labour, skills, and funding; hence, Holmes et al. (2008) acknowledge the high cost of this approach. Authors such as Gaertner et al. (2011), Ruwanza et al. (2013), and Froeschlin et al. (2022) have modelled active restoration and suggested several recommendations that should be taken into consideration. The active restoration strategy often includes planting native species, improving management measures (addition of fertilisers, reseeding, and ploughing), and manipulating disturbance regimes through thinning and burning (Atkinson and Bonser, 2020). Fill et al. (2017) and Hall et al. (2021) argued that active restoration, particularly native plant seed sowing, can improve vegetation recovery in IAP cleared areas.

Jones et al. (2018) and Holmes et al. (2020) report on the importance of clearly articulating restoration goals and first considering passive restoration. If passive restoration does not achieve the goals, then active restoration strategies should be applied. The most effective restoration method, however, depends on site-specific characteristics. The relevance of long-term monitoring and follow-up during restoration has been emphasised (McConnachie et al. 2012; Holmes et al. 2020), and this is to prevent scenarios that can hinder the restoration process. In this thesis, vegetation and soil recovery after *L. camara* clearing were examined with the aim of understanding passive restoration after clearing.

1.3. Rationale of the study

Even though much research has been done on IAPs in South Africa, it is evident that there are still several unexplored avenues pertaining to *L. camara* in the Eastern Cape province. Agricultural areas, particularly abandoned old fields in the moister regions, are dominated by *L. camara* (Jevon and Shackleton, 2015), yet little is known regarding its invasion process, impacts, and management. *Lantana camara*'s detrimental impacts have spurred global research efforts on this IAP (Shackleton et al. 2017; Hamad et al. 2022; Raphela and Duffy, 2022). It is therefore on this premise that this thesis seeks to further examine the dynamics of *L. camara* invasion in terrestrial habitats in South Africa's Eastern Cape. Planning and designing appropriate control and management strategies require an understanding of the various components linked to the *L. camara* invasion, particularly species-specific invasion mechanisms and impacts. This study examined the ecological effects of *L. camara* on several environmental attributes on farms in the Eastern Cape province of South Africa. The study focused on three ecological aspects: the invasion mechanism, impacts, and management of *L. camara*.

A few studies have been conducted on *L. camara* invasion in South Africa (Taylor and Kumar, 2014; Ruwanza, 2020; Raphela and Duffy, 2022), yet most of these studies have failed to examine invasion opportunities and impacts at the plant and community level. Invasion by IAPs is anticipated to have significant effects on species diversity and composition, yet only a handful of studies have been conducted to quantify the impacts of *L. camara* invasion on a community level or examine whether the effects vary among seasons. Generally, studies on community level impacts have reported negative impacts caused by IAPs (Ruwanza, 2020), a result that could be premature given that some studies have reported that effects could vary based on seasons and across different habitats (Alvarez and Cushman, 2002). In addition, impacts can vary based on the growth form of a particular native plant species as well as the growth form of the invader. Therefore, more comparative and experimental studies are needed to develop a comprehensive understanding of species-specific invasion opportunities and impacts at a plant and community level, an approach that was adopted in this study, with *L. camara* being used as the model IAP of interest.

No studies in South Africa have examined *L. camara* invasion mechanisms from the perspective of soil physicochemical properties and plant level across different seasons. A few studies, however, have examined how *L. camara* alters soil properties to favour its growth at the community level. For example, Ruwanza and Shackleton (2016) assessed the impacts of *L. camara* on both soil physical and chemical properties over three months. Most IAPs, such as *Acacias*, *Eucalyptus*, and *L. camara,* have been shown to change soil physical and chemical properties once they have invaded new ecosystems (Forsyth et al. 2004; Yelenik et al. 2004; Osunkoya and Perrett, 2011; Kerr and Ruwanza, 2016). An understanding of how IAPs change soil properties seasonally is needed if management interventions are to deal with soil legacy effects after IAP removal. Studies on soil effects following invasion have shown conflicting results of increases (Simba et al. 2013; Ruwanza and Dondofema, 2019; Kumar et al. 2021); decreases (Osunkoya and Perrett, 2011); and no changes (Stefanowicz et al. 2017) to soil properties. Therefore, there is a need to examine how individual IAPs change soil properties and which properties are most easily influenced. Part of this study, therefore, is motivated by the need to understand how *L. camara* changes soil physicochemical properties and how such changes can facilitate its proliferation.

Recognising the impacts of IAPs in South Africa resulted in the formation of the Working for Water (WfW) program (Hobbs, 2004; van Wilgen and Wannenburgh, 2016). Clearing priorities are based on species of interest, impacts, funding, environmental sensitivity, and benefits, i.e., both species benefits and clearing benefits such as water availability after clearing (Nkambule et al. 2017). Given the various clearing priorities, it is important for WfW to understand species-specific impacts so that investment is prioritised on IAPs that could have severe impacts on South Africa's economy. Indeed, *L. camara* is an aggressive invader (Vardien et al. 2012) that has adverse impacts on native vegetation and can also generate legacy effects via the suppression of native vegetation. Consequently, to come up with effective species-specific management strategies, it is important to understand the ecological dynamics of *L. camara* at a species and community level, especially in the Eastern Cape, where little research on *L. camara* has been conducted.

Rohr et al. (2018) report on how ecological restoration is described as a continuum from passive to active restoration. Various restoration models have been tested in South Africa to examine biodiversity recovery after clearing of IAPs (Holmes et al. 2000; Ruwanza et al. 2013; Ruwanza and Tshililo, 2019), yet few restoration studies have been conducted for *L. camara,* even though clearing is underway. Marais et al. (2004) and van Wilgen et al. (2022) document the clearing of several IAPs, including *L. camara*, by the WfW in South Africa. Given the financial costs related to active restoration, there is a need to evaluate passive restoration successes on both soils and vegetation. The spontaneous, autogenic recovery is referred to as passive restoration, and Le Maitre et al. (2011) report on how it can occur when the resilience of an ecosystem is still intact. Rohr et al. (2018) acknowledge how passive restoration requires minimal management and is a more cost-effective method than active restoration. However, if the site being restored has minimal recovery, then other management strategies are needed to be applied. Hence, some studies (Hall et al. 2021; Lamb et al. 2022) on restoration after removing an IAP often propose implementing active restoration if low passive restoration potential is anticipated. The assumption that once the IAP is removed, natural systems will recover on their own has produced mixed results (Blanchard and Holmes, 2008; Ruwanza et al. 2013), prompting researchers to conduct species- and site-specific context studies. It is possible that under passive restoration, new novel ecosystems may emerge, especially where secondary invaders are a challenge (Hobbs et al. 2006). Novel ecosystems tend to be comprised of different ecosystem functions and processes that might not be desirable (Hobbs et al. 2006; Richardson and Gaertner, 2013). Therefore, monitoring of IAP cleared sites is important so that interventions can be put in place to avoid the emergence of novel ecosystems. One of the research chapters in this thesis assesses passive restoration after *L. camara* removal, with the aim of examining both soil and vegetation recovery. Results will contribute towards an understanding of restoration trajectories after *L. camara* clearing, which is anticipated to benefit the South African government, particularly the

WfW programme, so that effective *L. camara* clearing and restoration guidelines can be developed.

1.4. Conceptual framework

This thesis is structured into three main topics: (i) understanding invasion mechanisms and impacts at a species level; (ii) evaluating invasion impacts at a community level; and (iii) assessing invasion management and restoration (Figure 1.1). To understand invasion mechanisms, effects, and management options, *L. camara* was used as a study species. This study acknowledges that the invasion mechanisms, effects, and management interventions are species- and site-specific; therefore, the results presented in this thesis are mostly applicable to *L. camara* at these sites; however, it is possible that the knowledge gained in this study can be used to manage IAPs in general. The invasion mechanism section examined how changes in soil properties can facilitate the impacts associated with the *L. camara* invasion. Previous research has demonstrated that alterations in soil properties are a common IAP trait, yet they are hardly tested for problematic IAPs such as *L. camara* (Ruwanza and Shackleton, 2016). The study further examined two invasion impacts of *L. camara*, namely effects on aboveground vegetation as well as effects on soil seed banks. Although the effects of IAPs on vegetation have been extensively studied in South Africa (Tererai et al. 2013; Yapi et al. 2018; Ruwanza and Dondofema, 2019; Ntshuxeko and Ruwanza, 2020), only a few studies have examined the effects of *L. camara* at a community level on both the aboveground (Jevon and Shackleton, 2015; Ruwanza, 2020) and belowground (soil seed banks) (Ruwanza, 2016). The last section is comprised of one experimental study that addressed a passive restoration management approach where both soil and vegetation recovery after clearing *L. camara* were assessed.

This study aligns with the niche hypothesis, resource availability, opportunity windows, and invasion meltdown hypotheses. Some of these theories are interconnected and may act in concert, as reported by Enders et al. (2020). Hence, Shea and Chesson (2002) documented that invasion is not a result of a single aspect but a combination of aspects. For example, temporal resource fluctuations may lead to heterogeneity when there is an increase in resource availability. This might improve niche opportunities and reduce interspecific species competition. This generally promotes IAP invasion success and species coexistence. The degree of this success, however, depends on species-specific traits that give these IAPs an advantage and make them good competitors.

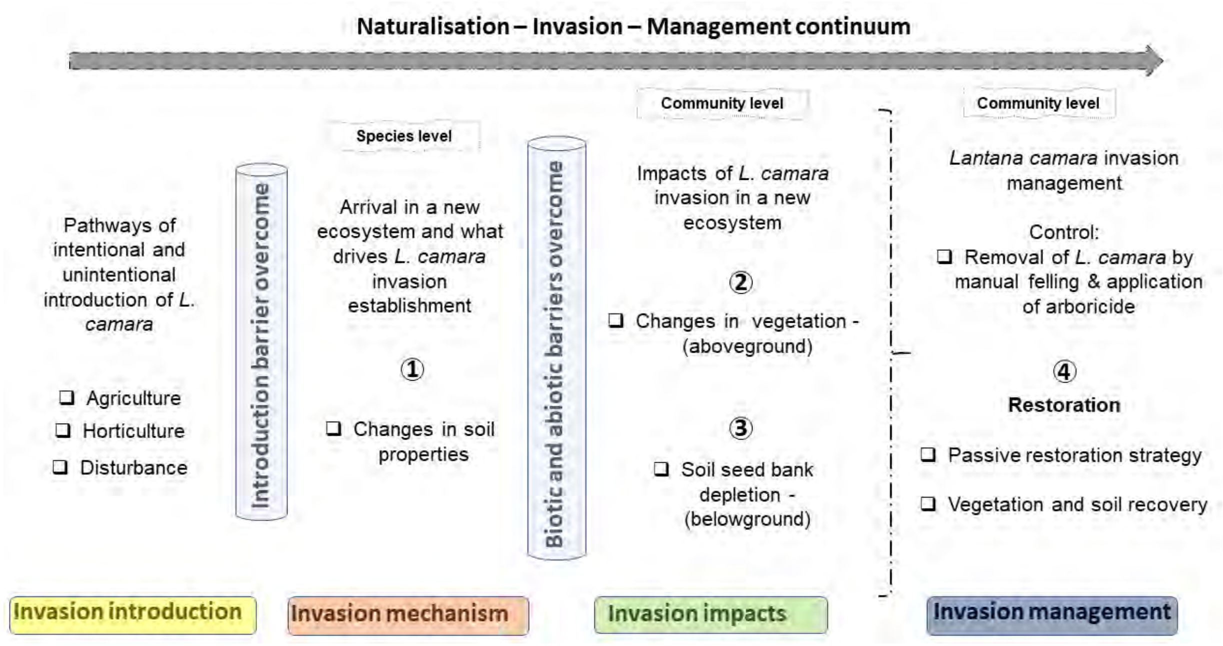

Figure 1.1: A schematic illustration of the invasion and restoration models used in the study. The research questions marked in black circles 1–4 are those that this study addresses.

1.5. Research aims and hypothesis

Since understanding invasion mechanisms, impacts, and management efficacy is important, the study started by examining *L. camara* invasion mechanisms and impacts on soil physicochemical properties at the plant level. Secondly, the study examined the effects of *L. camara* on the community level, where *L. camara*'s impacts on the aboveground vegetation as well as the belowground (soil seed banks) were assessed. Evidence of invasion impacts on native species is presented following a comparison of invaded and uninvaded areas. Lastly, the study examined the passive restoration strategy, i.e., whether *L. camara* removal increases native vegetation and improves soil physiochemical properties. The following research questions were assessed in three research sections:

(i) Invasion impacts and mechanisms at species level

- Does *L. camara* invasion affect soil physicochemical properties?
- Are there variations in soil physicochemical properties visible across the different seasons?

Hypothesis:

- *Lantana camara* invasion will have a negative impact on soil physicochemical properties.
- The impact of *L. camara* on soil physicochemical properties will vary seasonally.

(ii) Invasion impacts (above-and-belowground) at community level

- In what way does *L. camara* affect aboveground native vegetation abundance, diversity, composition, and cover?
- Does species composition, density, richness, and diversity of soil seed banks differ between the *L. camara* invaded and uninvaded areas?

Hypothesis:

- *Lantana camara* invasion results in a decline in the aboveground native species richness, diversity, and cover.
- Native soil seed bank abundance, composition, density, and diversity are lower in soils under *L. camara* invaded conditions compared to the uninvaded conditions.

(iii) Invasion management and restoration

- How does *L. camara* clearing influence soil physicochemical properties and native vegetation recovery?

Hypothesis:

- The soil physicochemical properties and vegetation will recover along a positive trajectory (improving over time or achieving desired outcomes) after *L. camara* clearing.

1.6. Thesis structure and outline

This thesis is comprised of seven chapters, with Chapters 3 - 6 written as scientific papers that are ready for publication.

- Chapter 1 is the general introduction chapter that presents an overview of the topic and general background information. It also discusses some of the research theories associated with IAPs and outlines the problem statement, the research conceptual framework, and the research questions. It also briefly describes the remaining chapter outlines.

- Chapter 2 is a literature review of some of the dynamics associated with *L. camara* invasion globally and in South Africa. Specifically, the chapter discusses how *L. camara* is invasive, its invasion traits associated with ecology, impacts, management, and control strategies that have been used in the past.

- Chapter 3 reports on an experimental chapter that is presented in the form of a publishable paper. The general purpose of the study is to examine how *L. camara* affects the physicochemical properties of the soil under different positions on three farms at Bathurst.

- Chapter 4 is an experimental study that is presented in the form of a publishable paper. The general purpose of the chapter is to assess the impacts of *L. camara* on aboveground native vegetation. This is a comparative study that examined *L. camara* invaded and uninvaded conditions on three farms in Bathurst.

- Chapter 5 is an experimental study that is presented in the form of a publishable paper. This chapter presents the findings of a greenhouse experiment that assessed the effects of *L. camara* invasion on belowground soil seed banks.

- Chapter 6 is also an experimental study that is presented in the form of a publishable paper. The general purpose of the chapter is to assess the influence of *L. camara* clearing on native vegetation diversity and soil physicochemical properties at two farms near Makhanda.

- Chapter 7 is a synthesis chapter that consolidates and synthesises the main findings, provides an overall conclusion, and draws recommendations for future research.

Given how the thesis is structured, it is possible that some sections, e.g., study area, are repeated in some research chapters. This was deliberate since all research chapters (3–6) are written as papers that are ready for publication.

1.7. Thesis incentive and significance

To make informed decisions and come up with potential management strategies, it is crucial to understand the dynamics of a particular IAP. Therefore, the knowledge gained from the studies presented in this thesis could assist researchers, ecologists, landowners, the WfW programme, and policymakers in understanding *L. camara* invasion and restoration potential. Moreover, this thesis provides baseline information that can be used in future studies. *Lantana camara* was chosen as the study species for this thesis because it is one of the most highly invasive species in South Africa and is currently listed as a category 1b IAP under the National Environmental Management: Biodiversity Act (NEM:BA A&IS Regulations of 2020). This means *L. camara* must be removed and destroyed immediately once identified, and no trade of the plant is allowed. Yet, there are few or no studies documenting its impacts on vegetation and soil at the species and community level. Moreover, there are no studies on the restoration trajectory after its removal, despite the millions of Rands that have been invested to manage the species. To my knowledge, only a limited number of studies have examined the effects of *L. camara* in South Africa, especially in the Eastern Cape. Most published studies have focused mainly on the impacts of multiple IAPs, rarely examining the dynamics of *L. camara* alone.

Chapters 3, 4, and 5 of this thesis were conducted at the same sites, and chapter 6 was conducted on a separate site. Chapter 3 explored the *L. camara* invasion mechanism and its impact on a species level. This is the first study in South Africa on *L. camara* to examine invasion dynamics at the plant level. Chapters 4 and 5 examined *L. camara* on a community level, and the interest of this thesis was both in the above-and-belowground communities. Powell et al. (2011) emphasised the importance of investigating the impacts of IAPs across spatial scales, hence the focus on community level changes. For chapter 6, this thesis initially planned to clear the sites used in the first three research chapters (3, 4, and 5), however, due to COVID-19 restrictions, this was unfeasible. Thus, sites already cleared by the WfW programme were chosen and used to assess vegetation and soil recovery after *L. camara* removal. It was not possible to conduct all soil nutrient measurements that are necessary, e.g., examination of nitrates, because soil analyses were limited by the financial resources available since this analysis was conducted at a commercial lab (Bemlab Pty Ltd).

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Chapter 2: Literature review on invasion mechanisms, impacts, and management dynamics of the noxious, invasive alien weed *Lantana camara*

2.1. Introduction

Human activities such as urbanisation, agriculture, development, tourism, and trade act as driving forces of environmental change and thus facilitate the movement of invasive alien species (IAS) (McKinney and Lockwood, 1999; Faulkner et al. 2020; Skocajic et al. 2020). Invasive alien species are one of the largest threats to ecosystem composition, processes, and function globally (Ehrenfeld, 2003; Osunkoya and Perrett, 2011; Le Roux et al. 2020). Globalisation, particularly the increased trade and travel of goods and humans has facilitated the spread of invasive alien plants (IAPs) globally (Meyerson and Mooney, 2007; Hapca, 2011). As a result, climate change, habitat loss, and invasion by IAS are considered the key drivers of biodiversity loss (Lowe et al. 2000). Ealry et al. (2016) estimated that invasive species threatened 17% of the global terrestrial surface, with close to 16% of the global biodiversity hotspots being threatened by biological invasions. Globally, a majority of biomes in South Africa (such as fynbos, Karoo, savanna, and grassland) are under threat from IAPs (van Wilgen et al. 2008; Le Maitre et al. 2016). Richardson et al. (2000) and, more recently, van Wilgen et al. (2020) described IAPs as plant species that have naturalised, can produce huge numbers of fertile offspring at a great distance from the parent plant, and hence can proliferate across a broad range.

Disturbance is a key factor that facilitates alien plant invasion in various habitats, but there are other supplementary mechanisms that facilitate it as well (D'Antonio et al. 1999; Eschtruth and Battles, 2009). For example, Reinhart and Callaway (2006) describe how changes in microbial soil organisms can increase the invasion success of some IAPs. Environmental change and habitat destruction are expected to drive plant invasion, and invasive plant species (IAPs) establish themselves through species-specific traits that enable their invasive behaviour. These species-specific traits include a high reproductive rate, effective seed dispersal, a persistent soil seed bank, the capability to germinate under a broad range of environmental conditions, vigorous growth, dynamic vegetative growth, and long flowering periods (Reichard, 1996; Pysek and Richardson, 2007; Moravcova et al. 2015). Invasive alien plants are known to be more competitive for resources that include light, nutrients, and water than native species (Daehler, 2003; Mangla et al. 2011), hence their ability to colonise gaps in ecosystems, which leads to the formation of monospecific stands.

Like many IAPs, *Lantana camara* is one of the noxious IAP species, causing damage to the environment (Wells and Stirton, 1988; Bhagwat et al. 2012). The Global Invasive Species Information Network (2011) identifies *L. camara* as one of the top ten most widespread IAPs globally. It has a tropical origin and the greatest diversity in the Caribbean Islands and Central and South America (Day et al. 2003). It has naturalised in about 60 countries in the tropical, subtropical, and temperate regions of the world, and has become a problem in those countries as it invades and forms dense thickets that have adverse effects on ecosystems (Day et al. 2003; Goncalves et al. 2014). In Australia, China, India, New Zealand, and South Africa, it affects many aspects of the ecosystem (Baars, 2002; Day et al. 2003; Zalucki et al. 2007). *Lantana camara* was first recorded in the mid-18th century in South Africa and in the 19th century in East Africa (Day et al. 2003). In Africa, Shackleton et al. (2017) reported how the species is associated with negative effects on biodiversity and the environment, especially in disturbed ecosystems such as old agricultural fields where it dominates.

Figure 2.1:*Lantana camara* invasive alien plant (Photographs by Uviwe Bolosha and ARC).

Lantana camara thrives well in disturbed areas, tolerates a wide variety of environments, and grows under a broad range of climatic conditions and soil types (Sharma et al. 2005; Abebe, 2018; Agaldo, 2018; Lakshmi and Sekhar, 2018). For instance, in Zimbabwe, Tarugara et al. (2022) observed how *L. camara* prevalence was associated with human activity clearing for settlement and agricultural activities. The study mentioned above found that *L. camara* cover correlated with specific land cover types; for instance, drainage lines, hills, and shrubs exhibited the highest canopy covers at 21.5%, 20.8%, and 19.6%, respectively, compared to other land cover types with less than 17% canopy cover. Furthermore, in South Africa, Henderson (2007) and Vardien et al. (2012) have observed that it occurs mostly in the grassland and savanna biomes. It primarily infests roadsides, road-river interchanges, riparian areas, farmland, abandoned agricultural lands, grazing areas, and protected areas because of its disturbance and broad ecological tolerance (Vardien et al. 2012; Schmitt et al. 2019; Ruwanza and Mhlongo, 2020). Using remote sensing and geospatial techniques, Dube et al. (2020) detected and mapped *L. camara* in disturbed ecosystems and reported how changes in climate will influence its spread and invasion dynamics. In another study, Goncalves et al. (2014) predicted and observed potential *L. camara* invasion vulnerabilities in African countries and concluded that Cameroon, the Central-African Republic, and the Democratic Republic of the Congo are highly vulnerable. Similarly, Akin-Fajiye and Akomolafe (2021) predicted several eastern and southern African countries that would be extremely vulnerable to *L. camara* invasion, including Angola, Ethiopia, Kenya, Madagascar, South Africa, Tanzania, Uganda, Zambia, and Zimbabwe. Ncube et al. (2020) predicted a 3–33% increase in *L. camara* invasion in the Matabeleland South Province of Zimbabwe. At the global level, Qin et al. (2016), Mungi et al. (2020), and Saranya et al. (2021) predicted the potential distribution and spread of *L. camara* on continents and countries such as India, Australia, and South America. In most of the above-mentioned studies, the driving factors linked to *L. camara* invasions were mostly associated with human-mediated disturbances and climate change.

2.2. Traits that make *L. camara* invasive

2.2.1. Species-specific traits

Invasive alien plant species usually have specific traits or a combination of traits mentioned above that allow them to invade and outcompete native vegetation (Pysek and Richardson, 2007; Mathakutha et al. 2019). For instance, their fast growth rate, high dispersal ability, phenotypic plasticity, and rapid reproduction rate is identified as species-specific traits that enhance plant invasion (Vardien et al. 2012; Goyal et al. 2018; Goyal and Sharma, 2019). Under ideal environmental conditions, *L. camara* can flower all year, although most flowering occurs during the wet summer months (Totland et al. 2005). *Lantana camara* produces a vast number of seeds and can reproduce both sexually and vegetatively. *Lantana camara*'s dispersal mode varies, i.e., humans, water, and animals (primarily birds), which can result in rapid spread over considerable distances (Bitani et al. 2022). All the afore-mentioned species-specific traits have been linked to the *L. camara* invasion. Although seed regeneration and seed bank dynamics are key species-specific traits that are linked with alien plant invasion, little is known about *L. camara* seed regenerative capacity and seed bank dynamics (Muvengwi and Ndagura, 2015; Ruwanza, 2016), thus the need for more studies on soil seed bank dynamics.

Lantana camara also modifies the surroundings through allelopathy. It produces large amounts of litter that contain allelochemicals such as triterpenes, flavonoids, and phenolic compounds (Mishra, 2015), which, when released into the environment, act as a defence mechanism and prevent the growth of other plant species. According to Urban et al. (2011), approximately 58 allelochemicals have been identified in several *L. camara* cultivars. Allelopathy is described as an interference-competition mechanism that affects the environment and promotes invasion (Ruwanza and Shackleton, 2016). Thus, the invasive traits of this species give it an advantage over most native species. Ruwanza and Shackleton (2016) also showed that *L. camara* litter can facilitate changes in some soil properties, thus favouring its own growth. Based on Ruwanza and Shackleton (2016) observations, *L. camara* invasion seems to be consistent with the theory of fluctuating resource availability proposed by Davis et al. (2000), which suggests that invasion increases as nutrient resources are available in high supply and the invasive species can uptake and utilise the resources effectively.

2.2.2. Ecosystem-based traits

Lantana camara has a broad geographic range and a wide ecological tolerance, as a result, it can occur in diverse communities and habitats. According to Vardien et al. (2012), its invasion success is also linked to habitat susceptibility. Firstly, climatic suitability where *L. camara* usually prefers warm and wet areas in most African countries, including South Africa, where it is present in seven out of nine terrestrial biomes. In South Africa, *L. camara* is more noticeable in the eastern parts since they are moister compared to the arid western parts. Hence, Urban et al. (2011) and Mukwevho et al. (2018) reported that the species invades the Eastern Cape, Gauteng, KwaZulu-Natal, Limpopo, Mpumalanga, the North West, and the southern parts of the Western Cape provinces. Shackleton et al. (2017) also mapped the distribution of *L. camara* in Eastern Africa, where it was widespread around Lake Victoria and patchy invasions were noted in Kenya and the Ethiopian highlands, areas that tend to be warm and moist. Secondly, *L. camara* is known to exploit and favour disturbed ecosystems, particularly human-mediated disturbed areas such as old agricultural fields. It mostly colonises and invades disturbed areas such as roadsides, grazing areas, road-river intersections, and riparian areas (Vardien et al. 2012).

2.3. Impacts of *L. camara* on ecosystems

Invasive alien plants have the potential to have a significant negative and positive influence on ecological, social, and economic systems. Thus, *L. camara* also has a diverse range of socioecological and economic impacts across several continents and countries, such as Africa, Australia, India, and New Zealand (Sundaram et al. 2012; Vardien et al. 2012; Ntalo et al. 2022). Changes in ecosystem processes, structure, functioning, and composition, as well as a loss of native species diversity, are among the most well-documented negative impacts of *L. camara* (Egoh et al. 2020). Discussed below are some of the impacts associated with the *L. camara* invasion globally.

2.3.1. Ecological impacts

2.3.1.1. Disrupts succession and decreases biodiversity

Multiple studies have reported that *L. camara* invasions have negative effects on biodiversity. Biological impacts include *L. camara* forming dense, impenetrable thickets, which affect native communities, composition, and processes, resulting in substantial negative ecological impacts on invaded habitats. Ambika et al. (2003) and Ruwanza (2016) reported how *L. camara* contains allelochemicals (e.g., alkaloids and phenolic compounds) that can hinder the germination and seedling survival of other species, thereby displacing and threatening native biodiversity. Several studies have documented how *L. camara* can negatively influence vegetation characteristics, for example, Dobhal et al. (2010) reported how *L. camara* interfered with the growth of *Justicia adhatoda* and *Murraya koenigii* in northern India by outcompeting these species, resulting in decreased populations. Gooden et al. (2009) also documented how *L. camara* invasion in south-eastern Australia caused a decline in native species diversity, and this was prevalent in ferns, which decreased by 70% in the *L. camara* invaded sites compared to the uninvaded sites. Qureshi et al. (2021) also reported how *L. camara* can cause a decrease in diversity indices, for example, the species richness of native plants was reported to be low in the *L. camara* invaded sites compared with the uninvaded sites. Similarly, vegetation diversity was almost double in the uninvaded sites (2.56 ± 0.27) than in the *L. camara* invaded sites (1.56 ± 0.65). As a result, a 65% dissimilarity was observed between the *L. camara* invaded and uninvaded sites. Ruwanza (2020) also reported on how the vegetation cover of all growth forms (trees and shrubs, forbs, and grasses) was less than 50% in the *L. camara* invaded sites compared to the uninvaded sites. Moreover, the same above-mentioned study reported that *L. camara* invasion resulted in a decrease in native species richness in the invaded sites compared to the uninvaded sites. A combination of factors contributed to these changes, i.e., competition for resources, microclimatic changes, and allelopathic effects.

Lantana camara invasion can also displace native species, and this was observed by Gooden et al. (2009), who reported that native shrub density was 10 times lower in the *L. camara* invaded sites than in the uninvaded sites. Similarly, Ruwanza (2016) also observed that the native seedling density in the *L. camara* invaded sites was half that of the uninvaded sites. There are also cases where no differences were observed between the *L. camara* invaded and uninvaded sites (Nangalelwa, 2010). Moreover, a few other studies have reported a positive effect on vegetation after *L. camara* invasions. For example, Schmerbeck and Gupta (2022) reported on how *L. camara* invasion can also have positive influences on some vegetation attributes, i.e., an increase in seedlings and sapling abundance with increasing *L. camara* cover. Therefore, *L. camara* can facilitate the establishment of some species, thus acting as a refuge or nurse plant. Although studies that show positive co-occurring and facilitation trends are few, these studies dispute the popular notion that *L. camara* has negative effects on native species abundance and diversity.

Furthermore, *L. camara* is likely to alter the suitability of habitat for animals in some communities. For example, Omeja et al. (2016) reported how its invasion posed a threat to the habitat of *Hippotragus niger* (sable antelope) in Kenya, as well as how it altered the forest ecosystem. In contrast, *L. camara* can co-occur with native vegetation, indicating that it does not eliminate native species in some communities but rather serves as a refuge (Ruwanza, 2020). In these altered habitats, some species can grow and thrive underneath *L. camara*, although this is invasion extent-dependent. The growth of some native species underneath *L. camara* can be advantageous during restoration because these species will serve as "restoration foci" on these sites, facilitating vegetation recovery.

From a biodiversity standpoint, *L. camara* has been associated with some benefits. Although tsetse flies spread sleeping sickness, *L. camara* invasion has also been linked to providing a haven for tsetse flies in sub-Saharan Africa (Syed and Guerin, 2004). The use of *L. camara* as a haven has also been reported for birds (Teucher et al. 2015; Habel et al. 2016). For example, the two above-mentioned studies reported that *Turdoides hindei* was observed using *L. camara* thickets as a surrogate habitat in Kenya (Teucher et al. 2015; Habel et al. 2016). In Australia, *Manorina melanophrys* also uses *L. camara* as a nesting habitat (Lambert et al. 2017). These studies seem to suggest that *L. camara* tends to provide some ecological benefits to the ecosystem.

2.3.1.2. Impacts on soil physicochemical properties

Although *L. camara* has been shown to have an impact on abiotic attributes, only a few studies have documented and emphasised the magnitude of this impact on soil physicochemical characteristics (Sharma and Raghubanshi, 2009; Fan et al. 2010; Simba et al. 2013; Ruwanza and Shackleton, 2016; Mahla and Mlambo, 2019; Kumar et al. 2021; Lone et al. 2021). For example, Fan et al. (2010) reported the impacts of *L. camara* on soil chemical properties (pH, total P, available P, total N, and available N) at the plant level and showed that *L. camara* invasion increased these properties. Another study by Ruwanza and Shackleton (2016) reported the effects of *L. camara* on the community level on both the soil physical (moisture content and water repellency) and chemical properties (total C and P), and the results were varied. For example, soil moisture under *L. camara* invaded sites increased by 3.1% compared to the natural sites, while penetration resistance levels were higher in the natural sites by 0.7 kg cm^{-2} compared to the *L. camara* invaded sites (Ruwanza and Shackleton, 2016). Osunkoya and Perrett (2011) reported a 2% increase in soil moisture under *L. camara* invaded sites compared to uninvaded sites. Additionally, soil chemical properties (pH, organic carbon, total carbon, and total nitrogen) also increased due to *L. camara* invasion (Osunkoya and Perrett, 2011). Decreases in these soil properties have also been observed, for instance, Osunkoya and Perrett (2011) documented a more than 30% decrease in soil nutrients such as iron (Fe) and manganese (Mn) in the *L. camara* invaded sites compared to the uninvaded sites. The above-mentioned varied results in soil properties seem to suggest that the influence of *L. camara* on soils is dynamic, however, these changes in soil properties could explain why *L. camara* proliferates in nutrient-poor ecosystems. Its ability to change soils, whether in increase or decrease, seems to work to its advantage, thus allowing the species to proliferate. However, to properly understand the underlying mechanisms of *L. camara* invasion on soil properties, more research is needed at different sites and ecosystems. Few studies have examined changes in microbial activities following *L. camara* invasion (Wang et al. 2015; Kumar et al. 2021). These studies have reported that *L. camara* litter can influence soil bacteria, fungi, and earthworm activity underneath the plant, leading to changes in soil properties (Wang et al. 2015; Kumar et al. 2021). For example, the increase in litter content underneath *L. camara* plants can result in increased soil moisture content, which in turn creates suitable conditions for increased bacterial activity. Under increased bacterial activity, litter decomposition increased, resulting in increased soil nutrients, and thus improving soil fertility and nutrient cycling. However, it is important to note that microbial changes in soils are season-dependent, so changes in microbial activities underneath the *L. camara* invasion could be season-dependent.

2.3.1.3. Impacts on agriculture

Due to its ability to invade disturbed areas and its unpalatability, *L. camara* has been identified as a menace in agricultural areas globally (Priyanka and Joshi, 2013; Nkambule et al. 2017; Abebe, 2018). It also has a direct and indirect impact on food security by encroaching on natural pastures and forming dense, impenetrable, thorny thickets, reducing grazing capacity and land values (Day et al. 2003; Bufebo et al. 2016). Taylor et al. (2012) reported that the presence of *L. camara* in vast areas may eventually lead to extensive agricultural lands being regarded as unproductive and worthless, which might have significant consequences for local people who rely on ecosystem goods and services. Furthermore, under a high *L. camara* invasion, van Wilgen et al. (2008) reported an 80% reduction in grazing capacity in five biomes in South Africa. Prasad (2012) also concurs with these findings and reports on how *L. camara* can reduce grazing grass, which is a vital source of food for herbivores. Other studies have also reported on the influences of *L. camara* on crops and croplands, for example, Ambika et al. (2003) and Hamad et al. (2022) documented the impacts of *L. camara* on crops through allelopathy and competition for resources, i.e., the growth inhibition ranged from 4–55% in *Eleusine coracana* (finger millet), 19–34% in *Pisum sativum* (peas), and 29% in *Zea mays* (maize). Shackleton et al. (2017) reported on how *L. camara* can invade croplands, resulting in 26%–50% reductions in crop yields. Kifetew and Woldu (2021) also documented that 83% of respondents in Ethiopia associated *L. camara* invasion with reduced crop production through encroachment on farmlands. Therefore, all the above-mentioned studies show that *L. camara* invasion has a negative effect on crop production.

Lantana camara has also been noted to be poisonous to animals, and poisoning may occur accidentally or intentionally (Botha and Penrith, 2008; Kumar et al. 2018; Negi et al. 2019; Barik et al. 2020). The availability and abundance of poisonous plants such as *L. camara* in pasture lands reduces the amount of food available to livestock and wildlife. Recently, Machado et al. (2023) reported on the deaths of 74 heifers out of 170 in Uruguay that ingested *L. camara* because of a lack of forage at a site where they took refuge during a storm. This confirms that indeed, *L.* camara synthesises toxic chemical compounds such as lantadenes, which are preserved in the leaves and are poisonous to livestock if ingested (Nkambule et al. 2017). When ingested by animals, the toxins attack the liver and kidneys of ruminants, resulting in a weakened immune system and thus exposing these animals to other diseases (Ide and Tutt, 1998; Shackleton et al. 2017). However, in contrast, few other studies have reported on how some livestock may intentionally prefer and consume *L. camara* as compared to other plant species. For example, Shackleton et al. (2017) documented how 74% of respondents in a study done in eastern Africa observed no negative impacts of *L. camara* on goats. Furthermore, a review by Ntalo et al. (2022) recently reported on how goats can be resistant to lantadenes found in *L. camara* leaves, thus making the species an alternative forage for these browsing animals. Overall, *L. camara* poisoning in livestock may differ depending on the animal.

Several other studies have also noted that *L. camara* can fuel fires by being more ignitable than some native species (Hiremath and Sundaram, 2005; Berry et al., 2011), which is likely to affect agricultural productivity. Fires can directly damage or destroy crops, leading to significant economic losses for farmers. Additionally, fires can alter soil chemistry and stimulate the growth of invasive alien plant species (IAPs), thus creating a cycle of repeated fires and increased IAP dominance. A mechanism by which *L. camara* can increase fire occurrences has been observed in the Australian dry rainforest by Berry et al. (2011), where it introduced flammable material to a generally non-flammable system, causing an increase in the availability of fuel by introducing an additional > 80% fuel cover. The increase in fire intensity following *L. camara* invasion has the potential to affect grazing grass, leading to negative effects on livestock. Besides the loss of grazing grass, increased fire intervals and intensity can have a negative impact on endemic native plants and soil-stored seed banks.

2.3.2. Socio-economic impacts

Both positive and negative social effects of *L. camara* have been reported, and they have a varied impact on local communities and livelihoods (Shackleton et al. 2017). The negative impacts, however, are the most frequently mentioned effects, and most communities perceive *L. camara* as a nuisance. For example, 90% of respondents in a study conducted in Ethiopia perceived *L. camara* as a disadvantaging species, and most of those respondents wanted the plant to be removed (Alemu and Terefe, 2015). The negative effects of *L. camara* may have an influence on the delivery of ecosystem services and the benefits that they provide to residents. In many communities, the spread of *L. camara* has restricted access to natural resources (water, fuelwood, agricultural, and forest products), as well as sacred natural sites, disrupting ecosystem services and, as a result, livelihoods (Jevon and Shackleton, 2015).

Several known positive impacts (benefits) of *L. camara* include its use as a traditional medicine (Day et al. 2003; Magwede et al. 2019; Negi et al. 2019; Ajao et al. 2022); use for fuelwood and furniture making (Tabuti et al. 2003; Patel, 2011; Negi et al. 2019); use as a boundary hedge and garden ornament (Ghisalberti, 2000; Kifetew and Woldu, 2021); and use as soil mulch and manure that can improve soil fertility and moisture retention (Shackleton et al. 2017; Negi et al. 2019). In contrast to other woody invasive alien trees and shrubs, in some countries, *L. camara* is rarely sold for economic benefit, thus making it a low-value economic species (Shackleton et al. 2017). Furthermore, since *L. camara* is being utilised in some communities, van Wilgen et al. (2011) and Kannan et al. (2016) advocated for the recognition of utilisation as a management strategy. Even though *L. camara* may have benefits in some regions (mostly rural), the cost of managing it outweighs the potential benefits (Alemu and Terefe, 2015; Shackleton et al. 2017). As a result, a growing body of literature appears to agree on regulating and controlling *L. camara* so that its negative impacts on biodiversity and natural ecosystems can be reduced (van Wilgen et al. 2011; Ntalo et al. 2022).

Lantana camara is also known as an economically destructive plant and is associated with economic pros and cons. The economic cost associated with *L. camara* invasions usually depends on its intensity. Day et al. (2003), Alemu and Terefe (2015), and Bufebo et al. (2016) point out how *L. camara* invasion directly and indirectly results in economic consequences such as losses in agricultural productivity, i.e., reduction in the quality and quantity of crop production, loss of grazing capacity, and decreasing carrying capacity and land values. Concerning this, Pratt et al. (2017) estimated economic losses of about US $0.9 to almost 1.1 billion associated with the IAS in Eastern Africa and reported on how this could be a threat to food security. Bang (2022) also recently reported on the substantial financial burdens that are imposed by IAS in India and how they amount to US $182.6 billion. Other economic impacts associated with *L. camara* include management costs. For example, Love et al. (2009) documented how controlling this species is usually time-consuming and requires long-term management plans, meaning that continuous financial support is needed. Erasmus and Clayton (1992) and Babu et al. (2009) reported on the high cost associated with controlling *L. camara*. Furthermore, Shackleton et al. (2017) documented how several households in eastern Africa spent approximately R8,500 per year (cost of labour and some household chemical control) on controlling *L. camara*. Bhagwat et al. (2012) also reported on the indirect economic loss in the agricultural sector due to the *L. camara* invasion. The monetary benefits are also linked to *L. camara* by Patel (2011), where furniture and baskets made from *L. camara* are sold to earn a living. Kannan et al. (2014) also documented how some communities in India earned money (46% of their income) by making use of forest resources such as *L. camara.*

2.4. Management of *L. camara*

Once IAPs such as *L. camara* have invaded an area and established themselves, a series of management measures are required to control them and ensure native vegetation regeneration success. It is important to note that there is no single standard strategy to manage IAPs, which may be related to the fact that these IAPs have distinctive traits that make management objectives difficult to achieve (Katembo, 2018). Hence, it is essential to first get a better understanding of the plant species (their presence, distribution, characteristics, and impacts) before considering management strategies (Witt et al. 2018). Mechanical, chemical, and biological management strategies and procedures have all been advocated for controlling *L. camara* (Urban, 2010; Priyanka and Joshi, 2013; Negi et al. 2019)*,* with the most common globally used method being mechanical control (Love et al. 2009).

In South Africa, *L. camara* is listed as a category 1b species under the South African National Environmental Management: Biodiversity Act (NEM:BA A&IS Regulations of 2020), which is the principal legislative tool that guides the management of IAS. This entails the species having to be controlled, removed, and destroyed where possible, and any trade or planting of the plant species is prohibited. Given the above listing category in the country, several management interventions have been put in place for IAPs, including *L. camara*. Mechanical and chemical control of *L. camara* involves several approaches, which include clearing of *L. camara* by manual removal; felling and spraying of stumps using various herbicides such as phenoxy acid, benzoic acid, and pyridine groups that are mixed with additives to improve their performance (Vardien et al. 2012). The spraying aims to reduce the coppicing of *L. camara* (Love et al. 2009). According to Erasmus and Clayton (1992), there are about six registered herbicides in South Africa that are used to control *L. camara.* Both mechanical and chemical control methods are costly, time-consuming in sites where *L. camara* is dense (Abebe, 2018), and require a lot of follow-ups since neither address soil-stored seed banks, which is known to trigger re-invasion. Vardien et al. (2012) also highlighted how the efficacy of chemical control is affected by the time of application, plant size, and application method. Despite this, mechanical and chemical control of *L. camara* has been the most widely used approach by the WfW program in South Africa. The WfW programme is the main programme that manages IAPs in South Africa, and they mostly fell the plants using chainsaws, spray the cut stems with a herbicide to reduce resprouting, stack the felled plants, and burn them when they are dry (Beater et al. 2008). In other countries, *L. camara* is managed by fire through burning the plants, but this method is used as a short-term approach (Ramaswami and Sukumar, 2013; Debuse and Lewis, 2014). Where fire is used as a control measure, it must be used with caution as it burns native soil seed banks, negatively affects soil properties (triggers soil repellence), burns co-occurring native remnant species, and creates suitable conditions for secondary invasion and re-invasion by *L. camara* (Chemari and Orikiriza, 2013; Hiremath et al. 2018).

Biological control is the most explored approach to controlling *L. camara*, and it involves the use of insects and microorganisms to suppress IAPs (Motooka et al. 2002). *Lantana camara* biocontrol involves about 45 biocontrol agents globally, with 13 in South Africa (Katembo et al. 2020). The biological control of *L. camara* in South Africa involved releasing a number of agents, which include, but are not limited to, *Aceria lantanae* (gall mite), *Coelocephalapion camarae* (weevil), *Hypena laceratalis* (moth), *Longitarsus bethae* (flea beetle), *Ophiomyia camarae* (fly), *Octotoma scabripennis* (leaf beetle), *Passalora lantanae* (fungi), *Puccinia lantanae* (fungi), *Septoria* spp. (fungi), *Teleonemia scrupulosa* (bug), and *Uroplata Girardi* (beetle) (Cilliers and Neser, 1991; Baars and Neser, 1999; Zalucki et al. 2007; April et al. 2011; Urban et al. 2011; Day, 2012; Mukwevho et al. 2017; Mukwevho and Mphephu, 2020; Simelane et al. 2021; Katembo et al. 2022). Even though biological control is regarded as the most researched control method, with numerous studies done (Schwarzlander et al. 2018; Simelane et al. 2021; Thomas et al. 2021), the agents often have limited success, and the fungal pathogens often fail to establish themselves. Effective biological control, however, together with the integration of other management strategies, can help control selected priority IAPs, including *L. camara*, and can prevent its further spread, and hence reduce its negative impacts on biodiversity and livelihoods (Katembo et al. 2022). According to Vardien et al. (2012), there are > 50 *L. camara* varieties in South Africa, which multiplies the complexity of managing *L. camara* using biocontrol. This highlights the need for exploring ecological restoration approaches and adopting an integrated approach that has the potential to successfully manage *L. camara*. Prior to that, however, an understanding of both the belowground and aboveground communities is crucial so that informed and improved species-specific and community-based management strategies can be formulated.

Managing IAPs is an issue globally, and studies have demonstrated that managing *L. camara* is generally expensive and requires long-term investments. As a result, proper planning is critical. Some studies by Ruwanza (2017) and Mukwevho and Mphephu (2020) have proposed the use of integrated approaches, which can improve the prospects of a successful restoration effort. Various ecological restoration methods have been attempted following the removal/clearing of IAPs, and these studies have yielded both successes and failures (Blanchard and Holmes, 2008; Ruwanza et al. 2013). For instance, Blanchard and Holmes (2008) recorded how a fell and removal strategy can result in higher species richness and diversity compared to other removal strategies such as fell only and fell and burn, thus being recommended as the preferred strategy to promote vegetation recovery. While Ruwanza et al. (2013) observed an absence of seedling recruitment during passive restoration, when active restoration was assessed, low germination rates (below 30%) of targeted native species in the treatments were also recorded. Morris et al. (2008) have demonstrated how clearing of *L. camara* and other IAPs improves native biodiversity; for instance, there was an 80% decrease in IAP density after clearing and an increase in native species in previously invaded sites. Other studies have documented that clearing *L. camara* can decrease its populations (van Wilgen et al. 2017), leading to native plant recovery. Even though there are limited studies on *L. camara* and there is still little documented effectiveness of the restoration process on other IAPs, most of these studies (e.g., Gooden et al. 2009; van Wilgen et al. 2020) document how management interventions can result in recovery.

Maintaining native seed banks is critical for successfully recovering cleared areas. The most common cause of failed recovery is a lack of native seeds of target plant species, with most of the cleared sites containing seeds of non-target plants (Simberloff and Holle, 1999; Kulmatiski, 2006; Pearson et al. 2016). Le Maitre et al. (2011) noted how native seed depletion following plant invasion can hinder passive recovery. In circumstances where native seed banks are limited, active restoration through the addition of native seeds is frequently suggested. According to Richardson et al. (2007), an effective restoration approach needs an understanding of the drivers and dynamics that have resulted in ecosystem alteration. Thus, proper planning that involves a systematic approach must be done to attain effective recovery thresholds (Holmes et al. 2020). Furthermore, an integrated management approach should be used to improve restoration effectiveness. Lastly, detailed monitoring and follow-up treatments should be done to prevent secondary invasion and re-invasion of the cleared plant areas (Ruwanza et al. 2018; van Wilgen et al. 2020).

Several factors, or a combination of these factors, have the potential to influence or hinder restoration efforts following *L. camara* removal. These include the intensity and duration of the *L. camara* invasion, ecosystem processes in the communities or sites that have been invaded, clearing methods used, abiotic environmental factors, and seed banks (Ruwanza, 2016). It is therefore crucial to take note of these factors during restoration processes after *L. camara* removal. Based on the literature reviewed, it is evident that more research needs to focus on evaluating the ecological impacts of *L. camara* on soil physicochemical properties and soil seed banks to gain deeper knowledge, since physicochemical properties are known to take several years post-clearing to return to their pre-invasion levels. Further, several other management approaches still need to be investigated, i.e., restoration approaches such as clearing, passive restoration, active restoration, soil manipulation techniques (soil transfer, topsoil removal, addition of relevant fertilisers), and an integration of management approaches that have the potential to recover ecosystems to their near-pristine conditions. Moreover, long-term studies focusing on secondary invasion after *L. camara* removal should also be done.

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Chapter 3: The effects of *Lantana camara* invasion on soil physical and chemical properties

Abstract

Invasive alien plant species modify the structure and functioning of natural ecosystems. *Lantana camara* is no different; it has traits that make it invasive and uses several mechanisms, such as soil nutrient changes, to successfully invade some habitats. Thus, to develop efficient management approaches, it is essential to understand invasion drivers, including how *L. camara* affects soil properties. To better understand the mechanisms by which *L. camara* affects soil properties, the study aimed to examine how *L. camara* invasion affects soil physicochemical properties across different seasons. The study sought to answer the following two research questions: (i) does *L. camara* invasion affect soil physicochemical properties under different sampling positions? (ii) are soil physicochemical property changes discernible across different seasons? Topsoil was collected at three sampling positions: under the *L. camara* individual plant canopy, on the canopy edge of the plant, and away from the plant. The soils were assessed for soil moisture content, penetration resistance, infiltration, and water repellency over four seasons and for pH and soil nutrients once in autumn (April 2020). Results for soil moisture content showed no significant differences between the three *L. camara* sampling positions, though seasonal differences were observed. The soil under and on the edge of *L. camara* canopies was less compact compared to the soil away from *L. camara* plants. In addition, seasonal variations in soil compaction were observed. Soil infiltration rates differed significantly across *L. camara* sampling positions, with faster infiltration rates recorded under and on the edge of *L. camara* canopies than further away, with the above being visible across all seasons except in summer (December). While variations in soil water repellency were noted during spring (September) and summer (December), only the summer period demonstrated significant differences. Most of the slightly repellent soils were found across all *L. camara* plants in spring (September), but in summer, slightly repellent soils were underneath and away from *L. camara* plants. The soil chemical properties showed no significant differences between the sampling positions. The study concludes that *L. camara* modifies some soil physical properties rather than chemical properties, although such physical property modification varies seasonally. The observed modifications in soil physical properties could explain how the alterations in soil physical properties can contribute to its competitive advantage, thus enabling it to grow and outcompete native plant species in the invaded areas.

Keywords: allelopathy; *Lantana* invasion; soil modification; soil penetration; soil properties

3.1. Introduction

Invasive alien plant species (IAPs) are found in various ecosystems, often possessing broader environmental tolerance and competitive traits that enable them to invade and spread in natural and disturbed habitats (Rejmanek and Richardson, 1996; Pattison, 2016; Liu et al. 2017; Nunez-Mir et al. 2019). The traits that cause plant invasiveness depend on both the invading species and the invaded habitats (Pysek and Richardson, 2008). For instance, *Lantana camara* produces numerous seeds and has long taproots, making it more invasive (Shah et al. 2020). Once IAPs establish in a new habitat, they alter the ecosystem structure and functioning, potentially leading to the loss of beneficial ecosystem services (Ricciardi et al. 2017; van Wilgen et al. 2020). Invasive alien plants can also modify and displace native plant species and alter soil physicochemical properties (Bever, 2003; Vila et al. 2011; Simberloff et al. 2013). Moreover, they can transform natural communities by altering abiotic and biotic properties, often resulting in negative socio-economic effects (Richardson et al. 2020; Rai and Singh, 2020).

Alien plant invasion mechanisms have been studied, but further research is required due to the variation in invasion mechanisms caused by factors like disturbance and climate change (Blumenthal, 2005; Rai, 2015). The novel weapon hypothesis suggests that IAP success is linked to plant biochemical weapons, specifically antimicrobial root exudates that interfere with new plant-soil microbial interactions, promoting allelopathy (Callaway and Ridenour, 2004; Choyal and Sharma, 2011). Invasive alien plants such as *Rhus typhina* release allelopathic compounds that prevent native species recruitment, while root allelochemicals modify soil physicochemical properties (Liu et al. 2017; Qu et al. 2021). Additionally, IAP traits such as high seed production, germination, and growth rates increase IAP survival and competitiveness (van Kleunen et al. 2010). For example, IAPs such as *L. camara*, *Acacia* species, and *Solanum mauritianum* flower and reproduce earlier, with a higher germination and growth rate, increasing their survival and spreading chances in new environments (Richardson and Kluge, 2008; Gibson et al. 2011; Priyanka and Joshi, 2013; Negi et al. 2019; Ruwanza, 2021).

Plant-soil feedback (a process where a plant alters biotic and abiotic soil properties and takes advantage of these alterations to maximise its growth) and how these facilitate alien plant invasion still need to be better understood (Ricciardi et al. 2017; Gundale and Kardol, 2020). They play an important role in plant dynamics, and they can affect ecological processes such as primary production and biogeochemical cycling, resulting in direct and indirect effects on both the invader and the invaded communities (Bever et al. 2010). Wang et al. (2015)

documented the interactive feedback between IAPs and abiotic soil properties to understand the mechanisms of successful invasion. This concept explores how the presence and activities of IAPs influence the soil abiotic properties, which subsequently influence the growth and success of the IAPs. The above-mentioned study noted that IAPs such as *Acacia* alter soil N-cycles, microbial communities, and litter decomposition to their advantage (Wang et al. 2015). Vila and Weiner (2004) reported that the successful establishment of IAPs is facilitated by their strong competitive capability for soil nutrients compared to native plant species. Most studies seem to agree that changes in soil properties are a driving factor behind invasion success (Novoa et al. 2013; Si et al. 2013; Rai, 2015; Ruwanza and Dondofema, 2020). Since IAPs can modify an environment to facilitate their own growth, some of the major soil-related changes include modifications in soil physical properties, alteration of nutrient concentrations, alteration of biogeochemical cycling, and modification of soil biota community composition (Duke and Mooney, 2004; Pysek et al. 2012; Soti and Jayachandran, 2016; de Souza et al. 2018; Wang et al. 2019).

Simba et al. (2013) and Gibbons et al. (2017) studied how IAPs can alter soil properties, creating optimal conditions for growth. Complementing this, Stefanowicz et al. (2017) highlighted through meta-analyses how IAPs can influence nutrient pools (C, N, and P), thus enhancing nutrient cycling, litter decomposition, and mineralisation. Researchers such as Chapuis-Lardy et al. (2006) and Ruwanza and Dondofema (2020) also investigated how species such as *Solidago gigantea* and *Psidium guajava* (respectively) can modify soil properties to favour their invasion. However, Ruwanza and Dondofema (2020) noted that changes in soil physicochemical properties post-IAP invasion vary based on the invasive species, invasion scale, ecosystem type, and external factors, emphasising the need to assess species-specific impacts for effective management strategies. Notably, studies have shown that *L. camara*, like many other IAPs, alters soil properties to support its invasion success (Wang et al., 2015; Ruwanza and Shackleton, 2016). Therefore, this calls for more research to ascertain the nature of soil property changes in various sites and landscapes for management purposes.

Ehrenfeld (2003) reported that the effects of IAPs are not universal. Similarly, Vanderhoeven et al. (2006), Tharayil et al. (2013), Tererai et al. (2015), Gibbons et al. (2017), and Comole et al. (2021) acknowledged that the effects of IAPs on soils are often species, site, and season specific, thus the need to conduct research across various sites and seasons to gain knowledge that can inform effective control methods and seek broader patterns. For instance, with regards to seasonal-specific variations, Herr et al. (2007) documented seasonal differences in soil pH and P fractions in *S. gigantea* invaded areas. Similarly, Tharayil et al.

(2013) also reported how the effects of *Polygonum cuspidatum* invasion were more pronounced in spring, i.e., slow N cycling, reduced accumulation of inorganic N, and increased organic forms of nitrogen. Researchers have shown significant interest in the global ramifications of *L. camara*, given its devastating effects. However, there is a scarcity of information in South Africa regarding the correlation between *L. camara* and soil physicochemical properties, particularly assessing season variations. The pressure that *L. camara* exerts on the environment and soils points to the need to better understand this species and how it affects soil changes over different seasons. Therefore, the main research objective of this study was to examine how *L. camara* invasion affected soil physicochemical properties across different seasons in Bathurst, Eastern Cape province of South Africa. The two research questions were: (i) does *L. camara* invasion affect soil physicochemical properties under different sampling positions? and (ii) are the variations in soil physicochemical properties visible across different seasons?

3.2. Methods

3.2.1. Study species

Lantana camara L., commonly known as *Lantana*, is a tropical plant native to Central and South America (Day et al. 2003). Under favourable conditions it grows up to two meters tall and is characterised by its aromatic nature and prickly stems. The leaves of *L. camara* are rough-textured and emit a pungent odour when crushed, while the flowers display a variety of colours such as pink, white, red, yellow, and violet (Ghisalberti, 2000; Patel, 2011). Fruit and flower production occur year-round, with birds serving as the primary seed dispersers (Agaldo, 2018). *Lantana camara* thrives in a diverse range of environments, adapting to various climates, habitats, and soil types, including both poor and fertile soils (Negi et al. 2019). It prefers open, unshaded areas and is commonly found in disturbed environments like roadsides, agricultural lands, and riparian fringes. Despite its versatile uses in traditional medicine for treating conditions like itchy skin, chicken pox, asthma, and ulcers, *L. camara* is known for its invasive behaviour, disrupting the regeneration process of native vegetation through allelopathic suppression and alterations in soil properties (Fan et al. 2010; Ruwanza and Shackleton, 2016). In South Africa, *L. camara* was introduced as an ornamental plant in 1858 and has since invaded close to two million hectares, with significant infestations in the Eastern Cape, Limpopo, Mpumalanga, and KwaZulu-Natal provinces (Urban et al. 2011).

3.2.2. Study area

The study was conducted on three farms located around Bathurst town, in the Eastern Cape province of South Africa. The sites were: Site 1, located in Lyndhurst Farm (-33.45647; 26.88134); Site 2, located in Amargh Farm (-33.44776; 26.88707); and Site 3, located in Summerhill Farm (-33.50713; 26.84736) (Figure 3.1). The farms are mostly used for livestock farming and crop production. The vegetation within these farms is classified as both the Albany Coastal Belt and the Kowie Thicket, both within the Albany Thicket Biome (Mucina and Rutherford, 2006). This biome has deep, well-drained, fertile sandy loam soils (Cowling, 1983), and the vegetation is determined by the complexity of interrelated factors such as soil moisture and soil type. Rainfall in the area is unpredictable, and droughts lasting several months are common; the mean annual rainfall is approximately 720 mm, with most of the rain falling in the austral summer months between October and April (Mucina and Rutherford, 2006; Puttick et al. 2011). The mean monthly minimum and maximum temperatures are 5.6 °C and 35.0 °C, respectively. The Albany Thicket vegetation is currently extremely transformed and shows excessive levels of degradation, mostly due to extensive grazing and farming (Mucina and Rutherford, 2006).

The sampling sites were selected based on their *L. camara* invasion (> 65% cover), availability of open, uninvaded areas, and them having similar slopes and soil types. The soil texture within the sampling sites ranged from being loamy to sandy. The Lyndhurst Farm has a footprint of approximately 65.1 ha and is used for both crop production (pineapples) and cattle farming, and the site is heavily invaded by *L. camara*. According to Heshula (2005), the *L. camara* invasion in the area dates from 2005, and its expansion has been observed over the years. Mechanical (bulldozing) and chemical (spraying) attempts have been made to control *L. camara* in some areas, but re-invasion and secondary growth were noted in those areas. Biological control experiments were also conducted on the farm using *Falconia intermedia* (Heshula, 2005). The dominant native trees are *Searsia* spp., *Vachellia natalitia*, and *V. karroo*. The Amargh Farm is mainly used for livestock farming (cows, pigs, and goats). The site is heavily invaded by *L. camara* together with other woody IAPs such as *Acacia mearnsii*, *Jacaranda mimosifolia*, *Melia azedarach*, and *Pinus* spp. The invasion of *L. camara* on this site mostly occurs in areas where frequent livestock grazing occurs. Some of the native trees and shrubs dominating the site are *Azima tetracantha*, *Scutia myrtina*, *Searsia* spp., and *Zanthoxylum* spp. The Summerhill Farm is mostly used for pineapple production, and huge patches of *L. camara* were found close to old pineapple fields, together with other IAPs that included *A. mearnsii* and *Arundo donax*. Native tree species dominating the farm include *V. karroo* and *V. natalitia*.

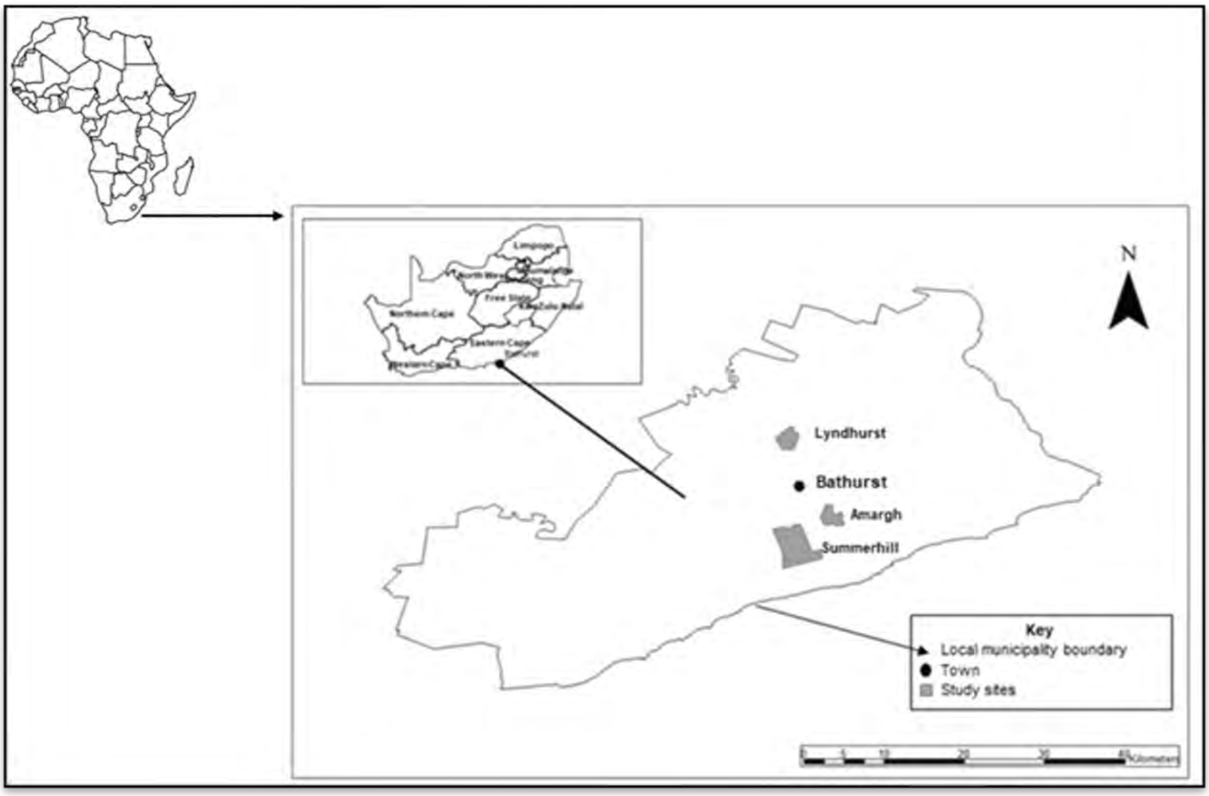


Figure 3.1: The study area showing the location of sites on three farms located near Bathurst in the Eastern Cape province of South Africa.

3.2.3. Experimental design and soil sample collection

At each farm, we purposely selected areas invaded by *L. camara*; thereafter, the mature *L. camara* plants were selected based on the following criteria: (i) having a height of > 100 cm; (ii) having a diameter at breast height (DBH) of more than 3 cm; and (iii) having an average crown of above 2 m. The selected individual plants were approximately 50 m apart within each site. Underneath each identified *L. camara* plant, soil cores were collected at three different positions (namely sampling positions), i.e., (i) beneath the *L. camara* canopy (30 cm from the stem), and these were referred to as 'canopy' soils; (ii) on the canopy edge of each *L. camara* plant, and these were referred to as 'edge' position; and (iii) 30 m away from the *L. camara* individual, and these were referred to as 'out' as they were in an uninvaded area with no *L. camara* influence (these acted as the control soils). At each site, the above-mentioned soil sampling positions were replicated six times, i.e., six plants per site. At each sampling position, soil samples were collected at four points (north, south, east, and west) 30 cm apart, as well as one in the middle, and mixed into one soil sample. In total, 54 soil samples (six individual plants × three sampling positions × three sites) were collected for each sampling month. Soil samples were collected using a soil core measuring 10 cm in diameter and 10 cm in depth after careful hand removal of debris and stones. Immediately after soil collection, soils were packed in labelled brown bags and transported to a laboratory at Rhodes University in Makhanda for analysis. Soil sampling for physical properties, namely soil moisture content, penetration resistance, infiltration, and water repellency, was done seasonally in the same sampling positions in April (autumn), July (winter), September (spring), and December (summer) 2020. Due to financial restrictions and the assumption based on literature that no soil chemical property variations were expected over one-year, chemical property measurements, namely pH, total C, total P, total N, NH_4, and NO_3, were only taken once in April (autumn).

3.2.4. **Soil measurements and analysis**

Before conducting laboratory measurements, roots and organic matter were removed from the soil samples by sieving them through a 2 mm sieve. Soil moisture content was analysed using the Black (1965) method and expressed as a percentage (%). To determine the gravimetric soil water content, soil samples were weighed wet, oven dried at 105 °C for 72 hours, and re-weighed to obtain the water content. Soil compaction was measured on site using a pocket penetrometer (SOILTEST, Inc., Evanston, Illinois, USA). The penetrometer was pressed into the soil, and the red metal ring was pushed up the scale due to compaction force, thus marking the penetration resistance value at kg cm^{-2} (Leung and Meyer, 2003). Soil infiltration rate was measured on site using a mini-disk infiltrometer, which is an acrylic tube with a semipermeable plastic disk and a rubber stopper. In this study, the suction rate (suction or negative pressure applied to the infiltrometer when measuring unsaturated hydraulic conductivity and infiltration rates) was adjusted to 2.0 cm based on the soil type. The two chambers of the infiltrometer (upper suction area and lower) were both filled with water, and measurements were taken by placing the infiltrometer on the soil surface after hand removal of plant litter. The drop in water in the lower chamber was monitored and used to measure the water infiltration rate in ml over five minutes. Therefore, infiltration measurements were manually recorded at 30-second intervals for five minutes. The measured cumulative infiltration over time was used to calculate the infiltration rate using the method suggested by Zhang (1997). Under laboratory conditions, soil water repellency was measured using the Water Droplet Penetration Time (WDPT), which measures the rate of wetting and retention of water in soils. The sieved soil was placed in petri dishes and air-dried for seven days under laboratory conditions at varied room temperatures due to seasonal temperature variations. The WDPT test was conducted by placing five drops of distilled water on the surface of the soil samples (Doerr and Thomas, 2000; Doerr et al. 2006) using a syringe and measuring the penetration time for each single drop. The average of the five drops was taken as the average for each sample. The following WDPT classes listed in Table 3.1 were used, and these were adopted from Bisdom et al. (1993) and Ruwanza and Shackleton (2016).

Table 3.1: The classification of the Water Droplet Penetration Time (WDPT) method used in this study.

Classification	Infiltration time (seconds)	Class
Wettable	< 5	1
Slightly repellent	5–60	2
Strongly repellent	60–600	3
Severely repellent	600–3 600	4
Extremely repellent	> 3 600	5

All soil chemical properties were measured at a commercial laboratory, namely Bemlab (PTY) Limited. Soil pH was analysed in a 1:5 soil KCl extract as described by Rhoades (1982). The total phosphorus (P) was measured using a Bray II extract as reported by Bray and Krutz (1945). Soil total carbon (C) was measured using the modified Walkley-Black method, whilst soil total nitrogen (N) was analysed by complete combustion using an elemental analyser. Soil ammonium (NH_4) content was analysed based on the Berthelot reaction involving phenol, and soil nitrate (NO_3) content was analysed by nitration of salicylic acid (Cataldo et al. 1975).

3.2.4. **Statistical analysis**

All data were analysed using TIBCO Statistica 14 (TIBCO Software Inc., 2019). Proof of normality and homogeneity was tested at a 5% confidence level ($p > 0.05$) using the Kolmogorov-Smirnov and Levene's tests, respectively. Soil physical properties that were measured for four seasons were analysed using repeated measures ANOVA since data were collected repeatedly at the same sampling position. The soil water repellency categories across the different sampling positions and seasons were analysed using the chi-squared test based on the WDPT categories. To analyse the changes in soil chemical properties, comparisons were made across the three sampling positions (canopy, edge, and out) using one-way analysis of variance (ANOVA), since data were collected only once. Where ANOVAs were significantly different, the Tukey Honestly Significant Difference (HSD) post hoc test was used at $p < 0.05$.

3.3. Results

3.3.1. Soil physical characteristics

The soils at the different sampling sites and positions ranged from loamy to sandy, and the mean soil moisture content for the canopy sampling position was 6.99 ± 0.68%, 6.72 ± 0.64% for underneath the canopy and 6.85 ± 0.64% for *L. camara* canopy. Statistical comparisons of the three sampling positions showed no significant ($p > 0.05$) differences (Figure 3.2). Soil moisture content significantly ($p < 0.001$) varied among the seasons, with high soil moisture content being recorded in the wet (December) and autumn (April) seasons as compared to the dry winter (July) and spring (September) seasons. A Tukey test indicated that moisture content was significantly higher between the seasons except in July and September, where $p > 0.05$. The above-mentioned seasonal variations were observed across all the sampling positions at all three sites. The interaction between sampling positions and season showed no significant ($p > 0.05$) differences (Figure 3.2).

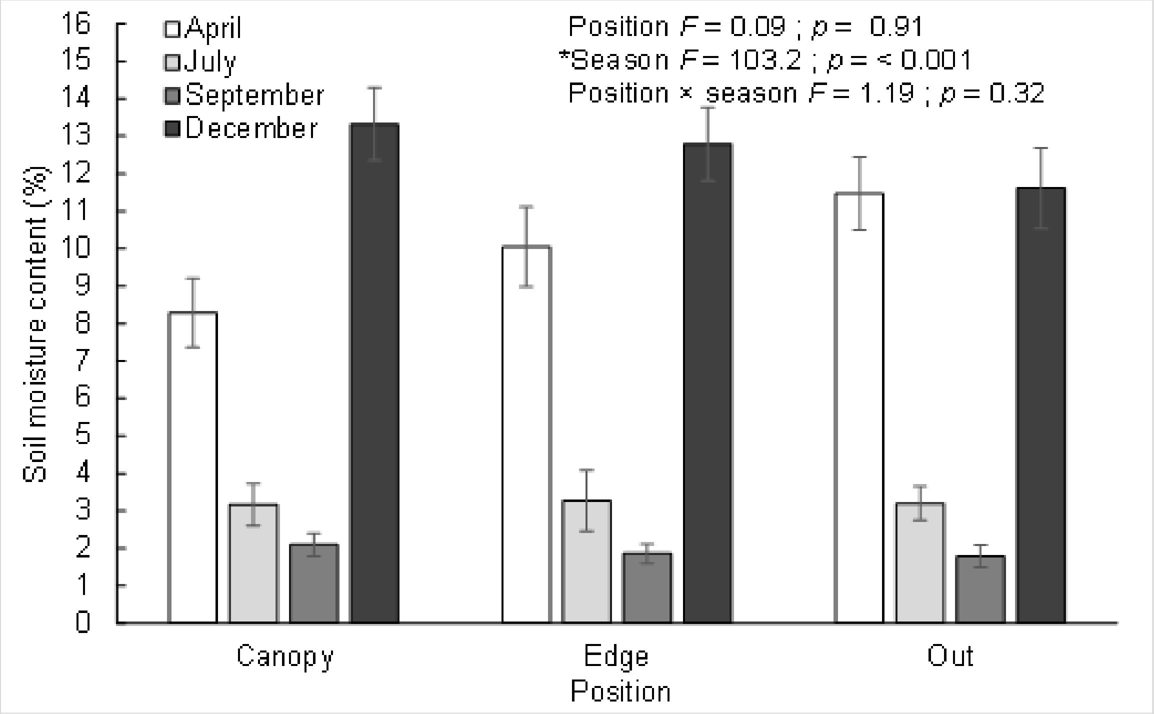


Figure 3.2: Moisture content of soil samples taken for three positions (canopy, edge, and out) across four seasons. Mean ± SE are shown and (*) shows a significant difference at $p < 0.001$ (n = 54).

The soil penetration resistance varied across the three sampling positions (Figure 3.3), with significantly ($p < 0.01$) higher soil penetration resistance away from the *L. camara* canopy as compared to soils collected from beneath *L. camara* and on the edge (Figure 3.3). These results were consistent across all the sampling seasons. The Tukey test showed that penetration resistance was significantly different ($p < 0.05$) between the three positions, where the canopy had a mean of 1.97 ± 0.11 kg cm^{-2}, the edge had a mean of 2.32 ± 0.14 kg cm^{-2}, and the area outside the canopy had a mean of 3.07 ± 0.14 kg cm^{-2}. Statistical seasonal comparisons showed that the soil was significantly ($p < 0.001$) more compact in the dry (July – 3.05 ± 0.41 kg cm^{-2}) and spring (September – 3.19 ± 0.43 kg cm^{-2}) seasons than in the wet (December – 2.09 ± 0.28 kg cm-^{2}) and autumn (April – 1.46 ± 0.12 kg cm^{-2}) seasons (Figure 3.3), and Tukey's post hoc test showed that soil penetration resistance was significantly different ($p < 0.05$) between the seasons, except between July and September. The interactions between sampling positions and seasons for soil penetration showed no significant ($p > 0.05$) differences (Figure 3.3). Overall, both sampling position and seasons influenced soil penetration resistance, with more compact soils being observed outside *L. camara* sampling positions than underneath the canopy edge in the dry than wet seasons.

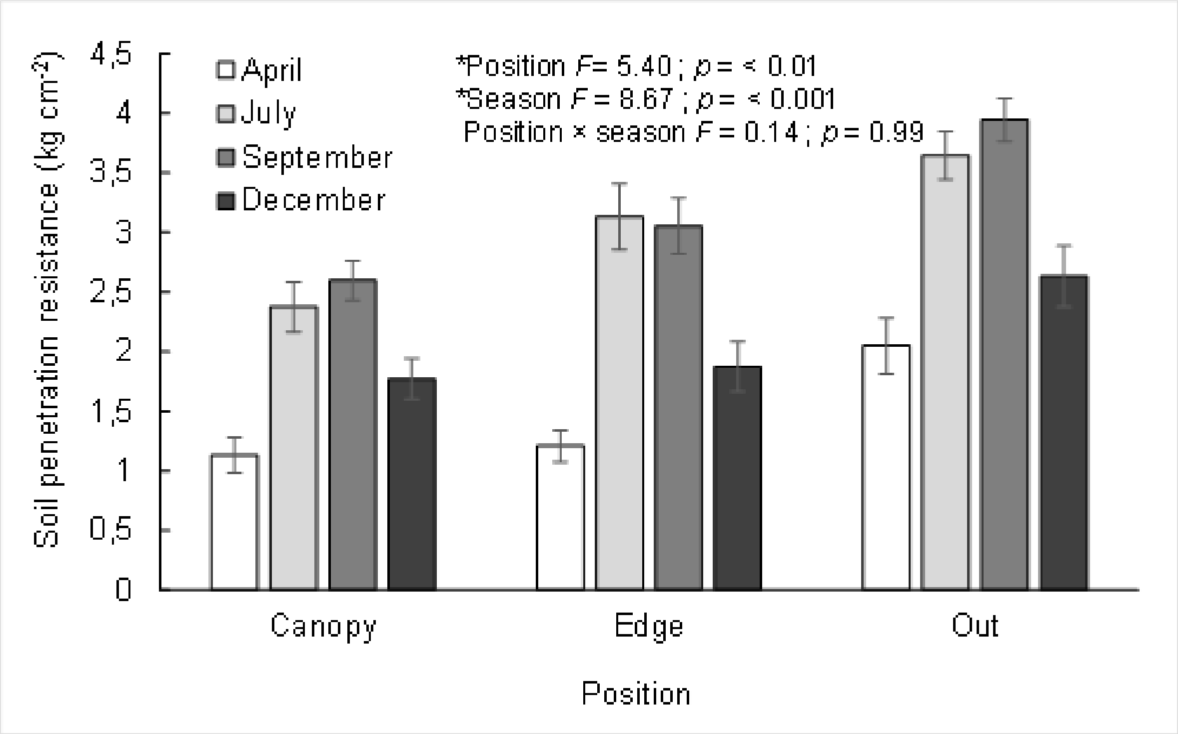
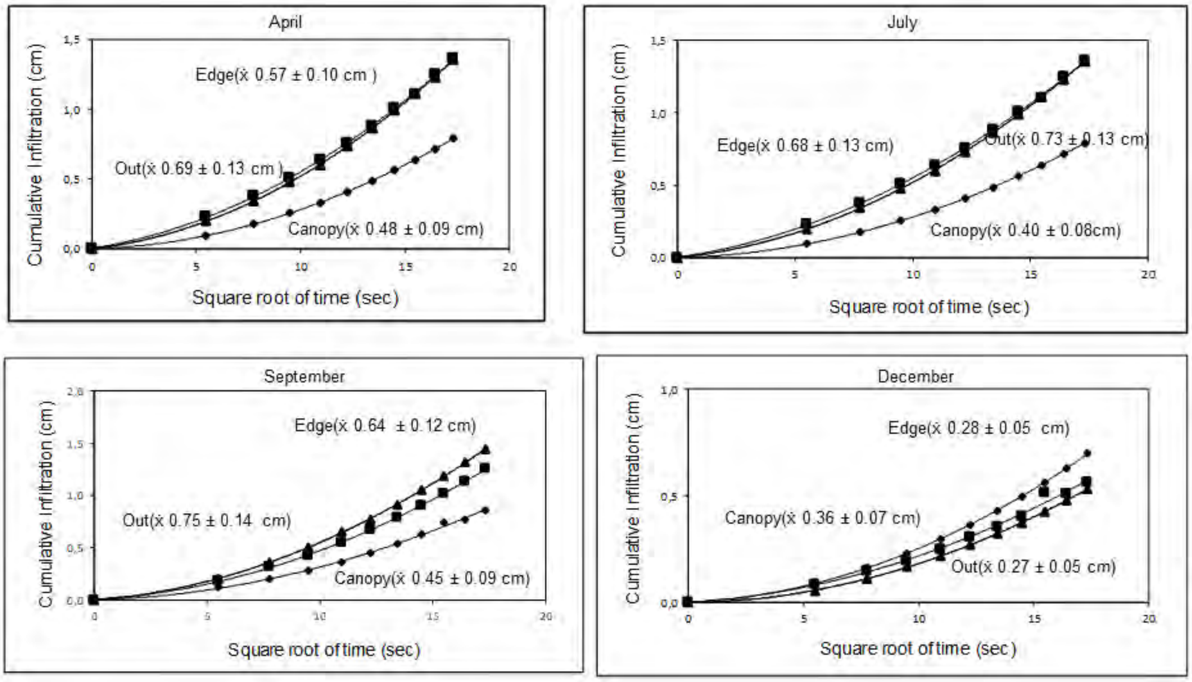


Figure 3.3: Penetration resistance levels of soil on three *L. camara* positions (canopy, edge, and out) across four seasons. Mean ± SE are shown and (*) shows a significant difference at $p < 0.001$ (n = 54).

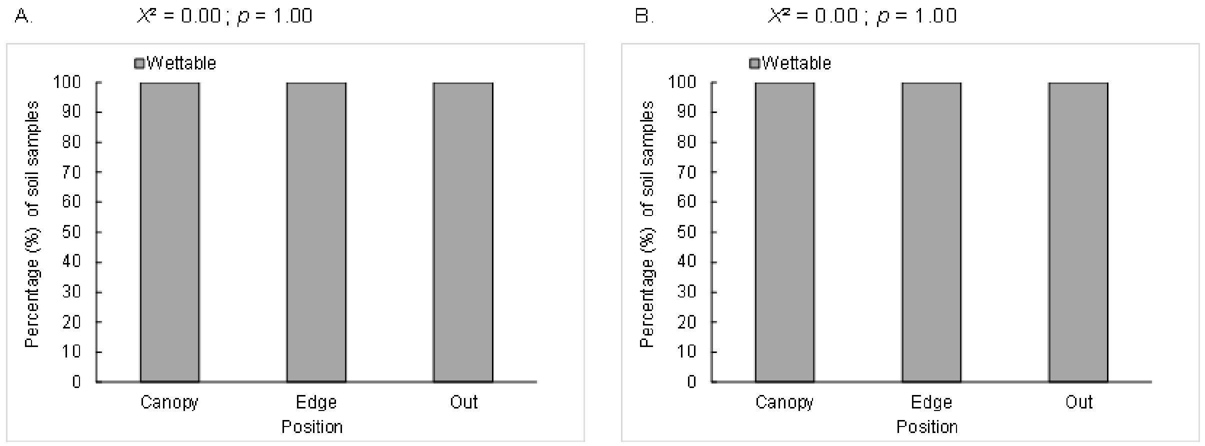
The mean soil infiltration rates ranged from 0.36 ± 0.06 cm–0.47 ± 0.09 cm for soils collected under the *L. camara* canopy, to 0.28 ± 0.05 cm–0.68 ± 0.13 cm for soils collected on the canopy edge, and 0.27 ± 0.05 cm–0.75 ± 0.14 cm for soils collected away from *L. camara* plants. Average soil infiltration rates showed significant ($p < 0.001$) differences between the different sampling positions, with faster infiltration rates being recorded underneath the *L. camara* canopy (0.42 ± 0.04 cm) and on the edge (0.52 ± 0.06 cm) than in the out position (0.61 ± 0.06 cm) (Figure 3.4). Seasonal comparisons also showed significant differences in soil infiltration, with significantly ($p < 0.001$) faster infiltration rates in summer (December = 0.30 ± 0.03 cm) than in any other season (Figure 3.4). The interactions between sampling positions and the seasons for soil infiltration rates showed significant ($p < 0.001$) differences (Figure 3.4). Overall, the soil infiltration rate was higher underneath the plant than outside the plant. Also, the wet summer month of December recorded higher infiltration rates than the other seasons.



*Position $F = 17.28$; $p = < 0.00$
*Season $F = 26.90$; $p = < 0.001$
*Position × season $F = 5.09$; $p = < 0.001$

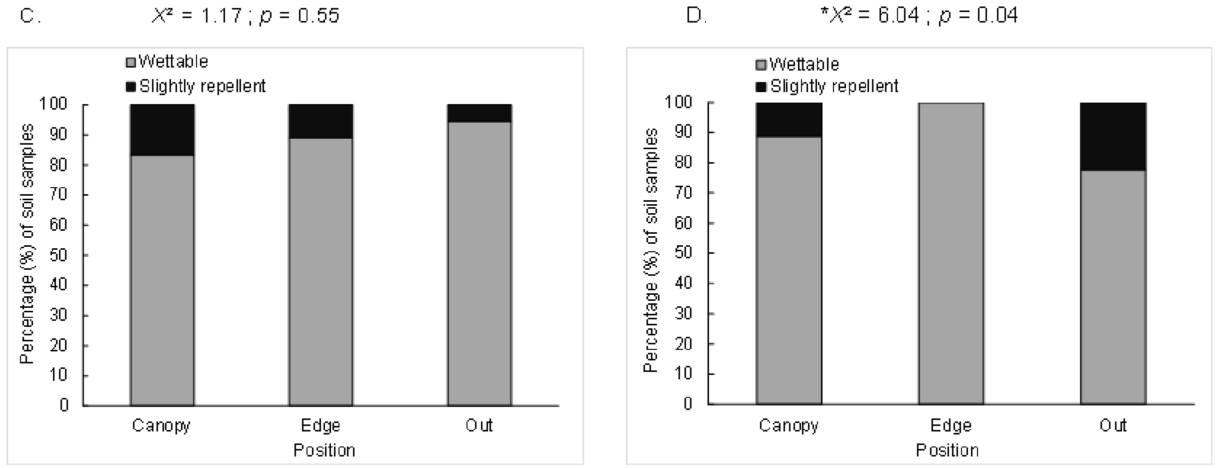
Figure 3.4: Mean infiltration levels for soil samples taken in three different *L. camara* positions (canopy (◆), edge (■), and out (▲)) across four seasons. (*) shows a significant difference at $p < 0.001$ (n = 54).

The bulk of soil collected under the canopy, edge, and out sampling positions was mostly wettable (80–100%), and the chi-squared analysis results of WDPT in April, July, and September showed no significant ($p > 0.05$) differences between sampling positions (Figure 3.5). Only December showed significant ($p < 0.05$) differences in WDPT scores (Figure 3.5). In April and July, the soils were all wettable (100%) as compared to September and December, where both wettable and slightly repellent soils were recorded (Figure 3.5). No strongly, severely, or extremely repellent soils were recorded in the sampling positions across all the seasons.



April

July



September

December

Figure 3.5: Water drop penetration times of soils collected from different sampling positions across four seasons. Chi-squared results are shown and (*) indicates significant difference at $p < 0.05$ (n = 54).

3.3.2. Soil chemical characteristics

The soil pH from all sampling positions ranged from 3.9 to 7.2, with the *L. camara* canopy and edge positions being moderately acidic (5.73 ± 0.25; 5.60 ± 0.25), and the soil collected in the out position being slightly acidic (6.00 ± 0.20). However, no significant ($p > 0.05$) differences in soil pH were observed across the three sampling positions (Table 3.2). Statistical comparisons showed no significant ($p > 0.05$) differences among the canopy, edge, and out sampling positions for all the measured soil nutrients (Table 3.2). Overall, all the measured soil nutrient properties showed no significant differences across all three sampling positions.

Table 3.2: Soil chemical properties results of soil samples taken under three sampling positions (n = 54). One-way ANOVA results are shown.

Soil chemical properties	**Position**			**F-value**	**P-value**
	Canopy	**Edge**	**Out**		
pH	5.73 ± 0.25	5.60 ± 0.31	6.00 ± 0.20	0.62	0.54
Total P (mg/kg)	172.87 ± 12.67	171.98 ± 14.16	219.49 ± 30.73	1.69	0.19
Total C (%)	2.38 ± 0.38	2.32 ± 0.44	2.39 ± 0.31	0.01	0.99
Total N (%)	0.24 ± 0.04	0.21 ± 0.03	0.22 ± 0.03	0.19	0.83
NH_4 (mg/kg)	5.36 ± 0.48	6.11 ± 0.91	7.35 ± 1.74	0.74	0.49
NO_3 (mg/kg)	7.14 ± 1.99	6.73 ± 2.65	6.40 ± 1.24	0.03	0.97

3.4. Discussion

This study has presented evidence that *L. camara* alters and modifies some soil properties, in this case, physical properties such as soil penetration resistance, infiltration rate, and repellency in communities it invades. These modifications in soil physical properties also vary depending on the season. These results concur with preceding studies reporting that soil underneath *L. camara* is less compact but repellent (Ruwanza and Shackleton, 2016). Generally, studies on the effects of IAPs on soil properties have reported varied results, with some IAPs, such as *Acacia* species., modifying soil properties by fixing soil N and C (Yelenik et al. 2004), whilst other studies on *Eucalyptus camaldulensis* reported no soil changes (Tererai et al. 2015). Based on Stefanowicz et al. (2018) findings, the magnitude and direction of soil changes caused by IAPs differ depending on the specific IAP and the invaded landscape conditions. For example, in this study, alterations in soil physical properties varied according to sampling positions and season and indicate that not all physical properties change in the same direction (increase or decrease), and such changes are seasonally affected. According to Niu et al. (2007), the modification of soil physical properties often provides favourable conditions for further invasion by *L. camara* and by IAPs generally. Also, Ruwanza and Shackleton (2016) showed how *L. camara* can alter soil physical properties such as moisture and repellency, thus potentially creating better conditions for their growth.

Soil moisture content changes were mostly visible across seasons rather than *L. camara* sampling positions. These results are in contrast with observations by Ruwanza and Shackleton (2016), who observed that the soils underneath *L. camara* were moister than those in the open. Similarly, studies on other IAPs, such as *Psidium guajava*, observed higher soil moisture content underneath IAPs than away from the plant, a result that this study did not observe (Ruwanza and Dondofema, 2020). Other studies have reported that high soil moisture content underneath IAPs could be driven by high litter content that can hold moisture in the soil. Although not tested in this study, it is possible that soil moisture levels are similar across the different sampling positions because *L. camara* is a multiple-branched scrambling plant that can allow sunlight penetration underneath it, thus allowing the soil to dry at similar rates to open, uninvaded areas. In this study, key soil moisture differences were recorded across different seasons. Indeed, differences in soil moisture content have been associated with seasonal variations, particularly temperature and rainfall patterns, where high moisture contents were found during the wet months (December and April) and low moisture contents were recorded in the dry months (July and September). Seasonal variations in soil moisture content underneath IAPs were also observed by Ruwanza and Dondofema (2020), who reported high soil moisture content during the wet months under the invasive plant *P. guajava*.

Various effects of soil compaction on plants have been documented, and in most case studies, soil compaction usually restricts root growth and decreases accessibility to nutrients (Nawaz et al. 2013). The soil compaction levels reported in this study clearly show how *L. camara* modifies soil compaction. The soil underneath the *L. camara* canopy and edge had reduced soil compaction compared to the soil further away. This shows how *L. camara* results in the loosening of the soil; this is anticipated to be an influence of an increase in organic matter due to litter fall and its decomposition (Sharma and Verma, 2000). Indeed, previous studies have shown that *L. camara* releases more litter underneath it (Sharma et al. 2003; Fan et al. 2010), and as the litter decomposes, it has the potential to soften the soils and make them less compacted. This is also linked to microbial activity during the litter decomposition process, as microbial activity increases soil porosity, thus making the soil less compact (De Gryze et al. 2006). Kyle et al. (2007) reported how low soil compaction underneath IAPs promotes root growth, which enhances access to soil resources. The reduced soil compaction was more evident in the wet months, and this may have been influenced by rainfall patterns and the ability of the plant to hold soil moisture during the wet season. Since soil compaction is associated with changes in soil porosity, infiltration rates, and soil aggregates (Kozlowski, 1999), Kozlowski emphasised how soil compaction negatively influences plant performance, impacting nutrient and water uptake. The lower compaction underneath *L. camara* plants can potentially lead to an increase in nutrient absorption and uptake. Therefore, the low soil compaction underneath *L. camara* soils may contribute to its competitive advantage, thus enabling it to grow and outcompete native plant species. Ruwanza and Shackleton (2016) reported on how *L. camara* can take advantage of other benefits associated with compaction, such as improved soil porosity and enhanced nutrient uptake.

Soils were slightly repellent underneath *L. camara* during spring (September) and summer (December), but not in autumn (April) and winter (July). An increase in soil repellency underneath IAPs (although seasonal in this study) has been observed in other studies and for other IAPs (Scott, 2000; Ruwanza and Shackleton, 2016; Ruwanza, 2020). This is common, particularly for IAPs that have allelopathic abilities, as chemical compounds released by the plant may solidify during the dry season, resulting in soil hydrophobicity, which is known to increase soil water repellence (Doerr et al. 2000; Olorunfemi et al. 2014). Santos et al. (2016) found an inverse correlation between soil water repellency and soil moisture content. Ruwanza et al. (2013) also linked repellent soils to high summer temperatures that can cause a reduction in soil moisture, thus leading to increased soil repellency. The soil water infiltration rate was higher under the *L. camara* canopy and the edge positions compared to the out position. This could be attributed to soils under IAPs being associated with reduced compaction levels. For instance, Yapi et al. (2018) and Ruwanza and Dondofema (2020) recorded high infiltration rates in invaded sites, and these were linked to several factors, including soil compaction, earthworm burrowing, and soil porosity.

Literature reports on how IAPs may alter soil chemical properties (Weidenhamer and Callaway, 2010; Stefanowicz et al. 2018; Huangfu and Li, 2019; Mandiporeva et al. 2023), and soil fertility beneath IAP canopies is usually higher than in nearby open areas (Kahi, 2004; Mussa et al. 2016). Contrary to the above assertions and what was observed by Ruwanza and Shackleton (2016) for *L. camara*, the results of this study did not find significant differences in measured soil chemical properties across the different sampling positions. It is not clear why there were no differences in soil chemical properties across different sampling positions; however, it could be linked to factors such as external disturbance (e.g., grazing or fire), soil texture, soil type, and structure. For example, Rousk et al. (2009) reported how acidic sandy soils tend to have low bacterial and fungal activity and thus result in low decomposition rates, consequently influencing soil nutrient content. The soil at the different study sites was acidic and generally nutrient deficient, this is likely to explain the reported soil chemical property results. The observed chemical properties may also be due to the fact that soil chemical properties were sampled once, and usually soil nutrients can exhibit significant temporal variability. For instance, Olojugba and Fatubarin (2015) and Tomaz et al. (2022) report on how soil chemical properties can change over time, often seasonally, due to factors such as temperature, microbial activity, plant uptake, and precipitation, to mention just a few. So basically, soil chemical properties can fluctuate throughout the year. It is also possible that external factors, such as fire and grazing, could have contributed to the observed soil nutrient levels. For example, fire has the potential to increase or decrease soil nutrients through litter combustion and volatilisation, whereas grazing can decrease the availability of soil organic matter, and trampling can increase erosion, leading to nutrient leaching.

Rai and Singh (2020) document how IAPs alter the soils they inhabit to increase their own fitness relative to that of native species. However, the effects of IAPs on soil physicochemical properties can be variable. Dassonville et al. (2008) and Stefanowicz et al. (2017) acknowledge how soil nutrient changes following invasion depend on factors such as the invading species, invasion duration, invasion extent, seasonality, and site-specific variations. Given that *L. camara* is a fast-growing IAP, it can leverage the altered soil properties to its growth advantage in comparison to slower-growing IAPs or native plant species (Simba et al. 2013). A few studies have documented how *L. camara* modifies and alters soil properties, and this is associated with several factors such as increased litter deposition, allelochemicals, and the creation of microclimates underneath the plant that are rich in microbial activity, soil moisture, and soil nutrients (Fan et al. 2010; Ruwanza and Shackleton, 2016). These factors are known to alter soil properties, as shown by Fan et al. (2010) and Ruwanza and Shackleton (2016), where these soil physicochemical properties have been shown to regulate both biotic (living) and abiotic (non-living) components of the community.

These changes may persist even after clearing *L. camara* through soil legacy effects, thus limiting re-colonisation by native species, as observed by Nsikani (2017) for *A. saligna*. Such changes may also create positive feedbacks that may stabilise or accelerate the invasion, thus making it more challenging to re-establish native plant communities. Moreover, over time, these soil changes may slow down restoration initiatives where *L. camara* is removed for passive restoration purposes. In areas where *L. camara* is not managed, e.g., agricultural areas where it dominates, changes in soil physical properties caused by *L. camara* can affect cultivation and crop output. For example, Tadele (2014) and Enyew and Raja (2015) reported on how *L. camara* can negatively influence crops such as *Eleusine coracana* (finger millet), *Triticum turgidum* (wheat), and *Zea mays* (maize) by outcompeting crops for nutrients and influencing soil properties. This negative impact mostly occurs when *L. camara* establishes itself in agricultural areas, thus leading to competition for resources such as water, nutrients, and sunlight. Therefore, these detrimental effects are more likely to occur in agricultural settings when *L. camara* competes with crops for essential resources.

In other examples, Shackleton et al. (2017), Barik et al. (2020), and Ntalo et al. (2022) emphasised how *L. camara* is an emerging threat to forage production for livestock, thus causing a major problem for farmers. This is also likely linked to its ability to modify invaded ecosystems, including soils.

3.5. Conclusion

The findings highlight how *L. camara* causes changes in some soil physical properties, such as soil penetration and water repellency. The changes observed in this study were across different sampling positions and were season-dependent. This study contributes to an enhanced understanding of how *L. camara* can modify soil properties in the invaded environment, specifically soil physical properties. Seasonal variations in soil properties also highlight how environmental conditions, especially temperature and rainfall patterns, can influence soil physical properties. Sampling of soil chemical properties was conducted only once, limiting a more representative assessment of the soil chemical properties and also limiting the availability of data for seasonal comparisons. Therefore, additional research is warranted to evaluate and contrast the variability in soil chemical properties.

The changes in soil properties can have important implications for ecosystem processes and the success of restoration efforts. Furthermore, Afzal et al. (2023) mention how any alterations in soil properties caused by IAPs can lead to profound changes in vegetation composition and structure. Given the reported effects of *L. camara* invasion on soil physical properties, it is recommended that *L. camara* be managed through clearing, even when the changes appear relatively minor. The removal of *L. camara* is recommended to prevent further spread and protect the integrity of the ecosystem and biodiversity. Lastly, since *L. camara* can reshape soil properties, in this case, soil physical properties, more studies are needed to explore the mechanisms behind *L. camara* soil property modifications. It is therefore recommended that future research be conducted at the plant level to examine drivers of soil property changes, e.g., allelopathy, litter release, microbial activities, and plant-soil interactions underneath *L. camara* and other invasive plants.

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Chapter 4: Effects of *Lantana camara* invasion on native vegetation

Abstract

This study examined how *Lantana camara* affects native vegetation on three farms located near the town of Bathurst in the Eastern Cape province of South Africa. Detailed vegetation surveys were conducted in *L. camara* invaded and uninvaded conditions across 36 plots within three farms. All species were enumerated and identified, and their cover was visually estimated. The results showed that the species richness and Shannon-Wiener diversity index were not affected by *L. camara* invasion. The diversity of trees and shrubs was significantly higher in the *L. camara* invaded condition than in the uninvaded condition. The mean vegetation cover for trees and shrubs was also significantly higher in the *L. camara* invaded condition compared to the uninvaded condition; however, the cover of forbs and graminoids in the *L. camara* invaded and uninvaded conditions showed no significant differences. Nevertheless, *L. camara* invasion displaced some native species, such as *Citronella* spp. and *Azima tetracantha*. The mean plant height for trees and shrubs in the *L. camara* invaded condition was significantly lower than in the uninvaded condition. Furthermore, the diameter at breast height between the *L. camara* invaded and uninvaded conditions showed no significant differences. The results showed how *L. camara* created a suitable habitat and co-occurred with some native species and other IAPs such as *Acacia mearnsii*, *Jacaranda mimosifolia,* and *Bidens pilosa* that can compete with it. This study concludes that *L. camara* can co-exist with other species (both native and IAPs), an indication that its impacts on vegetation are unpredictable and cannot be generalised. Therefore, management decisions to clear *L. camara* should consider measures to protect the refuge and co-existing native species. This can be achieved by implementing clearing methods that protect co-occurring native vegetation, e.g., selective removal of *L. camara* or thinning.

Keywords: biological invasions; co-occurrence; ecological impacts; invasive plants; native vegetation displacement

4.1. Introduction

Biological invasions, whether deliberate or unintentional, have significant global impacts on ecosystems, habitats, and biodiversity (Vila et al. 2011; Simberloff et al. 2013; Early et al. 2016; Vaz et al. 2017; IPBES, 2019; Richardson et al. 2020). Invasive alien plants (IAPs) have been reported to cause economic, environmental, and human harm (Pimentel, 2002). The proliferation of IAPs is linked to intentional introductions associated with globalisation and increased human movement (Hulme, 2009; Koutika et al. 2011; Boy and Witt, 2013; Faulkner et al. 2020). For example, many invasive eucalypts were intentionally introduced to South Africa in the 1820s for forestry purposes (Forsyth et al. 2004). Once introduced and established, IAPs often have negative impacts on the new ecosystem (Rai and Singh, 2020). Lockwood et al. (2013) define an impact as a change caused by invasive alien species (IAS) (in this case, plants) on the recipient ecosystem.

The definition of IAPs has been widely debated (Richardson et al. 2000). The National Invasive Species Council (NISC) of the United States defines IAPs as non-native plants introduced into an ecosystem that cause or are expected to cause socio-economic and environmental harm (NISC, 2001). Pysek et al. (2004) define IAPs as species introduced to an environment that are self-sustaining populations capable of producing seeds profusely and have the potential to spread and cover large areas. While there are multiple definitions of IAPs, it is generally accepted that these species are alien (non-native) to the environment and have negative socio-economic and ecological consequences on the invaded ecosystem (Richardson et al. 2020).

Several theories have been put forward to explain the invasion capacities and processes of IAPs (Davis et al. 2001; Keane and Crawley, 2002). Although these theories are effective at explaining alien plant invasion, it is important to note that species and ecosystem-based traits play a role in why some species thrive in new ecosystems. For example, species and ecosystem-based traits such as high reproduction rate, capability to germinate under fluctuating environmental conditions, vigorous growth, effective seed dispersal, long-term persistence of seeds, dynamic vegetative growth, the ability of seeds to germinate easily, long flowering periods, and climatic suitability have been used to explain invasion by alien plants (Montana, 1990; Rejmanek et al. 2005; Pysek and Richardson, 2008; Vardien et al. 2012). For instance, several studies have reported that traits that make *Acacias*, *Eucalyptus*, and *Lantana* invasive in South Africa include their ability to grow fast, early reproduction, soil nutrient alterations, and tolerance of disturbance (van Wilgen et al. 2011; Vardien et al. 2012; Hirsch et al. 2020). In the case of *Lantana*, its ability to tolerate disturbance, allelopathy, the production of abundant viable seeds, its preference for high rainfall and temperature regions, and resource availability have been noted as some of the species- and ecosystem-based traits that make the plant more invasive (Vardien et al. 2012).

Various studies examine the impact of invasive alien plants (IAPs) on vegetation, noting declines in species diversity, richness, structure, and composition (Pysek et al. 2012; Dong et al. 2015; Richardson et al. 2020). Contrary findings, documented by Sax and Gaines (2003) and Dong et al. (2015), suggest IAPs can increase diversity and richness or cause no change, a phenomenon termed the invasion paradox by Valone and Wyers (2019). Pysek et al. (2012) link invasion co-occurrence to invasion history, community characteristics, and disturbance. However, Sax and Gaines (2003) acknowledge the mixed evidence on diversity variation post-invasion, which may differ at regional and local scales. Thus, impacts caused by IAPs on native vegetation are usually idiosyncratic and dependent on several factors that range from the species invader to the ecosystem being invaded. Invasive plant species such as *L. camara* are often associated with local scale ecosystem modifications, although co-occurrence has been observed (Ruwanza, 2020), resulting in the creation of new niche spaces that attract other species to co-exist with *L. camara*. The most reported mechanism that explains *L. camara's* ability to co-occur with other species is positive facilitation, where other species benefit from *L. camara*, e.g., through shade and protection from enemies (Ruwanza, 2020).

Lantana camara, a robust IAP, exhibits a multitude of traits contributing to its invasiveness (Day et al. 2003; Sharma et al. 2005; Mungi et al. 2020; Ntalo et al. 2022). Introduced as an ornamental species in Cape Town (South Africa) in 1858 (Urban et al. 2011), it has since spread extensively across humid regions of the country (van Wilgen and Wilson, 2018). Boasting wide ecological tolerances (Vardien et al. 2012), *L. camara* thrives in disturbed habitats such as grazing lands, forest edges, and abandoned fields, often outcompeting native flora for nutrient resources (Vardien et al. 2012).

Lantana camara invasion profoundly alters vegetation composition, structure, and function (Jevon and Shackleton, 2015; Ruwanza, 2020), often suppressing the survival and growth of native plant species (Sharma and Raghubanshi, 2010; Alemu and Terefe, 2015; Kumar et al. 2020). Sharma and Raghubanshi (2006) reported how *L. camara* undermines the health and regeneration of native plants by reducing their seed germination rates. Furthermore, it significantly hinders the germination of *Albizia lebbeck* and *Dalbergia sissoo* seeds (Manohar et al. 2017). Through allelopathic effects and other mechanisms, *L. camara* disrupts natural succession, leading to decreased biodiversity and native species richness (Day et al. 2003; Sharma and Raghubanshi, 2007; Singh et al. 2014; Mahla and Mlambo, 2019). Studies by Gooden et al. (2009) and Ruwanza (2020) reveal that *L. camara*-invaded sites typically exhibit lower species diversity, native plant richness, and altered composition and structure compared to uninvaded areas, though *L. camara* may offer refuge for certain native plants (Ruwanza, 2020).

Lantana camara invasion is extensive and affects some key economic sectors such as the agricultural sector in South Africa and Africa at large (Vardien et al. 2012). For example, *L. camara* is associated with a reduction in grazing lands, loss of crop yields due to weeding challenges, and the mortality of livestock (Vardien et al. 2012; Shackleton et al. 2017). Shackleton et al. (2017) reported that *L. camara* invasions cost rural communities a substantial amount of income from losses related to crop yields and livestock. Ntombela et al. (2016) pointed out how a loss in the agricultural sector affects not only food security but also the competitiveness of secondary and tertiary sectors in the country's economy and at the household level. Therefore, it is crucial to understand how IAPs such as *L. camara* influence ecosystems and biodiversity so that we can prioritise management efforts that are effective at preventing future introductions while at the same time controlling existing invasions (Blackburn et al. 2014).

Concerns have been raised regarding the management efforts of *L. camara* on various spatial scales around the world, and while numerous management approaches have been used to control *L. camara*, none have been successful in completely eradicating it. This is likely to be impossible given the current invasion extent. Even though *L. camara* is a known invader, there is still a knowledge gap regarding its impacts on native vegetation at a local scale, especially in the Eastern Cape province of South Africa, where it invades different habitats. As a result, there is a need to provide further insight into the impacts caused by *L. camara* at the site level to assist in developing site-specific interventions. Furthermore, previous research has shown that impacts can be site- and species-specific, indicating the need for impact studies at different sites to enhance understanding of the impacts and develop site- and species-specific interventions. Therefore, the specific objective of this study was to assess how *L. camara* influences natural vegetation in the Eastern Cape province, South Africa. This study provided insights into the effects of *L. camara* invasion on the local natural vegetation at a community level. The main question addressed was: does *L. camara* negatively affect native vegetation abundance, diversity, composition, and cover?

4.2. Materials and methods

4.2.1. Study area

This study was carried out on three farms that are currently used for crop and livestock farming. The farms are Lyndhurst Farm (-33.45647; 26.88134), Amargh Farm (-33.44776; 26.88707), and Summerhill Farm (-33.50713; 26.84736), located near Bathurst town in the Eastern Cape province of South Africa (Figure 4.1). The study sites were invaded by *L. camara* and each site had an invasive population of more than 65% *L. camara* cover. Adjacent to the *L. camara* invaded areas were uninvaded areas that had natural vegetation, which included woody species such as *Gymnosporia buxifolia*, *Vachellia karroo*, and *Zanthoxylum capense*, and graminoids such as *Eragrostis* spp. and *Sporobolus* spp. Vegetation in the area is categorised as Albany Coastal Belt and Kowie Thicket, which are both within the Albany Thicket Biome (Mucina and Rutherford, 2006). The Albany Thicket Biome is characterised by thorny, woody, dense, and semi-succulent vegetation, with woody species such as *Erythrina* spp., *Carissa* spp., *Grewia* spp., *Searsia* spp., and *Vachellia* spp. dominating (Mucina and Rutherford, 2006). The soils within the biome are sandy, well-drained, and of coastal dune origin (Mucina and Rutherford, 2006). About 51% of the biome has been transformed into other land uses, which include urban expansion, crop production, and livestock farming (Low and Rebelo, 1996). The temperatures in the area are mild, with mean monthly minimum and maximum temperatures of 5.6 °C and 35.0 °C, respectively (Mucina and Rutherford, 2006). The annual precipitation is approximately 720 mm, with most of the rain falling in the summer months between October and April (Mucina and Rutherford, 2006; Puttick et al. 2011).

4.2.2. Site description

The sampling sites were selected based on the cover of *L. camara* (> 65%), the availability of adjacent uninvaded areas, and having similar aspects and soil types. The elevation of the sites was approximately 250 m, and the soil texture ranged from loamy to sandy. Land use within the study sites was dominated by crop production, mainly pineapple, and livestock production. The Lyndhurst Farm has a footprint of approximately 65.1 ha and is used for both crop production (pineapples) and cattle farming. The site is heavily invaded by *L. camara* and the dominant native trees were *Searsia* spp., *V. karroo*, and *V. natalitia*. Amargh Farm is mainly used for livestock farming (cows, pigs, and goats). The site is heavily invaded by *L. camara*, but other woody IAPs such as *A. mearnsii*, *Jacaranda mimosifolia*, *Melia azedarach*, and *Pinus* spp. were present with small populations. The invasion of *L. camara* on this site mostly occurs in areas where frequent livestock grazing occurs. Several native species dominating the site include *Azima tetracantha*, *Scutia myrtina*, *Searsia* spp., and *Zanthoxylum* spp. Summerhill Farm is mostly used for pineapple production, and huge patches of *L. camara* were found close to old pineapple fields, together with small populations of other IAPs such as *A. mearnsii* and *Arundo donax*. Native tree species dominating the site include *V. karroo* and *V. natalitia*.

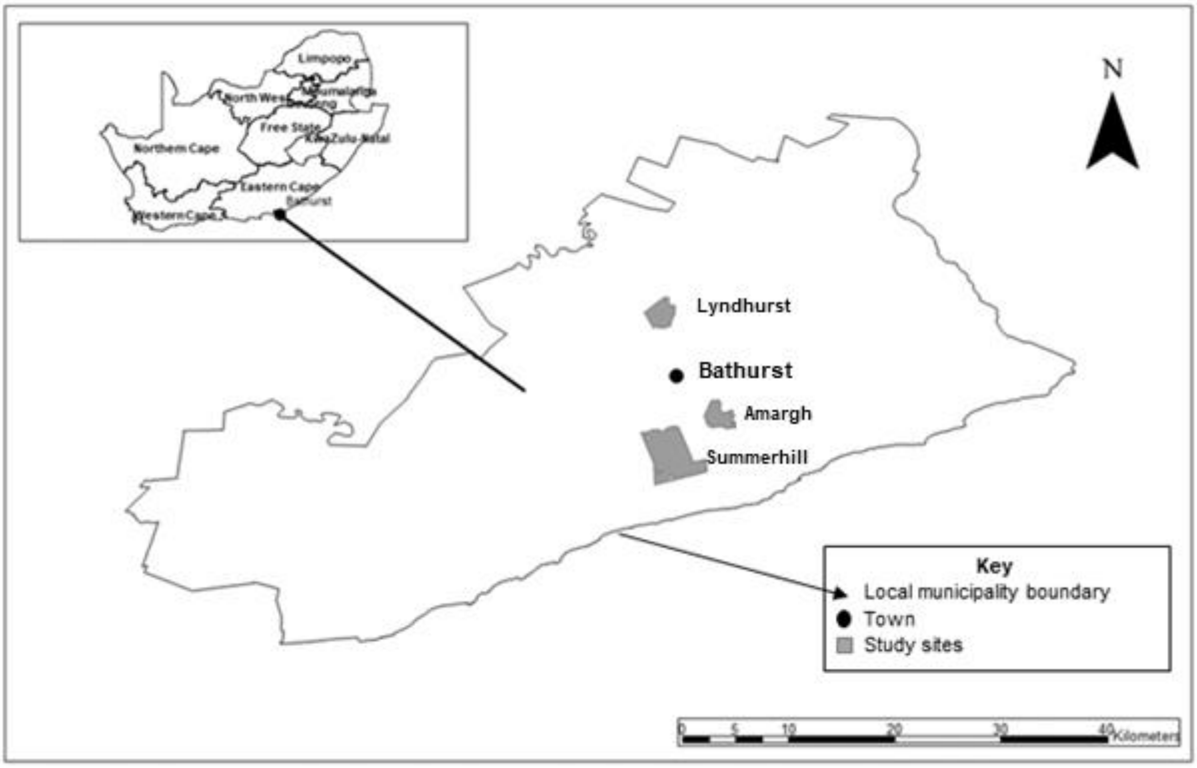

Figure 4.1: Location of the three study sites located at near Bathurst town, in the Eastern Cape province, South Africa.

4.2.3. Sampling design

In each of the three farms (referred to as sites), a *L. camara* invaded and an uninvaded area (referred to as invasion conditions) were identified for vegetation surveys. The invaded condition was defined by *L. camara* with a cover of more than 65%, whereas the uninvaded condition was dominated by native woody plants with the same cover status. In each of the invaded and uninvaded conditions, plots measuring 5 m × 5 m (25 m^2) were set up, with each plot replicated six times at each site (farm). Therefore, a total of 36 plots were set up (six plots × two invasion conditions (invaded and uninvaded) × three sites (i.e., three farms). The plots within each invasion condition were approximately 10 m apart, whereas the distance between the invaded and uninvaded conditions per site (within a farm) was 100 m (i.e., separated by farm roads).

4.2.4. Vegetation surveys

A detailed vegetation survey was conducted in February 2020, during the rainy season for effective identification. The total number of individual plant species found in each plot were counted to assess the species richness and density of all trees and shrubs. Forbs and graminoids were determined by counting the total number of individual plants available in a 1 m × 1 m quadrat that was placed at the centre of the plots. The cover of all plant species was visually estimated per plot and quadrat to the nearest 5% or 1% if less than 5%. This method estimated the percentage of ground covered by each plant species, and the estimation was done with a level of precision where the cover of plant species was rounded to the nearest 5% if the cover is greater than or equal to 5% and to the nearest 1% if the cover is less than 5%. For trees and shrubs, height (cm) and diameter at breast height (DBH) (cm) measurements were recorded using a tape measure and a vernier caliper, respectively. For multi-stemmed plants, only the height and DBH of the tallest stem was recorded. The height data of trees and shrubs was distributed into the following size classes: < 50 cm, 51–150 cm, 151–250 cm, 251–350 cm, and > 350 cm. Species were allocated to different growth forms, namely trees, shrubs, forbs, and graminoids, based on morphology. Plant samples were collected for identification at the Albany Museum herbarium in Makhanda, South Africa.

4.2.5. Statistical analysis

Data were analysed using TIBCO Statistica 14 (TIBCO Software Inc., 2019). Normality tests were conducted using the Shapiro-Wilk test, and data was normally distributed. In order to assess the effects of the *L. camara* invasion on plant diversity, species richness, Shannon-Wiener index, Simpson's index, and evenness index were calculated per plot and compared between invaded and uninvaded conditions. Differences in vegetation measurements, species richness, and diversity indices between the invaded and uninvaded conditions were analysed using a *t*-test since the data was collected only once. Species occupancy frequency percentages were calculated as the number of times a plant species was present per plot in the different invasion conditions.

4.3. Results

A total of 46 plant species were found in this study (trees, shrubs, herbs, and graminoids), and the identified plant species came from 27 different families across all plots, with the dominant ones being Poaceae, Fabaceae, and Malvaceae (Appendix 1). Apart from *L. camara*, other frequently occurring tree and shrub species (≥ 20% occupancy) in the invaded condition were *Carissa* spp., *Searsia* spp., *Scutia myrtina*, and *V. karroo*. In the uninvaded condition, the most frequently occurring tree species was *V. karroo* with an occurrence of more than 20% (Appendix 1). Some alien invasive trees and shrubs such as *A. mearnsii*, *J. mimosifolia*, *M. azedarach*, and *Pinus* spp. were recorded in the invaded condition, although they had low frequency occupancies of less than 6% (Appendix 1).

A total of 444 individual trees and shrubs were enumerated in the *L. camara* invaded condition across all study sites, of which about 54% were native species and 46% were alien species.

For alien species alone, *L. camara* dominated with 97%, with the remaining 3% of enumerated alien species coming from other growth forms. Both species richness and the Shannon-Wiener diversity index were significantly ($p < 0.001$) higher in the *L. camara* invaded condition compared to the uninvaded condition (Table 4.1). Species richness was almost twice as high in the invaded condition (11.67 ± 2.68) as in the uninvaded condition (7.76 ± 2.72). Both Simpson's and evenness indices showed no significant ($p > 0.05$) difference between the invaded and uninvaded conditions (Table 4.1). Species richness of trees and shrubs was three times higher in the invaded condition (3.16 ± 1.58) than in the uninvaded condition (0.77 ± 1.52; Table 4.1). Similarly, higher tree and shrub diversities were observed in the invaded than in the uninvaded conditions for the Shannon-Wiener, Simpson's, and evenness indices (Table 4.1). The richness of both alien and native trees and shrubs was significantly higher in the invaded condition than in the uninvaded condition, although this was more pronounced for alien trees and shrubs in the invaded condition since no aliens were present in the uninvaded condition (Table 4.1).

Table 4.1: Species richness and indices of diversity between *L. camara* invaded and uninvaded conditions in three sites located around Bathurst town in the Eastern Cape province of South Africa. Data presented as means ± SE and * represents a significant difference, N invaded = 18; N uninvaded = 18).

Species richness and diversity indices	**Invasion condition**		**T-test value**	
	Invaded	**Uninvaded**	***t***	***p***
	All species			
Species richness	11.67 ± 2.68	7.76 ± 2.72	4.44	≤ 0.001*
Shannon-Wiener diversity index *H′*	1.64 ± 0.38	1.16 ± 0.48	3.26	≤ 0.01*
Simpson's index of diversity *D*'	0.77 ± 0.10	0.68 ± 0.21	1.77	0.09
Pielou's evenness index *J*'	0.84 ± 0.09	0.84 ± 0.24	0.05	0.96
	Trees and shrubs			
Species richness (all)	3.16 ± 1.58	0.77 ± 1.52	4.62	≤ 0.001*
Species richness (alien)	1.11 ± 0.58	0.00 ± 0.00	8.08	≤ 0.001*
Species richness (native)	2.06 ± 1.51	0.72 ± 1.49	2.67	≤ 0.01*
Shannon-Wiener diversity index *H*'	0.73 ± 0.53	0.16± 0.52	2.90	≤ 0.01*
Simpson's index of diversity *D*'	0.49 ± 0.22	0.17 ± 0.29	3.82	≤ 0.001*
Pielou's evenness index *J*'	0.69 ± 0.28	0.20 ± 0.39	4.31	≤ 0.001*

The mean percentage of vegetation cover differed between the invaded (42.3 ± 4.52%) and uninvaded (35.1 ± 5.12%) conditions. The cover of trees and shrubs was more than double in the invaded condition than in the uninvaded condition ($p \leq 0.001$). The mean percentage cover for forbs in the *L. camara* invaded condition (14.3 ± 3.41%) and uninvaded condition (18.9 ± 6.15%) showed no statistical differences ($p > 0.05$). Similarly, the mean percentage cover for grasses also showed no significant differences ($p > 0.05$) (Figures 4.2b and c).

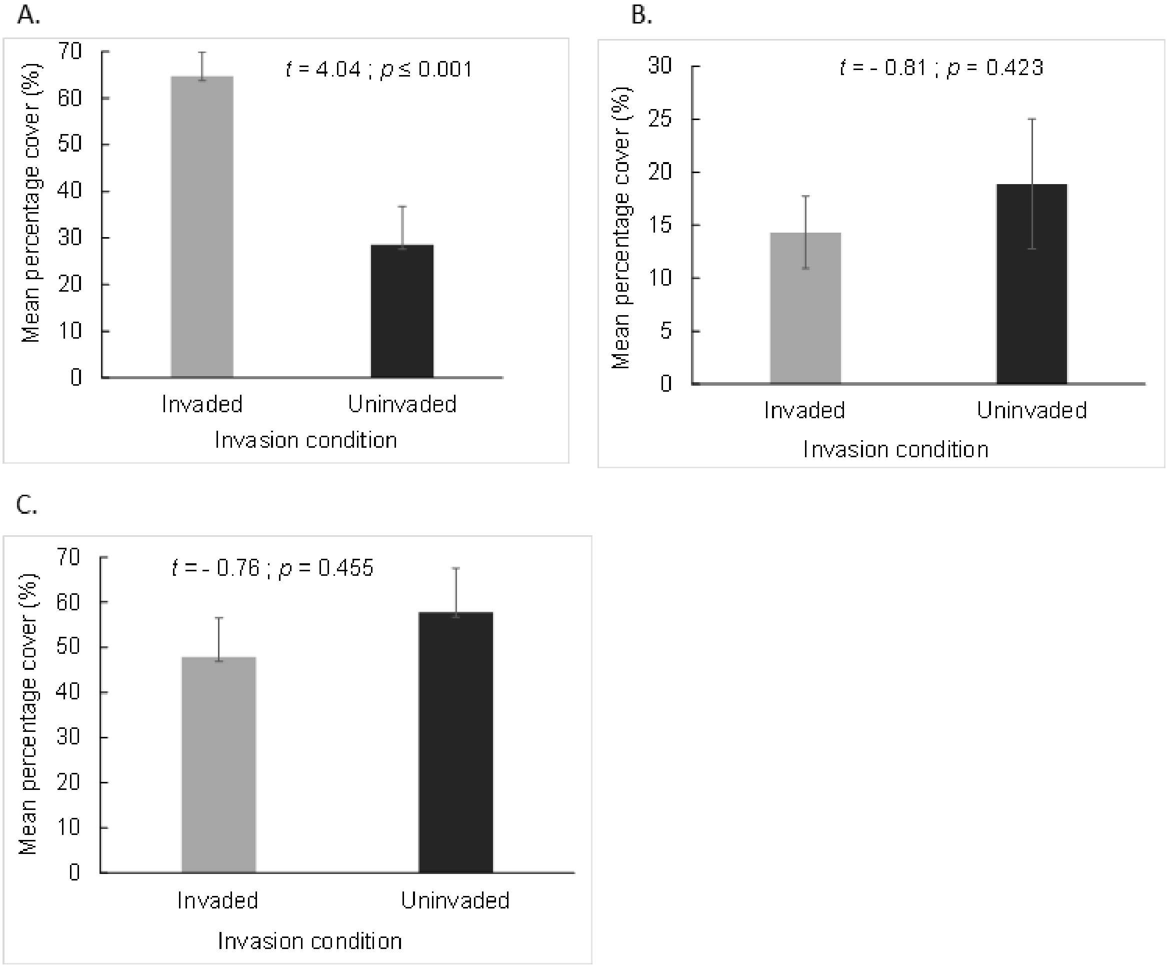

Figure 4.2: Mean vegetation cover in the *L. camara* invaded and uninvaded conditions for (a) trees and shrubs, (b) forbs, and (c) graminoids from three sites located near Bathurst town, Eastern Cape. (N invaded = 18; N uninvaded = 18). Bars represent the mean ± SE.

The mean plant height of trees and shrubs was significantly ($p \leq 0.001$) higher in the uninvaded condition than in the invaded condition (Figure 4.3a), with an average height of 82.5 ± 7.91 cm and 45.0 ± 2.60 cm, respectively. The mean DBH in the invaded condition and the uninvaded condition showed no significant differences ($p > 0.05$) (Figure 4.3b). Most of the trees and shrubs with an average height size below 250 cm were in the invaded condition rather than in the uninvaded condition (Figure 4.3c). A total of 382 seedlings (< 50 cm) were recorded in the invaded condition, compared to only 80 in the uninvaded condition. Tall trees and shrubs with an average height of more than 250 cm were mostly in the uninvaded condition rather than in the invaded condition (Figure 4.3c).

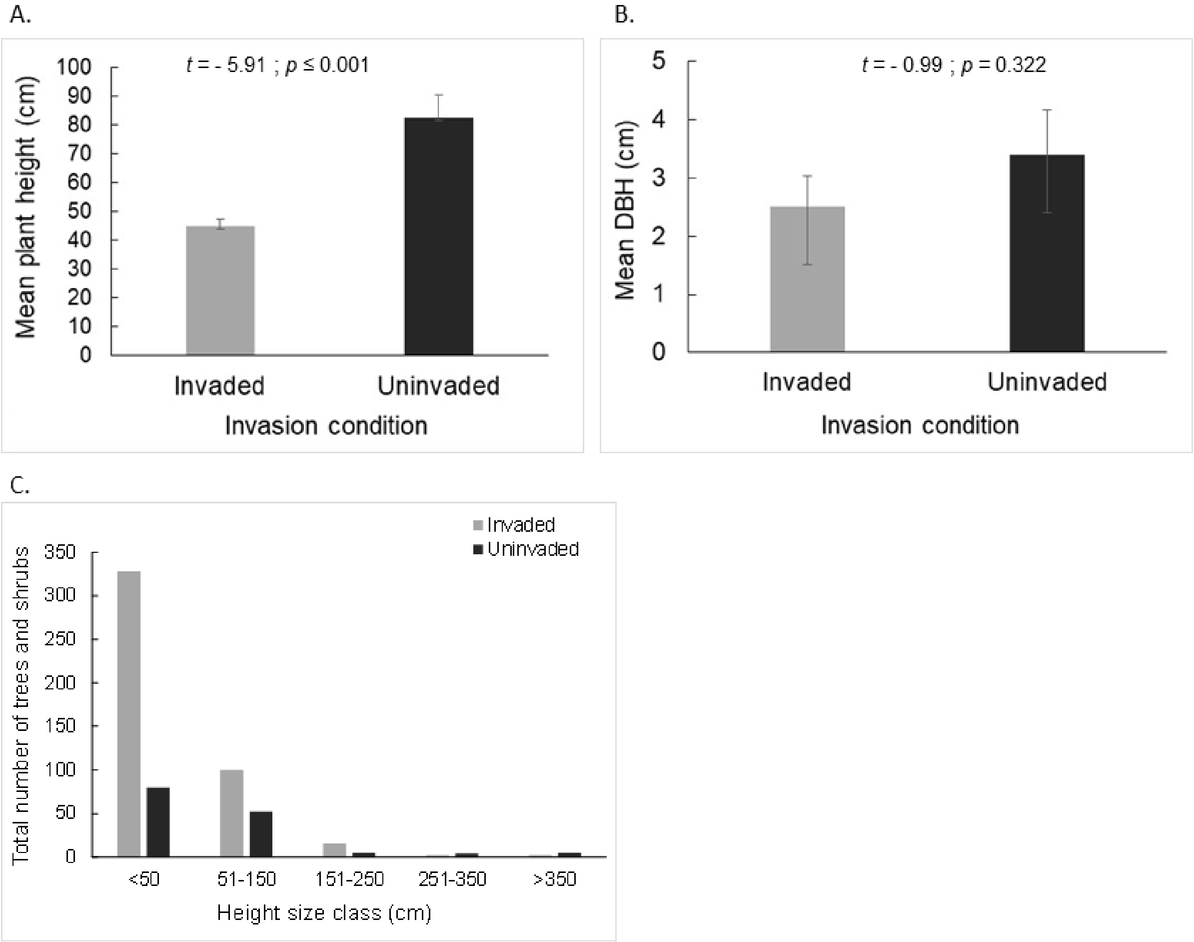

Figure 4.3: (a) Mean plant height, (b) diameter at breast height (DBH), and (c) total number of trees and shrubs per size class in *L. camara* invaded and uninvaded conditions observed in sites close to Bathurst town, Eastern Cape. Bars represent the mean ± SE.

4.4. Discussion

The main objective of this study was to examine the influence of *L. camara* on vegetation richness, diversity, and composition. The results of this study are varied, with both positive and negative impacts of *L. camara* being observed on vegetation richness, diversity, cover, height, and composition. For example, species richness and some diversity indices such as Shannon-Wiener were significantly higher in the *L. camara* invaded conditions, while Simpson's and Pielou's evenness showed no differences between the invaded and uninvaded conditions. The study also found that the effects of *L. camara* on vegetation cover were growth form dependent, with differences being noted for trees and shrubs but not for forbs and graminoids. These results contradict the popular notion that *L. camara* displaces native vegetation, resulting in reduced species diversity and composition where it invades (Zende et al. 2017; Bezabih et al. 2021). However, such varied results as observed in this study have been reported in the past (Zende et al. 2017; Ruwanza, 2020). It is also important to note that the duration of the invasion can influence the severity of the impacts on native plant vegetation. For instance, Valone and Weyers (2019) showed that the longer an IAP has invaded an area or site, the more likely it is to alter community composition and negatively influence native species richness.

Jevon and Shackleton (2015) and later Bezabih et al. (2021) report how *L. camara* invasion is linked to a significant decline in species richness, diversity, cover, structure, and composition. Studies that have reported on vegetation decline following *L. camara* invasion suggest allelopathy and changes in soil physical and chemical properties as the main drivers of native species decline (Jevon and Shackleton, 2015; Bezabih et al. 2021). In contrast to these previous studies, the results of this study show that *L. camara* invasion did not reduce species diversity and cover; rather, higher diversity was observed in the *L. camara* invaded condition. This could be due to several factors, such as *L. camara* being a refuge plant for other species or playing a positive plant-plant facilitation role that promotes the co-occurrence of species. The above assumptions are made because *L. camara* seemed to co-occur with some species such as *Centella asiatica*, *Cyperus* spp., *Digitaria eriantha*, *Searsia* spp., *Sporobolus africanus*, and *V. karroo* that had frequency occurrences of more than 40% in the invaded plots. Co-occurrence between invasive and native species has been reported in the past (Ruwanza, 2020), attributed to species being able to share resources such as nutrients, positive plant-plant facilitation, as well as the ability of these species to share affinity for disturbed conditions. Plant species that share affinity for disturbed conditions are usually species that are adapted to specific disturbances and can colonise those disturbed areas (Cilliers and Bredenkamp, 1999).

The co-occurrence of plant species can be facilitated by factors such as positive interactions, where an IAP either improves environmental conditions beneath their canopies or reduces competitive exclusion among other plants through facilitation mechanisms (Soliveres et al., 2015). The ability of *L. camara* to alter soil properties, as discussed in the preceding chapter, may have benefited understory vegetation. Furthermore, the litter produced by *L. camara* could also play a significant role in facilitating coexistence, potentially benefiting understory vegetation. Indeed, Wolkovich et al. (2009) noted that plant litter from invasive grass species facilitated the growth of the native *Artemisia californica*. Groves and Willis (1999) acknowledge that the effects of IAPs on native species are not linear, with some species being displaced while others are unaffected and some favoured by invasion. Therefore, there are various complexities in understanding the impacts of IAPs on native species (Ricciardi et al. 2013), and this study showed increased diversity of natives in the invaded condition. The co-occurrence of the above-mentioned species can also be linked with the competitive ability of these species, which is associated with traits such as resource use efficiencies and resource capture efficiency (Daehler, 2003).

At the growth form level, high species richness and cover were recorded for trees and shrubs in the *L. camara* invaded condition compared to the uninvaded condition. However, this did not apply to forbs and graminoids, which showed no differences between the invaded and uninvaded conditions. Results suggest that the impact of *L. camara* on vegetation could be growth form dependent, implying that *L. camara* acts as a refuge for some understory species. Although several studies have reported a decrease in understory species due to alien plant invasion (Lorenzo et al. 2011), others have demonstrated that some IAPs create native species refugia (Ruwanza, 2020). However, the ability of *L. camara* to act as a refuge for some species is only possible under low invasion extent, as reported by Ruwanza (2020). Under low invasion extent, other species can benefit from sunlight and reduced competition for nutrients with the IAPs. The cover of *L. camara* and its ability to modify soil physical properties create a suitable habitat for the co-occurring plant species. Several other factors have been linked to species interactions and co-occurrence, such as habitat heterogeneity and disturbance regimes (Ngondya and Munishi, 2021). In this study, disturbances linked to animal grazing at the sites were observed, and these could have promoted the co-occurrence of species through seed dispersal by animals. Moreover, the ability of *L. camara* to create suitable growth conditions for other species may also have facilitated co-occurrence. For example, Maskell et al. (2006) reported how the presence of IAPs resulted in the co-existence with common native plants, and Oduor et al. (2018) reported how *Opuntia ficus-indica* acted as a refuge for native plant species in habitats experiencing intense ungulate herbivory. Also, Ruwanza (2021) reported on how the invasive *Solanum mauritianum* co-existed with some native plant species, although this was not attributed to disturbances such as grazing.

In this study, I observed the presence of other IAPs such as *A. mearnsii*, *J. mimosifolia*, *M. azedarach*, and *Pinus* spp. in the invaded condition, although they occurred infrequently. Co-existence between native and alien species has been reported in invaded areas (Tererai et al. 2013; Ruwanza, 2020). Co-occurrence among IAPs could also be attributed to positive plant-plant facilitation. Additionally, the seeds of many IAPs can remain dormant in the soil and only germinate under suitable conditions. This has been observed in several soil seed bank studies (Tererai et al. 2015). The presence of these IAPs in the *L. camara* invaded condition can have a negative impact on *L. camara* management initiatives, as it can hinder the recovery process after *L. camara* removal. These IAPs have the potential to act as secondary invaders even after the invader has been removed. This could slow down the recovery of areas cleared of alien species (Nsikani et al. 2018). Secondary invaders are associated with well-known IAP traits, namely, persistent soil seed banks that can quickly recruit after IAP removal (Nsikani et al. 2018).

The study also noted that some specific native species were absent in the *L. camara* invaded condition, indicating that *L. camara* potentially eliminates and displaces certain native species, such as *Azima tetracantha* and *Zanthoxylum capense*, as well as the herb species *Citronella* spp. The displacement of native species by *L. camara* can result in the loss of native species and a reduction in genetic diversity. Stinson et al. (2007) reported on how native species vary in their resistance to invasion, with some species being more easily excluded from invaded communities than others. Several factors, including competition and allelopathy (Bhagwat et al. 2012; Vardien et al. 2012; Ruwanza, 2020), have been reported to contribute to the displacement of other plant species by *L. camara*. Although not tested in this study, allelopathic compounds produced by *L. camara* (Gentle and Duggin, 1997) have been observed to interfere with the physiological processes of native plants, resulting in their displacement (Kato-Noguchi and Kurniadie, 2021). This highlights how the allelopathic litter under *L. camara* invaded sites can inhibit the germination of certain plants beneath it. It may also affect the regeneration of native plant seedlings found in invaded habitats, thereby slowing down the likelihood of native vegetation succession. This could lead to the replacement of native vegetation and an increased likelihood of forming *L. camara* monodominant stands, although this is likely to occur only under high *L. camara* invasion conditions. Alternatively, the areas that provided suitable habitat for *L. camara* do not favour the species that were absent in the *L. camara* invaded condition. This is also linked to the aforementioned factors of allelopathy and competition, as well as the variations in soil properties (Wang et al. 2015). These factors can conjointly create an environment that is unfavourable for the growth of native species.

Trees and shrubs were taller in the uninvaded condition than in the *L. camara* invaded condition, while the total number of seedlings was higher in the invaded condition compared to the uninvaded condition. However, the decline in the number of trees and shrubs taller than > 205 cm clearly shows that *L. camara* could be promoting refugia for seedlings but suppressing their growth to maturity based on height as a measurement. A possible explanation would be that *L. camara* litter, which subsequently results in increased soil nutrients, could be benefiting seedlings, but *L. camara* shade could be suppressing growth. Thus, the reported low numbers of tall trees and shrubs. Therefore, *L. camara* invasions have the potential to create new populations dominated by seedlings and saplings (Osunkoya et al.

2013). The prevalence of seedlings and juveniles in the *L. camara* invaded condition has implications for native species recruitment. For example, seedlings are non-reproductive plants; therefore, their prevalence could mean limited native species seed rain, which is likely to result in the local loss of some native species (Osunkoya et al. 2013). This could result in a shift in vegetation structure within the invaded communities. Indeed, Gooden et al. (2009) reported on how *L. camara* can cause shifts in community structure, from tall forests to short-statured shrubland and forbs. Perhaps this could also explain the vegetation composition shifts that have been noted after the removal of IAPs (Gaertner et al. 2014), which potentially linked the dominance of seedlings during IAP invasion and the associated limited seed rain. Authors such as Gaertner et al. (2014) and Ruwanza et al. (2018) have discussed these ecological shifts in vegetation structure and composition pre- and post-invasion by IAPs, and they have concluded that invasion by IAPs often leads to changes in vegetation structure and composition, often resulting in a decrease in native plant diversity, changes in community dynamics, and shifts towards dominance by IAPs.

4.5. Conclusion

In conclusion, *L. camara* did not negatively affect species richness, diversity, or cover of native species. However, changes in some features of vegetation structure and composition were noted. *Lantana camara* seemingly created favourable conditions for some plant species that can co-exist with it, meaning that its known trait of changing soil properties (Ruwanza and Shackleton, 2016) could benefit some species. Our results show that the impacts of *L. camara* on vegetation are varied and do not have a predictable pattern. Some studies report significant negative effects (Vardien et al. 2012; Osunkoya et al. 2013), while others record positive or no effects (Ruwanza, 2020), although this is based on measured vegetation variables. Therefore, it is prudent to conclude that the effects of *L. camara* differ among measured vegetation variables and potentially among habitat types. Parepa et al. (2014) and Kunzi et al. (2015) acknowledge the above conclusion based on findings from other IAPs and point out how varied impacts of IAPs have been observed, and suggested factors such as site-specific factors, invasion extent, the invasive plant type, and invasion duration can explain these varied results. Hence, the impacts caused by IAPs on vegetation cannot be generalised, which highlights the need for various studies at different sites with varying invasion durations and extents.

Despite *L. camara* potentially facilitating co-existence with some native species, from a management standpoint, it is recommended that *L. camara* be removed due to its invasive nature and the significant impacts it poses on ecosystems. By removing *L. camara*, native species can have a better chance to recover and thrive without the competition and suppression imposed by this IAP. Removal of *L. camara* should, however, take into consideration the protection of refugia and co-occurring native species, implying that the removal method should be less destructive to avoid damaging the refugia and co-occurring native species. These refugia and co-occurring native species have the potential to act as restoration centres once *L. camara* has been removed. Restoration centres are important because they aid in seed dispersal and can serve as nurse plants. Lastly, more research is needed to examine the effects of *L. camara* at diverse sites and land use types to better understand the site-specific effects of the plant, for which the information can be used to make site-specific management plans that are effective at the site level.

4.6. References

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Supplementary materials

Appendix 4.1: The percentage frequency of plant species within Site 1–3, in both *L. camara* invaded and uninvaded conditions.

Plant species	Family	Invasion condition	
		Invaded	**Uninvaded**
	Trees and shrubs		
**Acacia mearnsii*	Fabaceae	■	-
Azima tetracantha	Salvadoraceae	-	■
Canthium spinosum	Rubiaceae	■	-
Carissa spp.	Apocynaceae	■■	-
Diospyros lycioides	Ebenaceae	■	■
Dovyalis spp.	Salicaceae	■	-
Gymnosporia buxifolia	Celastraceae	■	■
**Jacaranda mimosifolia*	Bignoniaceae	■	-
**Lantana camara*	Verbenaceae	■■■■	-
**Melia azedarach*	Meliaceae	■	-
Passerina rigida	Thymelaeaceae	■	■
**Pinus* spp.	Pinaceae	■	-
Rhamnus prinoides	Rhamnaceae	■	-
Scutia myrtina	Rhamnaceae	■■	■
Searsia spp.	Ebenaceae	■■■	■
Vachellia karroo	Fabaceae	■■■	■■
Zanthoxylum capense	Rutaceae	-	■
	Forbs		
**Alternanthera pungens*	Amaranthaceae	■■	■■
Amaranthus spp.	Amaranthaceae	■	■
Asparagus africanus	Asparagaceae	■	-
**Bidens pilosa*	Asteraceae	■■	-
Centella asiatica	Apiaceae	■■■	-
**Chenopodium album*	Chenopodiaceae	■	■■
Citronella spp.	Cardiopteridaceae	-	■
Clivia miniata	Amaryllidaceae	■	-
**Conyza bonariensis*	Asteraceae	-	■

Cucurbita spp.	Cucurbitaceae	■	-
**Datura stramonium*	Solanaceae	-	■
Helichrysum spp.	Asteraceae	■	-
**Malva parviflora*	Malvaceae	-	■
**Plantago lanceolata*	Plantaginaceae	■■	■■
Pteridium spp.	Dennstaedtiaceae	■■	-
Senecio ilicifolius	Asteraceae	■	■
Sida rhombifolia	Malvaceae	■	■■
**Solanum nigrum*	Solanaceae	■	■
**Trifolium repens*	Fabaceae	■	-
Graminoids			
**Arundo donax*	Poaceae	■■	-
Brachiaria spp.	Poaceae	■	■
**Cynodon dactylon*	Poaceae	■■■■	■
Cyperus spp.	Poaceae	■■■	-
Digitaria eriantha	Poaceae	■■■	■■■■
Ehrharta erecta	Poaceae	■	■
Eragrostis curvula	Poaceae	■■	■■■
Melinis repens	Poaceae	■	-
Panicum maximum	Poaceae	■	■■
Sporobolus africanus	Poaceae	■■■	■■

(■) - Indicates the presence of plant species based on calculated occupancy frequency that is categorised as follows: ■ (1–20%); ■ ■ (21–40%); ■■ ■ (41–60%); ■■■ ■ (> 60%); 0 – absence of species. (-) indicates that the species was not present in the invasion condition, and (*) shows non-native species that were identified using Bromilow (2010).

Chapter 5: Effect of *Lantana camara* invasion on soil seed bank dynamics in the Eastern Cape, South Africa

Abstract

Soil seed banks are crucial constituents of plant community dynamics, and for some species, they are the main promoters of invasion. Therefore, studying and understanding soil seed bank dynamics is vital to understanding alien plant invasion and, hence making management decisions. The impacts of *L. camara* on soil seed banks and the potential of the soil seed bank have rarely been studied. Thus, the objective of this study was to examine how *L. camara* invasion affects soil seed banks. Soil samples were collected from *L. camara* invaded and uninvaded plots on three sites located near Bathurst in the Eastern Cape province of South Africa. They were germinated under ambient greenhouse conditions for 10 months. The species composition, density, richness, and diversity of the seedlings that emerged from *L. camara* invaded and uninvaded conditions were recorded. The soil seed banks from both *L. camara* invaded and uninvaded conditions were dominated by herbaceous and graminoid species. The soil seed banks collected underneath *L. camara* and uninvaded conditions were similar, indicating that *L. camara* nurses some native herbs and grasses. The soil seed bank in *L. camara* invaded conditions also included other alien plants such as *Plantago lanceolata* and *Taraxacum officinale*, with occurrence frequencies of more than 50%. The total seedling abundance was significantly higher in the uninvaded condition than in the *L. camara* invaded condition, but there was no significant difference in seedling richness and diversity (Shannon-Wiener diversity index and Pielou's evenness index) between the invasion conditions. This study concludes that *L. camara* invasion negatively influenced the soil seed bank abundance of forbs and grasses. However, the presence of alien forbs and grasses in the soil seed bank under *L. camara* invasion could hinder vegetation recovery, as it has the potential to trigger secondary invaders. The limitations of this study, however, are that the short duration might not have captured every variety of seeds present in the soil, especially those that have longer dormancy periods or specific germination requirements.

Keywords: co-occurrence; germination; non-native plants; seed bank composition; seed recruitment

5.1. Introduction

Habitat loss and invasions by invasive alien species are serious global drivers of biodiversity loss (Lowe et al. 2000). They result in ecosystem degradation; hence, numerous studies are being conducted to better understand their adverse effects (Pimentel et al. 2000; Davis, 2005; Hedja et al. 2009; Pysek et al. 2012; Chen et al. 2018). Invasions by invasive alien plants (IAPs) frequently have adverse socio-economic and environmental impacts that are detrimental to human wellbeing (Langmaier and Lapin, 2020; Richardson et al. 2020; Diagne et al. 2021; Perez et al. 2022). Various plant and ecosystem traits have been used to explain plant invasions. For instance, the capability of IAPs to reproduce and disperse faster as well as adapt to new environments, particularly disturbed environments, has been used to explain the success of plant invasions (Inderjit, 2005; Richardson et al. 2020). Numerous studies emphasise how disturbance is one of the leading factors that intensifies plant invasions (Davis et al. 2000; Orban et al. 2021), as well as how it facilitates the spread of IAPs through changing resources, consequently creating suitable substrates for their growth in the absence of competitors.

Soil seed banks play a significant role in plant invasion, and hence (i) understanding them helps predict the long-term impacts of plant invasion, (ii) aids in developing measures to manage or control plant invasion, and (iii) helps in evaluating restoration potential after IAP removal (Gioria et al. 2012). For example, the plant recovery process after IAP removal might be centred on soil seed banks, seedling banks (seedlings and saplings already present), vegetative reproduction (re-sprouting of plant parts), remnant species (understory existing plants), and seed dispersal from intact areas (Garwood, 1989). Darwin (1859) noticed the potential of soil seed banks in plant recruitment, implying the need to understand soil seed bank dynamics for both invasion impacts and control. Given the importance of soil seed banks in managing alien plant invasion, research on the soil seed bank is a critical component of invasion ecology (Roberts, 1981; Simpson, 1989; Lang, 2006; Wang et al. 2013).

Studying soil seed banks can play several functional roles, such as (i) discovering plant species that might hamper restoration efforts, i.e., identifying alien species and the possibilities of these species dominating soil seed banks (Wetzel et al. 2001; Fisher et al. 2009; Gioria and Pysek, 2017); (ii) showing composition, richness, and abundance of local plant communities and whether the seed bank resembles the aboveground native vegetation; and (iii) providing information on environmental and ecological processes that hinder restoration of disturbed sites (Gioria et al. 2012; Shiferaw et al. 2018). Soil seed banks, however, rely on the seed production and composition of the seed sources, and most seeds come from plant communities in the aboveground vegetation and are dispersed either through abiotic or biotic mechanisms, i.e., anemochory (dispersed by wind), hydrochory (seed dispersal in water), epizoochory (seeds attached externally to animals), and endozoochory (diaspores with fleshy appendages or coverings that are consumed by animals and dispersed in excreted dung) (Bakker et al. 1996; Hyslop and Trowsdale, 2012; Milotic and Hoffmann, 2016). Most seeds are frequently found in the upper few centimetres of the soil and litter layer, and their density declines with soil depth (Bekker, 1998; Shiferaw et al. 2018).

According to Rayburn et al. (2016), assessing the similarity of species between soil seed banks and the aboveground vegetation is crucial for understanding the successional trajectory of a site following disturbance. In frequently disturbed sites, the aboveground vegetation and soil seed banks are usually similar, and in undisturbed sites, there is less similarity between standing vegetation and soil seed banks (de Villiers et al. 2003). Hopfensperger (2007) reported that the similarity between aboveground and belowground spheres can decrease over time following disturbance, as dormant seeds may lose viability with time. Hence, some scholars have concluded that relying only on the seed bank during restoration is not practical (Hopfensperger, 2007), thus the need for active restoration in situations where the seed bank has been depleted. Perhaps the most admirable thing will be to conduct soil seed bank studies before the IAP is removed so that decisions regarding the adoption of passive or active restoration are factored into restoration goals.

Mendes et al. (2015) document how soil seed banks in semi-arid ecosystems are classified by high spatial and temporal variability, thus being influenced by spatial patterns of vegetation and ecological niches. For example, Mukhongo et al. (2011) observed a high number of seeds and seedlings in grasslands compared with other vegetation types (i.e., shrubland, forest, and plantation), an indication that soil seed bank dynamics vary depending on vegetation type. Sanou et al. (2022) also observed variations in soil seed bank density in different vegetation types and microhabitats (bare soil, eroded soil, under plant canopy). Species diversity under the canopy was almost two to six times higher compared to the other microhabitats, an indication that the seed bank is dependent on aboveground vegetation since the compared sites had little to no vegetation. Moreover, seed density was also higher under the canopy (80.30 dm^{-3}) than outside tree canopies (44.59 dm^{-3} and 59.96 dm^{-3}). Seasonality can also strongly influence soil seed banks. For example, Abreu et al. (2021) reported on how high seed bank density and richness were observed during the wet season. Seed banks can represent seeds of both native and alien vegetation (Gioria et al. 2012) and a seed bank dominated by alien species may represent a notable barrier to restoration efforts, whereas a seed bank containing native species may accelerate restoration trajectories (Gioria and Pysek, 2016). Several studies have documented the different roles of soil seed banks in alien plant invasion habitats. For example, Goets et al. (2018) observed how soil seed banks of *Acacia mearnsii* were significantly higher than native vegetation, thus driving its invasion. Mndela et al. (2020) observed how the regeneration of IAP cleared sites was initiated by early successional plant species since they dominated the soil seed banks. Putri et al. (2021) documented how the soil seed banks underneath invaded areas were mostly comprised of IAPs, an indication that some invasive species act as refugia for other plant invaders. Lastly, Ruwanza (2016) concluded that the dominance of the *L. camara* seed bank reduced the density and diversity of other species, and this in turn can hinder vegetation recovery after removing *L. camara.*

Knowledge of the reproductive biology of IAPs is critical to managing invaded areas after clearing and developing strategies that will lead to their successful control. *Lantana camara* is no different from the other IAPs studied. It is an invasive shrub that typically grows about two m (Priyanka and Joshi, 2013), was introduced in South Africa in the 1850s, and has negative impacts on native plant species. *Lantana camara* is a highly adaptable species that can thrive in various ecosystems and can spread rapidly once introduced into a habitat (Negi et al. 2019). It consistently colonises disturbed areas such as roadsides, riverbanks, pasture lands, valleys, and forest edges (Ruwanza and Mhlongo, 2020; Ntalo et al. 2022). It produces seeds all year round that are 1-2 mm long and remain viable for years (Sharma et al. 2005). Seed germination of *L. camara* is usually stimulated by high soil moisture, warm temperatures, and high light intensity (Negi et al. 2019). The long-distance spread of *L. camara* is facilitated mostly by humans and endozoochorous birds that consume the fruit and seeds (Daehler et al. 2001). In South Africa, *L. camara* is designated as a category 1b invader that has invaded more than two million ha (Vardien et al. 2012). Category 1b invaders are plants that must be removed and destroyed immediately; no trade of this plant is allowed.

The seed bank dynamics of IAPs need to be understood at different sites if management interventions are to yield site-specific measures. Despite a strong appreciation of the ecological importance of soil seed banks, there is minimal knowledge of the seed bank dynamics of *L. camara* globally. Only recently has this gap started being addressed; for example, Muvengwi and Ndagurwa (2015) documented how high soil seed banks of *L. camara* in wetland ecosystems make them vulnerable to further invasion, particularly on the lower slopes of the wetland in Zimbabwe. Ruwanza (2016) also documented the soil seed bank dynamics of *L. camara* in agricultural areas and along roadsides and reported how *L. camara* reduces the seed bank of native species in South Africa.

Little is known about the seed bank dynamics of *L. camara* in South Africa. For example, Muvengwi and Ndagurwa (2015) found that *L. camara* exhibited high seed density in their study, which was linked to its biannual fruit production. They observed that the majority of *L. camara* seeds were concentrated in the top 5 cm of the soil profile. Globally, other studies have reported that *L. camara* is recognised for its persistent seed bank, enabling recruitment even after several years of its introduction (Vivian-Smith and Panetta, 2009; Negi et al., 2019). Given the above context, this study examined the effects of *L. camara* invasion on soil seed banks on three farms located near Bathurst in the Eastern Cape province of South Africa. I also assessed the availability of pioneer native species and IAPs in the soil seed banks with the aim of evaluating restoration or re-invasion potential after *L. camara* clearing. The specific research question was; does species composition, density, richness, and diversity of soil seed banks differ between *L. camara* invaded and uninvaded areas?

5.2. Materials and methods

5.2.1. Study area

The soil collection sites (Amargh, Lyndhurst, and Summerhill farms) were located within the Ndlambe Municipality, around Bathurst town, about 12 km inland from Port Alfred on the R67 road, in the Eastern Cape province of South Africa (Figure 5.1). The slope angle, soil type, and plant density were all similar across all three study sites. The sites lie within the Albany Coastal Belt and Kowie Thicket, within the Albany Thicket Biome. Van Wyk and Smith (2001) acknowledge how the Albany Thicket supports many endemic taxa and that it forms the core of the Albany Centre of Endemism. This biome's vegetation is typically dense, woody, semi-succulent, and thorny (Everard, 1987). The soils within this area are well-drained, sandy, and of coastal dune origin (Mucina and Rutherford, 2006). The annual precipitation is approximately 720 mm, with most of the rain falling in the summer months between October and April (Mucina and Rutherford, 2006). Temperatures within the area range from 13–29 °C in the austral summer to 1–12 °C in the austral winter (Mucina and Rutherford, 2006). The status of the study sites is extremely transformed and shows high levels of degradation, particularly because of ongoing agricultural activities, both crop production and animal grazing.

The Lyndhurst Farm has a footprint of approximately 65.1 ha and is used for both crop production (pineapples) and livestock farming (cows). Within the farm, there is a site that is heavily invaded by *L. camara*. Adjacent to the invaded site is the uninvaded area, that is dominated by native trees such as *Searsia* spp., *Vachellia karroo,* and *V. natalitia*. The Amargh Farm is mainly used for livestock farming (cows, pigs, and goats). The site is heavily invaded by *L. camara* together with a few other woody IAPs that include *Acacia mearnsii*, *Jacaranda mimosifolia*, *Pinus* spp., and *Melia azedarach*. The invasion of *L. camara* on this site mostly occurs in areas where frequent livestock grazing occurs. The adjacent uninvaded area is dominated by native trees and shrubs such as *Azima tetracantha*, *Scutia myrtina*, *Searsia* spp., and *Zanthoxylum* spp. Summerhill Farm is mostly used for pineapple production, and huge patches of *L. camara* were found close to old pineapple fields. The invaded site has a few other IAPs that included *A. mearnsii* and *Arundo donax*. An uninvaded patch is dominated by native trees, with the most abundant being *V. karroo*. On all three sites, the soil ranged from being loam to sandy, the elevation was approximately 250 m, and the sites/farms were more than 2 km apart. Common forbs and graminoids in all these sites include *Alternanthera pungens*, *Centella asiatica*, *Cynodon dactylon*, *Digitaria* spp., *Panicum maximum*, *Senecio* spp., and *Sporobolus africanus*.

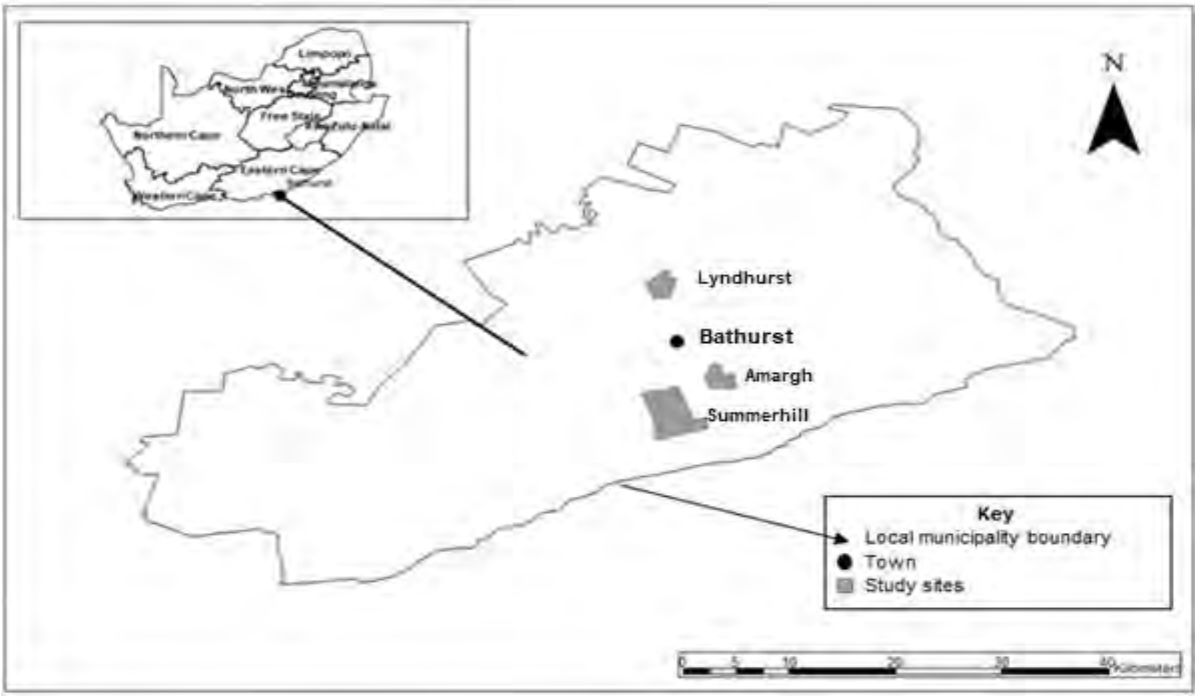

Figure 5.1: The location of the study area (three farms located around Bathurst town in Eastern Cape) where soil for the soil seed bank study were collected.

5.2.2. Soil seed bank sampling and assessment

Soils for the seed bank greenhouse experiment were collected in January 2021 at the three above-mentioned sites. The soil was collected from the *L. camara* invaded and uninvaded conditions. The *L. camara* invaded condition at all the three sites was dominated by *L. camara*, with an estimated cover of above 65%. The uninvaded condition was dominated by native plants and had an estimated cover of more than 65%. The distance between the invaded and uninvaded conditions per site was less than 10 m (separated by farm roads). At each site, 10 plots (5 m × 5 m each) were set up along a transect, with the distance between plots being approximately 1 m. Within each plot, five soil samples from the four corners and one from the centre were collected using a soil corer (10 cm in diameter and 10 cm in depth). Soil samples were thoroughly mixed to form one soil sample. Soil samples were then transported to the laboratory, where they were air dried for one week before being sieved using a 2 mm sieve to remove any coarse organic fragments and plant litter other than seeds to eliminate potential recruitment of any asexual fragments. In total, 60 soil samples (ten plots × two invasion conditions (invaded and uninvaded) × three sites (farms)) were collected and placed in germination trays (27 cm wide × 30 cm long × 11.5 cm deep) in the greenhouse. The trays were arranged based on the invasion conditions and sites for better experimental control, easier management, and efficient use of space, and the germination trays were rearranged monthly to expose them equally to variations in air temperature and light inside the greenhouse.

A seedling emergence approach was used in this study, and the germination trays were watered by hand every second day for 10 months (January to October 2021) to give any hard-coated seeds enough time to germinate. The temperatures within the greenhouse were similar to those outside throughout the day and night. The average daily temperatures during the warm season were above 24 ºC during the day, and the average daily high temperatures during the cool season were below 20 ºC. Every two months, the seedling emergence was monitored, with emerging seedlings counted, identified up to species level where possible, and removed to reduce competition. Some of the species were identified at the Selmar Schonland Herbarium at the Albany Museum in Makhanda, and species were categorised based on life form into trees, shrubs, forbs, and grasses. Bromilow (2010) was used to identify the non-native species. The variables considered per tray were species diversity, richness, evenness, density, and composition.

5.2.3. Data analysis

Data on seedlings that emerged were analysed for species richness and composition per tray. To facilitate abundance analysis, the total number of seedlings that germinated per tray was counted (seedlings m^{-2}). The data was analysed using TIBCO Statistica 14 (TIBCO Software Inc., 2019). Normality was tested using the Kolmogorov-Smirnov test. Species richness, Shannon-Wiener diversity index (H'), Pielou's evenness index (J'), and abundance between *L. camara* invaded and uninvaded sites were done per plot, and differences between the two invasion conditions were tested using a *t*-test. The species similarity between the *L. camara* invaded and uninvaded sites was calculated using the Sørenson similarity index (SI), which was expressed as Sørenson coefficient (%) (Magurran, 2004).

$$\text{*Sørenson coefficient (\%)} = \frac{2C}{A + B} \times 100$$

Where C is the number of species each sample has in common, and A and B represent the number of species found in each sample.

A Principal Component Analysis (PCA) was conducted using frequencies for the identified species to examine if *L. camara* changes species composition. The Principal Component Analysis was done using CANOCO for Windows 5 (Smilauer and Leps, 2014), and the seedling abundance of the most frequently occurring species was used.

5.3. Results

5.3.1. Seed bank composition and similarities between invasion conditions

The number of seedlings emerging per tray varied between the invasion conditions. In total, 1,666 seedlings of vascular plants were counted, and these were distributed across 17 families, with Asteraceae being the most abundant family, followed by Poaceae and Amaranthaceae (Table 5.1). The composition of the seed bank in the study area was as follows: 82% of the plants that germinated were forbs, 16% were graminoids, and 2% were trees and shrubs (Table 5.1). Commonly occurring forbs and graminoids were *Digitaria eriantha*, *Plantago lanceolata*, *Setaria* spp., *Solanum nigrum*, *Sporobolus africanus*, and *Taraxacum officinale* in the *L. camara* invaded soils, and *Aizoon* spp., *Conyza bonariensis*, *Cotula* spp., *D. eriantha*, and *Ehrharta erecta* in the uninvaded soils (Table 5.1). Seedlings that germinated from the *L. camara* invaded condition included four tree and shrub species, 26 forb species, and nine grass species. Out of these, 13 were exotic species. Seedlings that germinated from the uninvaded condition included two tree and shrub species, 28 forb species, and 10 grass species.

The Sorenson's similarity index showed that there was a high similarity of species between the *L. camara* invaded and uninvaded conditions (Sorensen's index = 79%). Furthermore, the PCA of *L. camara* invaded and uninvaded conditions limited distinction between the sites regarding species assemblage (Figure 5.2). Species such as *Aptenia* spp. (native forb), *P. lanceolata* (exotic forb), *Setaria* spp. (native graminoid), and *T. officinale* (exotic forb) had higher densities in the *L. camara* invaded condition compared to species such as *Aizoon* spp. (native forb), *Amaranthus hybridus* (exotic forb), *Cotula* spp. (native forb), and *Galinsoga parviflora* (exotic forb) that were more associated with the uninvaded condition (Figure 5.2).

Table 5.1: Species composition of seedlings that germinated from soil samples collected in the *L. camara* invaded (n = 30) and uninvaded conditions (n = 30) near Bathurst, Eastern Cape. * Plant species that are exotic to South Africa.

Plant name	**Taxonomic family**	**Percentage of frequently occurring species**	
		Invaded	**Uninvaded**
Graminoids			
**Cynodon dactylon*	Poaceae	0	20
Chloris spp.	Poaceae	7	10
Digitaria eriantha	Poaceae	47	43
Ehrharta erecta	Poaceae	23	33
Eragrostis spp.	Poaceae	3	10
Lolium spp.	Poaceae	3	13
Panicum maximum	Poaceae	3	3
Setaria spp.	Poaceae	17	0
Sporobolus africanus	Poaceae	13	13
Urochloa spp.	Poaceae	10	7
Other graminoids (Juncaceae, Cyperaceae, Restionaceae)			
Cyperus spp.	Cyperaceae	0	3
Forbs			
Aizoon spp.	Aizoaceae	30	53
**Alternanthera pungens*	Amaranthaceae	0	3
**Amaranthus hybridus*	Amaranthaceae	0	20
Amaranthus spp.	Amaranthaceae	0	10
**Amaranthus spinosus*	Amaranthaceae	7	3
	Aizoaceae	13	0
**Bidens pilosa*	Asteraceae	30	23
Centella asiatica	Apiaceae	3	0
Chamaesyce prostrata	Euphorbiaceae	3	0
**Chenopodium album*	Amaranthaceae	3	23

**Chenopodium* spp.	Amaranthaceae	3	7
**Conyza bonariensis*	Asteraceae	13	30
Cotula spp.	Asteraceae	33	53
**Cyclospermum* spp.	Apiaceae	10	3
Emex australis	Polygonaceae	7	10
**Galinsoga parviflora*	Asteraceae	0	13
Lippia spp.	Verbenaceae	0	3
**Malva parviflora*	Malvaceae	0	7
Oxalis spp.	Oxalidaceae	20	13
**Physalis angulata*	Solanaceae	10	3
**Plantago lanceolata*	Plantaginaceae	63	20
**Polygonum aviculare*	Polygonaceae	3	0
**Portulaca oleracea*	Portulacaceae	0	10
Senecio spp.	Asteraceae	20	10
**Solanum* spp.	Solanaceae	3	23
**Solanum nigrum*	Solanaceae	30	23
**Sonchus* spp.	Asteraceae	3	7
**Taraxacum officinale*	Asteraceae	60	13
Tephrosia capensis	Fabaceae	10	0
Tetragonia spp.	Aizoaceae	10	7
Unknown 1	-	7	10
Unknown 2	-	33	7
Unknown 3	-	20	10
	Trees and shrubs		
Erythrina caffra	Fabaceae	3	17
**Lantana camara*	Verbenaceae	27	0
Olea spp.	Oleaceae	3	0
Pappea capensis	Sapindaceae	7	0
Sideroxylon spp.	Sapotaceae	0	3

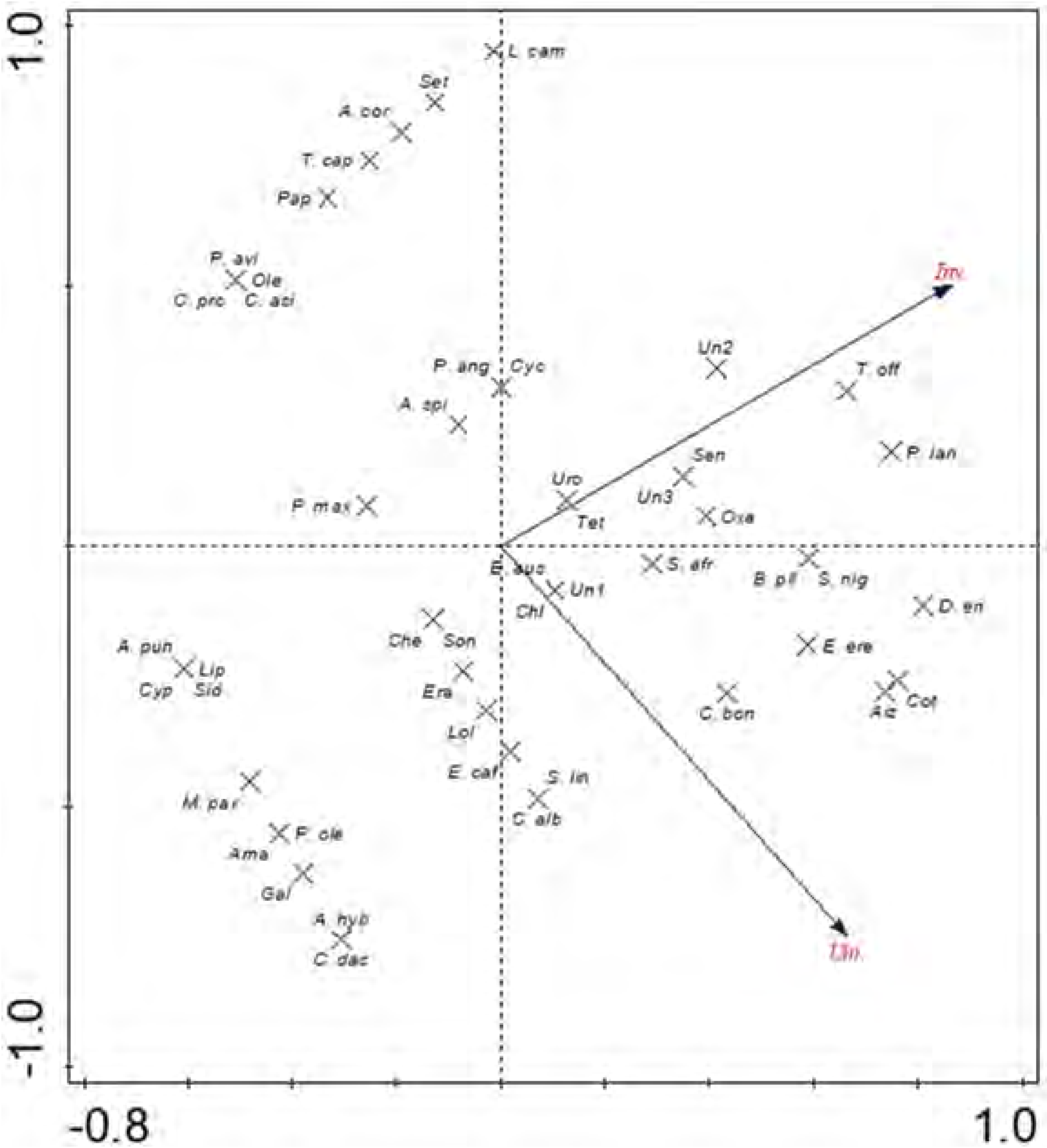

Figure 5.2: Principal Component Analysis (PCA) plot of all seedlings that germinated from different invasion conditions.

5.3.2. Seed bank abundance and diversity

The mean seedling abundance was 20.5 ± 2.01 m^{-2} for the *L. camara* invaded and 35.1 ± 4.59 m^{-2} for the uninvaded conditions, significantly ($p < 0.05$) higher in the uninvaded condition (Table 5.2). Comparisons of seedling abundance based on growth form showed significantly higher abundances for forbs and grasses in the uninvaded condition than in the invaded condition. The overall mean abundances based on growth form were 0.6 ± 0.14 m^{-2} for trees and shrubs, 22.4 ± 2.60 m^{-2} for forbs, and 4.8 ± 0.67 m^{-2} for grasses. Species richness of all species showed no significant differences ($p > 0.05$) between the *L. camara* invaded and uninvaded conditions (Table 5.2). Similarly, species richness per growth form (trees, shrubs, forbs, and grasses) did not show any significant variations ($p > 0.05$) between the invasion conditions (Table 5.2). The Shannon-Wiener and Pielou's evenness index did not show significant differences ($p > 0.05$) between the *L. camara* invaded and uninvaded conditions (Table 5.2). Apart from variations based on growth form, only seedling abundance was statistically different between the *L. camara* invaded and uninvaded conditions for all the seedlings, with the uninvaded condition averaging almost double the abundance of seedlings than the *L. camara* invaded condition.

Table 5.2: Seed bank abundance, richness, and diversity of soil collected in the *L. camara* invaded (n = 30) and uninvaded conditions (n = 30) (mean ± SE) at Bathurst, Eastern Cape.

Variables	**Invasion condition**		***T* - test value**	
	Invaded	**uninvaded**	***t***	***p***
	All species			
Species abundance (m^{-2})	20.47 ± 2.01	35.07 ± 4.59	- 2.90	0.005*
Species richness	4.90 ± 2.11	5.30 ± 2.19	- 0.72	0.48
Shannon-Wiener diversity index *H'*	1.29 ± 0.11	1.19 ± 0.11	0.55	0.59
Pielou's evenness index *J'*	0.74 ± 0.05	0.65 ± 0.05	1.36	0.18
	Species abundance per growth form			
Trees and shrubs (m^{-2})	0.47 ± 0.20	0.63 ± 0.19	-0.60	0.54
Forbs (m^{-2})	16.70 ± 1.78	28.13 ± 4.71	-2.27	0.03*
Grasses (m^{-2})	3.30 ± 0.53	6.30 ± 1.18	- 2.30	0.03*
	Species richness per growth form			
Trees and shrubs	0.17 ± 0.46	0.37 ± 0.61	-1.43	0.16
Forbs	3.53 ± 1.61	3.53 ± 1.79	0.00	1.00
Grass	1.20 ± 0.96	1.40 ± 1.04	- 0.77	0.44

The mean abundance of exotic seedlings was 9.3 ± 1.14 m^{-2} for the *L. camara* invaded and 9.0 ± 1.51 m^{-2} for the uninvaded conditions. Moreover, the mean abundance for native seedlings in the *L. camara* invaded and uninvaded conditions was 11.3 ± 1.61 m^{-2} and 25.6 ± 4.11 m^{-2}, respectively. The seedling abundance of exotic species did not show any significant differences ($p > 0.05$) between the invasion conditions (Figure 5.3a). In contrast, the abundance of native seedlings was significantly ($p < 0.001$) lower in the *L. camara* invaded conditions than in the uninvaded (Figure 5.3a). The total richness for both exotic and native plant seedlings showed no significant ($p > 0.05$) difference between *L. camara* invaded and uninvaded conditions (Figure 5.3b).

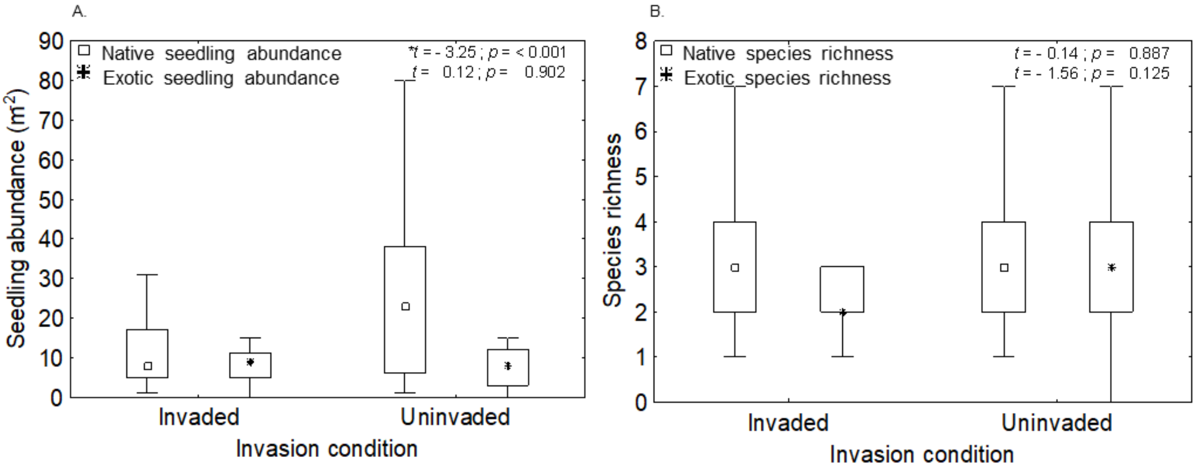

Figure 5.3: Seedling abundance (a) and species richness (b) of native (□) and exotic species (✱) in *L. camara* invaded (n = 30) and uninvaded conditions (n = 30) of soil collected in Bathurst, Eastern Cape. * Denotes significant differences. Bars indicate mean ± SE.

5.4. Discussion

This study assessed the differences in plant species composition, abundance, richness, and diversity of soil seed banks of *L. camara* invaded and uninvaded conditions. Results showed that *L. camara* influenced seedling abundance and composition but not species diversity and richness. This is evident through the decrease in seedling abundance of forbs and graminoids in the *L. camara* invaded condition. Similar results on other IAPs were observed by Vila and Gimeno (2007), where *Oxalis pes-caprae* invasion did not affect the species richness of the soil seed bank. Kundel et al. (2014) also recorded no significant reduction in species richness, diversity, and abundance in soil seed banks of *Solidago* invaded soils. Lastly, Obiakara et al. (2021) documented how *Tithonia diversifolia* invasion did not negatively affect seedling diversity. These results contradict studies that showed that *L. camara* negatively affects seedling diversity. For example, our results contradict suggestions by Ruwanza (2016) that *L. camara* invasion decreases species diversity in soil seed banks, resulting in native species depletion. It is not clear why *L. camara* had a negative effect on seedling abundance but not on diversity, but the suspicion is that this could be because of invasion extent and duration, which typically refers to the length of time that *L. camara* has been present in those areas. Previous studies have reported that soil seed bank variations and depletions are more visible under high invasion extent and after a long duration than when invasion extent is low (Tererai et al. 2015; Ruwanza, 2016).

From a growth form perspective, results seem to suggest that *L. camara* invasion reduces the seedling abundance of forbs and grasses, as these were low under *L. camara* compared to the uninvaded conditions. This result concurs with findings by Ruwanza (2016), who recorded a lower mean density (2 620 m^{-2}) of seedlings in soil collected under *L. camara* compared to the uninvaded sites (4 470 m^{-2}). *Lantana camara* is known to displace native vegetation through biological attributes such as allelopathy. *Lantana camara* releases allelopathic compounds in the soil that are responsible for changes in soil properties, which, in turn, influence the germination and growth of other seedlings (Kato-Noguchi and Kurniadie, 2021). Kato-Noguchi and Kurniadie (2021) have reported this aspect, where the allelopathic effects of *L. camara* suppressed and inhibited the germination and growth of native plant species, i.e., *Achyranthes aspera*. Sharma et al. (2005) and Gooden et al. (2009) also documented the allelopathic effects of *L. camara* and how it can reduce native seedling recruitment and growth. Therefore, it is possible that allelopathy is having a negative effect on seedling abundance, resulting in lower seedling abundance under the *L. camara* invaded condition than in the uninvaded condition. This low seedling abundance under *L. camara* has the potential to limit the chances of vegetation recovery through passive restoration once *L. camara* is removed.

Although the overall seed bank composition between the *L. camara* invaded and uninvaded conditions was similar, a closer look at the results shows some minor distinctions in species composition between the two invasion conditions. For example, some native species were absent from the soil collected underneath *L. camara*, however, the presence of seed banks of some species, particularly grasses and forbs, which were represented by *A. cordifolia*, *C. prostrata*, *Oxalis* spp., *Setaria* spp., and *T. capensis*, is an indication that *L. camara* also acts as a refugia for some native species. This shows that *L. camara* does not eliminate all native species but can co-exist with them. This has been observed by Ruwanza (2020), who showed that *L. camara* acts as a refuge and can co-exist with some native species. The co-existence of species is mediated by factors such as competition between species, the dispersal abilities of the co-existing species, shade tolerance, and environmental filtering. Most of the species associated with *L. camara* usually prefer the ideal habitats provided by *L. camara* so that they can mutually co-exist with it (Gioria and Pysek, 2016). Most seedlings that co-existed with *L. camara* in this study had a long effective dispersal and could tolerate a wide range of environments, including Poaceae, Fabaceae, and Asteraceae. It is possible that native seedlings that germinated and co-existed with *L. camara* in this study have the potential to compete with *L. camara* for resources. Gioria et al. (2021) document how some plant species can co-exist with IAPs in soil seedbanks because of functional similarities with native species, niche differences that allow them to overcome biofiltering, and fitness differences, which is the competitive ability of the species where some plant species are more competitive than others.

The results on the absence of some native species seedlings in the *L. camara* invaded condition corroborate previous studies that have concluded that *L. camara* can displace some native species but, at the same time, acts as a nurse plant for some species that can co-exist with it (Swarbrick et al. 1995; Ruwanza, 2016; Ruwanza, 2020). The absence of some species could likely have been associated with their displacement from the standing vegetation. Several studies on other IAPs have reported on how invasive species can negatively influence soil seed banks through several mechanisms (Kundel et al. 2014). Other indirect factors associated with habitat alterations, shading, agricultural practices related to frequent fire use, and livestock management can also result in the absence of some species in the soil seed bank (Tessema et al. 2011). For example, Bekele et al. (2000), Vosse et al. (2008), Lopez-Toledo and Martinez-Ramos (2011), Shiferaw et al. (2019), and Zida et al. (2020) also recorded similar findings where seeds of some native species (mostly woody pioneer species) were either absent or dormant in the soil seed bank, while seeds of other growth forms dominated. This observation may be attributed to the specific germination requirements of these species. The results of this study show how *L. camara* can have a competitive advantage against native seedlings. Furthermore, *L. camara* invasion also displaced the seed banks of some exotic species, such as *A. hybridus* and *M. parviflora*, and this may be linked with *L. camara*'s competitive ability and the inability of those species to reach maturity.

Gioria and Pysek (2016) reported on how the characteristics of IAP soil seed banks can vary, i.e., from no seed banks to transient seed banks or persistent seed banks. The establishment of persistent seed banks, however, plays a fundamental role in their successful invasion, as they usually take advantage of environmental conditions to maximise their germination and growth (Rejmanek et al. 2005). In this study, the seedlings of *L. camara* were observed under the *L. camara* invaded condition. Moreover, it was also observed that soils from the *L. camara* invaded condition had seeds of other exotic species, mostly forbs such as *B. pilosa*, *C. bonariensis*, *P. angulata*, *P. lanceoalata*, *Solanum* spp., and *T. officinale*. Previous studies (Ruwanza, 2016) have reported that the soil underneath *L. camara* often contains seeds from other alien species. The co-existence of alien plants has also been reported in the past and has earned several descriptions, such as secondary invasion, invasion treadmill, and invasion meltdown (Simberloff and Von Holle, 1999). Several studies (e.g., Daehler, 2003; Kuebbing et al. 2013; Gioria et al. 2014; Grewel et al. 2019; Ruwanza, 2020; Zenni et al. 2020) have reported on the co-occurrence of plant invaders, including *L. camara*, in both aboveground vegetation and soil seed banks.

The limitations of this study include the following: (1) Germination conditions in the greenhouse may not represent field conditions, thus some seeds in the soil seed bank may require specific environmental conditions to germinate; (2) temporal dynamics, where this short-term study may not have captured the long-term dynamics of the soil seed bank and dormant seeds may not germinate during the study period; (3) seed viability, where there is a possibility that not all seeds may have been viable for germination. Nevertheless, considering that soil seed banks are known to be determinants of vegetation dynamics in plant communities (Templeton and Levin, 1979), the presence of *L. camara* and exotic plants on the seed banks of the studied sites could have implications for *L. camara* management and native restoration of these sites should these plant invaders enhance each other's impacts. Early detection of these non-target seedlings and their control can be more effective during the restoration process of these sites since secondary invasion after removing or clearing a plant invader is common (Pearsons et al. 2016; Nsikani et al. 2020).

5.5. Conclusion and management implications

This study concludes that *L. camara* invasion negatively influenced soil seed bank seedling abundance of some species and composition but not diversity and richness, which did not differ between the *L. camara* invaded and uninvaded conditions. *Lantana camara* invasion also resulted in the displacement of some native seed banks, but at the same time, it co-existed with some native and alien plant species. From a management standpoint, these results have implications for restoration once *L. camara* is removed. Firstly, the observed impacts on some species have the potential to inhibit vegetation recovery after *L. camara* clearing. Secondly, the availability of alien forbs and grasses underneath the *L. camara* soil seed bank can trigger secondary invaders once the plant is removed. Thirdly, the presence of a few native species underneath the *L. camara* soil seed bank gives hope that remnant native species will germinate and kick-start vegetation recovery once *L. camara* is removed. Lastly, re-invasion by *L. camara* after its removal is possible since *L. camara* seedlings dominated the invaded condition.

When managing these sites after *L. camara* removal, active restoration, careful monitoring, and follow-up to remove secondary invaders that will germinate from the seed bank are recommended. Where active restoration is considered due to the low seed bank of native trees and shrubs, seeding should be taken into consideration, as it has been found to yield positive results (Ruwanza et al. 2018). If possible, *L. camara* clearing should be done in a way that the few native species existing in the seed banks should be protected, and this speaks to issues of the clearing method, i.e., the use of mechanical equipment where tractors should be limited to prevent disturbance of these native seed banks. From a research point of view, it is recommended that studies on *L. camara* soil seed bank dynamics be evaluated over long periods and different seasons since species composition, density, and richness can vary at different times during the year.

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Chapter 6: Ecological response and restoration implication of *Lantana camara* clearing

Abstract

Natural ecosystems are degrading at an alarming rate because of human-caused activities. This underscores the importance of putting in place ecosystem management strategies, such as ecological restoration, as one means of curbing continuous ecosystem degradation. This study was aimed at examining native soil and vegetation recovery following *Lantana camara* clearing and sought to answer the following research questions: (i) How does *L. camara* clearing influence soil physicochemical properties? and (ii) what effect does *L. camara* clearing have on native vegetation diversity? Three clearing conditions, namely *L. camara* invaded, *L. camara* cleared, and uninvaded, were selected on two sites near Makhanda, in the Eastern Cape province of South Africa. Clearing was done in 2019 and 2020 by manual felling and the application of arboricide to reduce re-sprouting. In both sites, 5 m x 5 m plots were set up for soil and vegetation measurements at each clearing condition. Over the course of three months, soil samples were collected from the three clearing conditions and analysed for soil gravimetric moisture content, penetration resistance, cumulative infiltration, Water Droplet Penetration Time, pH, and soil nutrients. Results show that there were substantial variances in soil moisture and penetration across the three months. Cumulative infiltration rates showed significant differences among the clearing conditions and months, with interactions observed. The soil pH was significantly lower in the *L. camara* invaded and cleared conditions than in the uninvaded condition. The vegetation characteristics showed lower species richness and diversity indices in the *L. camara* invaded and cleared conditions. The uninvaded condition had significantly more trees and shrubs than the cleared and invaded conditions, although most native species were observed in the *L. camara* cleared conditions than in the invaded conditions. The percentage cover for trees and shrubs was significantly higher in the *L. camara* invaded condition. This study concludes that *L. camara* clearing can promote soil and native vegetation recovery, but re-invasion by *L. camara* in the cleared conditions, as well as secondary invasion by other alien plants, could hinder the process. Active restoration should be considered to reduce the effect of secondary invaders. Long-term studies are also essential, considering that ecological restoration is a long-term process.

Keywords: legacy effect; natural vegetation; recovery; restoration; secondary invasion

6.1. Introduction

A wide range of human-induced activities are causing many ecosystems to decline at an accelerated rate, leading to widespread degradation (Vitousek et al. 1997; Myers et al. 2013; Costanza et al. 2014). Consequently, ecosystem management strategies such as ecological restoration are increasingly important as a response to ongoing ecosystem degradation (Young, 2000). Ecological restoration aims to restore degraded biodiversity and the ecological functions of native ecosystems (Van Diggelen et al. 2001). Gann and Lamb (2006) suggest that to achieve successful ecosystem management, ecological restoration must address four factors, namely: ecosystem productivity, biodiversity, human livelihoods, and empowering local people. This therefore means that the development of restoration goals that speak to both socio-economic and ecological benefits is important.

Management approaches for invasive alien plants (IAPs) generally include reducing the risks of importing or introducing alien species, controlling their movement and use, eradicating their range, and reducing their impact (Pysek and Richardson, 2010). From an impact reduction standpoint, Le Maitre et al. (2011) and Ruwanza et al. (2013) demonstrated how the management of IAPs can be complex; for example, low germination rates of native species, high seedling mortality rates, and competition from secondary IAPs have been shown to retard ecosystem recovery following IAP clearing as a reduction strategy. Also, Blanchard and Holmes (2008) reported on the vegetation recovery following the clearing of IAPs and noted the complexities associated with secondary invasion and re-invasion. In contrast, other restoration studies following IAP removal have shown successful soil and vegetation recovery, i.e., increases in measured soil properties and plant diversity (Ndou and Ruwanza, 2016; Ruwanza et al. 2018). For example, Ruwanza et al. (2018) reported a positive recovery trajectory post clearing *Eucalyptus camaldulensis* along the Berg River in the Western Cape province of South Africa. The above-mentioned examples seem to show that ecological restoration following IAP removal is not uniform, with both successes and failures being reported. Previous studies seem to suggest that the challenges of ecosystem recovery following IAP clearing are mostly attributed to re-invasion by secondary invaders, loss of native seed banks, changes in soil characteristics, and invasion legacy effects, particularly soil legacy effects where soil changes induced by the invader persist for some time even when the species has been cleared (Nsikani et al. 2017; Fill et al. 2018; Ruwanza et al. 2018).

To reduce IAPs and restore invaded ecosystems, the then Department of Environmental Affairs (DEA – now called the Department of Forestry, Fisheries, and the Environment - DFFE), in South Africa initiated a program called "Working for Water" (WfW), whose main goal is to implement manual IAP control operations to minimise their impacts on water resources and biodiversity and create employment in the process (Beater et al. 2008). The program has adopted an integrated control approach that involves both mechanical (such as cutting, slashing, scraping, ring barking, and hand digging) and chemical interventions (such as the painting of the stumps with arboricide to reduce resprouting) (Urban, 2010). These control methods, combined with biological control (suppression of damaging activities of one organism by using natural enemies, such as parasites, pathogens, or predators), have been employed in South Africa to manage IAPs, including *Lantana camara*, which is the species of concern in this study (van Wilgen et al. 2020). Since its inception in 1995, the WfW programme has cleared an average of 200 000 ha a year, with much of the clearing being done on *Chromolaena*, *Eucalyptus*, *Lantana*, *Prosopis*, and *Acacia* species (van Wilgen et al. 2020). Although the WfW programme is regarded as a successful initiative (Esler et al. 2008; van Wilgen et al. 2020), several challenges have been noted concerning issues of ecological restoration following IAP removal. For example, the few documented successes in IAP control following WfW clearing are an indication that the passive restoration model being implemented by WfW is yielding mixed results (van Wilgen et al. 2020). Therefore, numerous studies are required to assess whether WfW clearing is yielding passive soil and vegetation recovery or not. Lastly, some studies have reported that follow-up control that is done by WfW following IAP clearing is not being done effectively, thus resulting in some cleared areas being re-invaded (Ruwanza et al. 2018; van Wilgen et al. 2020).

There are various challenges globally to managing IAPs: mechanical and chemical control of *L. camara* is short-term, labour-intensive, requires ongoing follow-up treatments, and is costly (Day et al. 2003; Love et al. 2009; Negi et al. 2019). Therefore, adopting ecological restoration models to manage IAPs may be a useful approach for several reasons (Holmes et al. 2020). Restoration can either be active or passive; active restoration relies on active manipulation of the abiotic and biotic characteristics (planting seedlings, propagating materials, soil manipulation, etc.) to accelerate the process of ecosystem recovery (Le Maitre et al. 2011). In contrast, passive restoration refers to the process of allowing natural succession to take place within an ecosystem after removing or clearing IAPs (Vaughn et al. 2010; Gann et al. 2019). The latter restoration method is known to be difficult to achieve because it depends on significant drivers of recovery (such as seeds and dispersers), requires the removal of persistent disturbances, and takes longer, so it can be challenging to achieve the desired state (Holl and Aide, 2011; Atkinson and Bonser, 2020). Restoration ecology is sometimes criticised for focusing only on the visible signs of ecosystem degradation and giving little attention to the physicochemical and biological components (Buckley, 2008). Hence, it is critical to consider both vegetation and soil characteristics when restoring an ecosystem (Heneghan et al. 2008). As previously stated, several studies have been conducted on vegetation restoration (Lamb et al. 2005; Pretorius et al. 2008; Ruwanza, 2017; Mekuria et al. 2018; Shimamoto et al. 2018; Festin et al. 2019); however, there is a lack of research on soils that could provide insights into vegetation recovery. Studies on soil recovery following the removal of IAPs seem to suggest that soil legacy effects tend to slow down ecosystem recovery (Ruwanza et al. 2013; Nsikani et al. 2017). Many studies have documented invasive effects on soil chemistry and microbial communities, i.e., Pickett et al. (2022) highlight quantifiable and persistent soil legacy effects of invasive *Phalaris aquatica* that outcompetes and displaces native plants in Southern California. Their study emphasised the importance of understanding these soil legacy effects to facilitate restoration efforts. Suseela et al. (2016) also reported on the legacy effects of *Polygonum cuspidatum*. Their research emphasised the importance of understanding the mechanisms through which IAPs influence soil carbon dynamics, and they documented how restoration efforts may not be fully realised until legacy effects are resolved. Lastly, Grove et al. (2015) also discussed the soil legacy effects following the removal of a nitrogen fixing invader, *Cystisus scoparius*, in Mason County, Washington, and how the positive fertilisation favoured secondary invasion of fast-growing invasive grasses and herbs. Basically, all these studies highlight how crucial it is to manage soil legacies for successful ecosystem restoration.

The soil legacy effect depends on several factors, such as invasion extent and duration, diversity of secondary invasion after removal of IAPs, and diversity of recruiting native species (Nsikani et al. 2017). Several techniques to reduce the soil legacy effect after IAP clearing have been suggested, including soil transfer, tillage, and soil nutrient manipulation, e.g., sucrose addition to counter soil N deposited by N-fixing plants (Ruwanza et al. 2013). However, the bulk of these suggestions have not been tested, so their effectiveness in changing soil nutrients after IAP removal remains unknown. Therefore, more studies to understand soil changes after IAP removal are needed if restoration projects such as the WfW clearing are to yield positive outcomes.

Lantana camara L. (Verbenaceae), native to South America, is an invasive flowering plant commonly known as *Lantana*, wild or red sage (Nanjappa et al. 2005; Negi et al. 2019). It is described as an evergreen shrub reaching about two m in height with a potent smell and features various flower colours - pink, yellow, white, and red (Ved et al. 2018). Its oval leaves are hairy with toothed margins, and its seeds are fleshy, initially green, turning blue-black when ripe (Kato-Noguchi and Kurniadie, 2021). *Lantana camara* is notorious for its aggressive invasion of habitats, thriving in open, unshaded, disturbed areas such as old fields (Sharma et al. 2005). It dominates moist regions in South Africa but has rapidly spread to various habitats (Vardien et al. 2012). Management strategies include mechanical, chemical, and biological control methods, with Working for Water (WfW) primarily conducting physical clearing in South Africa, supplemented by biological control through the release of *Aceria lantanae* and *Falconia intermedia* (Day et al. 2003; Sharma et al. 2005; Urban, 2011; Alemu and Terefe, 2015; Simelane et al. 2021). In around 1858, *L. camara* was introduced to South Africa as an ornamental plant (Urban et al. 2011).

Despite the billions of Rand spent on controlling IAPs by WfW in South Africa (Marais and Wannenburgh, 2008; Working for Water, 2013; van Wilgen et al. 2012, 2020), research on ecological recovery following *L. camara* removal is still needed to further understand the potential of recovery after clearing to develop effective management strategies. *Lantana camara* is one of the major invaders in South Africa, and a significant effort has been made to control it (Marais et al. 2004; Vardien et al. 2012; Simelane et al. 2021). To our knowledge, no study has examined how both soil and vegetation recover after *L. camara* removal for restoration purposes. Therefore, there is a need to monitor how both soil and vegetation recover after *L. camara* clearing to guide future restoration initiatives. This study evaluated changes in soil properties and vegetation after clearing *L. camara* from terrestrial habitats in the Albany Thicket Biome near Makhanda, Eastern Cape province, South Africa. The study goals were to evaluate soil and vegetation responses following *L. camara* clearing in comparison to invaded and uninvaded conditions. This study's two research questions were: (i) How does *L. camara* clearing influence soil physicochemical properties? and (ii) what effect does *L. camara* clearing have on native vegetation diversity?

6.2. Materials and methods

6.2.1. Study area and experimental design

The study was carried out on two farms (referred to as sites) near Makhanda, in the Eastern Cape province of South Africa. The two sites are Balcraig Farm (Site 1) (33°20'56.22" S; 26°33'34.94" E) and Fairewood Reserve (Site 2) (33°19'31.83" S; 26°33'22.92" E) (Figure 6.1). The sites were in the Kowie Thicket vegetation type, which is within the Albany Thicket Biome (Mucina and Rutherford, 2006). The Kowie Thicket is characterised by thorny shrubs, woody plant species, and succulent euphorbias and aloes. Due to low radiation intensity, the herbaceous layer is poorly developed. The dominant woody species within the study area are *Azima tetracantha*, *Carissa bispinosa*, *Cussonia spicata*, *Euclea undulata*, *Gymnosporia polyacantha*, *Schotia latifolia*, *Vachellia karroo,* and *V. natalitia* (Mucina and Rutherford, 2006). Approximately 7.5% of the Kowie Thicket has been transformed by agricultural practices.

Temperatures in the area range from 13–29 °C in the austral summer to 1–12 °C in the austral winter (Mucina and Rutherford, 2006). The annual rainfall ranges from 340 to 650 mm, with most of the rain falling in the austral summer (Mucina and Rutherford, 2006).

The sites are located within the Makana local municipality and were selected because they had *L. camara* cleared by WfW in 2019 and 2020. At each site, three clearing conditions, namely *L. camara* invaded, *L. camara* cleared, and uninvaded (reference site), were selected for soil and vegetation surveys. The soil types within the study sites ranged from loam to sandy. The Balcraig Farm is mainly used for livestock grazing, especially in uninvaded conditions. The vegetation within the farm was dominated by trees and shrubs such as *A. tetracantha*, *Canthium spinosum*, *Cussonia* spp., and *Euphorbia* spp., as well as grasses such as *Cynodon dactylon* and *Sporobolus africanus*. The study sites have also been invaded by a few *Acacia* spp. and *Opuntia* spp., and most of the clearing was done for *L. camara* since they were the most dominant IAP on site. The Fairewood farm is approximately 100 ha in size, and wildlife is found on site. The site was dominated by native flora, with the dominant species being *Gymnosporia* spp., *Searsia pyroide*s, *V. karroo*, and *V. natalitia*. *Lantana camara* was the most abundant IAP; however, a few IAPs such as *A. mearnsii*, *Pteridium* spp., and *Tagetes minuta* were also present in small populations. Common forbs on site include *Alternanthera pungens*, *Centella asiatica*, and *Senecio* spp.

Lantana camara clearing at both study sites was conducted by the WfW in 2019 at Balcraig Farm and 2020 at Fairewood Farm. Clearing was done by manual felling of the plants using hand tools, and this was done before the seeds had matured. Arboricide was also applied immediately after cutting to reduce re-sprouting. The felled *L. camara* plants were stacked on site and burned. After clearing, follow-up treatments were conducted every six months to remove all recruited IAP saplings by hand pulling. Surveys were done before clearing, and clearing was done on selected areas or units based on the availability of funding.

It was difficult to estimate the extent of *L. camara* invasion prior to clearing, but based on the visible cut stumps and Google Earth images prior to clearing, it was estimated that the *L. camara* cover was approximately 75%. An adjacent *L. camara* invaded condition was chosen based on the extent of *L. camara* invasion, which was above 75% cover. The invaded condition was predominantly invaded by *L. camara*; however, there were a few other IAPs present. The uninvaded conditions were chosen because they did not have any *L. camara*. The uninvaded condition acted as the reference or control site, which provided compositional and structural information on the vegetation in the area. Within each site, the clearing conditions were less than 200 m apart, and the distance between the two sites (farms) was approximately 3 km to provide a measure of site independence (Galatowitsch and Richardson, 2005). In each of the above-mentioned clearing conditions, five plots were set up with each plot measuring 5 m × 5 m with a 5 m buffer zone. Therefore, a total of 30 plots were set up for this study (5 plots per clearing condition × 3 clearing conditions, namely invaded, cleared, and uninvaded × 2 sites). The 25 m^2 plots were used because of the limited *L. camara* cleared sites that were near both invaded and uninvaded sites.

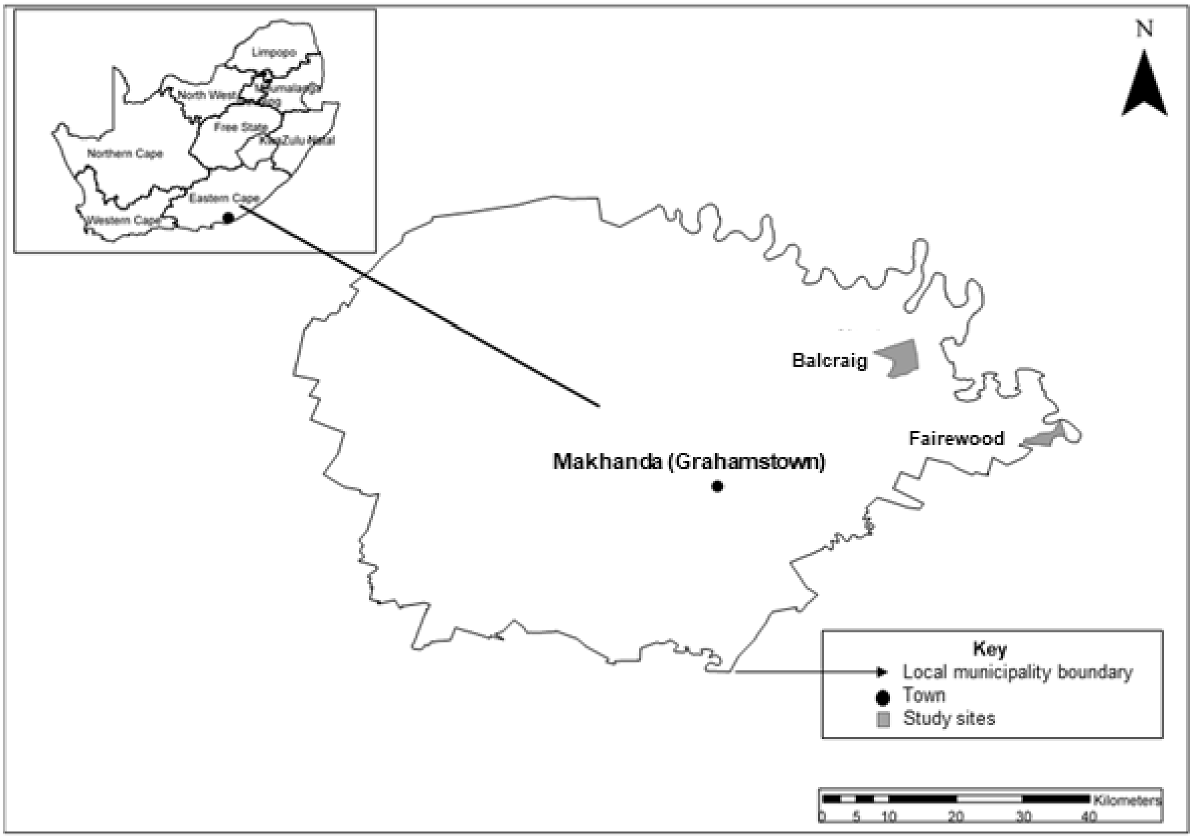

Figure 6.1: The locations of the two study sites near Makhanda town, in the Eastern Cape province of South Africa.

6.2.2. Data collection

6.2.2.1. Soil sampling

Soil samples were collected six months to a year post clearing from each plot's four corners as well as one in the middle, and these were combined into a single soil sample. Soil was collected using a soil corer measuring 10 cm in diameter and 10 cm in depth. Soils were collected after the removal of litter and debris. Soon after collection, all soils were labelled and sent to the laboratory for analysis. Soil sampling for physical properties was done for three months, i.e., July, September, and November, to warrant repeated assessments. However, chemical properties were only taken once because no changes were expected during these months and to reduce financial costs since chemical analysis was done using a commercial laboratory.

6.2.2.1.1. Soil physical properties

Soil moisture and repellence were measured under laboratory conditions, whilst soil penetration resistance level and infiltration rate were measured under fieldwork conditions in each plot. Soil moisture was measured in terms of gravimetric soil moisture, which was expressed as a percentage. Soils were weighed wet, oven-dried at 60 °C for 72 hours, and re-weighed to obtain the water content (Black, 1965). Soil penetration resistance was measured in all plots using a hand penetrometer that was pushed into the soil, allowing a red metal ring to be forced to scale and mark the penetration resistance value in kg cm^{-2} (Leung and Meyer, 2003). Soil infiltration rate and hydraulic conductivity were measured with a mini-disk infiltrometer (Decagon Devices, Pullman, WA, USA). The infiltration rate was determined using the Zhang (1997) methods and was measured by the cumulative rate of infiltration over time. Soil water repellency was measured using the Water Droplet Penetration Time (WDPT) method (Doerr and Thomas, 2000; Doerr et al. 2006), where soil samples were placed in petri dishes, levelled, and air dried for seven days. Five drops of distilled water were applied with a hypodermic syringe to the soil surface, and the penetration time of each water drop was recorded, averaged, and taken as a representative of the WDPT for each soil sample. The soil samples were categorised as follows based on water droplets diffusing into the soil: wettable (within 5 s), slightly repellent (5–60 s), strongly repellent (60–600 s), severely repellent (600–3 600 s), and extremely repellent (> 3 600 s) (Bisdom et al. 1993; Ruwanza and Shackleton, 2016).

6.2.2.1.2. Soil chemical properties

All soil chemical properties were measured at Bemlab (PTY) Limited, a commercial laboratory in Cape Town, South Africa. Soil pH was analysed in a 1:5 soil KCL extract as described by Rhoades (1982), soil total nitrogen was analysed using the complete combustion method where a Eurovector Euro EA Elemental Analyser was used, soil phosphorus was analysed using the Bray II extraction method as described by Bray and Krutz (1945), and soil carbon was analysed using a revised Walkley Black method as described by Chan et al. (2001). Soil exchangeable cations such as calcium (Ca), sodium (Na), potassium (K), and magnesium (Mg) were extracted in a 1:10 ammonium acetate solution and then analysed (Thomas, 1982).

6.2.2.2. Vegetation surveys and analysis

Detailed vegetation surveys were done on all 30 plots in July 2021, and the species richness and density of all trees and shrubs were determined by counting the total number of all individual plants present in the plots. Species richness for other growth forms (forbs and grass) was determined from counts of the total number of individual plants present in a 1 m × 1 m quadrat that was located at the centre of each plot. Plant species cover was visually estimated, and each species was assigned to its growth form (trees, shrubs, forbs, and grass) and origin status (native or alien). All plant samples were collected and identified at the Selmar Schonland Herbarium in Makhanda.

6.2.3. Statistical analysis

Data were analysed using TIBCO Statistica 14 (TIBCO Software Inc., 2019). Statistical significance was determined at $p < 0.05$, and data were first tested for normality using the Kolmogorov-Smirnov test. For each clearing condition, species richness and diversity were analysed. The Shannon-Wiener H' index, Simpson index D', and Pielou’s evenness index J' were also used to examine the effects of clearing conditions on species diversity. One-way analysis of variance (ANOVA) was used to test and compare the differences among the clearing conditions among different vegetation and soil chemical parameters because they were measured once. Soil physical properties were analysed using repeated measures of ANOVA since they were collected repeatedly over three months. Soil repellency categories were analysed using a chi-squared test. Species frequency of occurrence was calculated as the number of times a species occupied the different plots independent of their abundance, and this was calculated as a percentage. To determine the differences between clearing conditions, Tukey’s Honest Significant Difference (HSD) test at $p < 0.05$ was used.

6.3. Results

6.3.1. Soil physicochemical characteristics

The soil at the clearing conditions ranged from being loam to sandy soil. The mean soil moisture for the cleared condition was 11.25 ± 1.09% (cleared condition), 10.01 ± 2.41% (invaded condition), and 10.92 ± 2.53% (uninvaded condition) and no significant differences ($p > 0.05$) were observed among the clearing conditions (Figure 6.2). Comparisons among the months showed that July (7.67 ± 0.82%) and November (5.59 ± 0.64%) had significantly lower ($p < 0.001$) soil moisture compared to September (18.92 ± 3.05 %), when a very high soil moisture content was measured in all three clearing conditions. The interaction between clearing conditions and months of soil moisture content showed no significant ($p > 0.05$) differences (Figure 6.2).

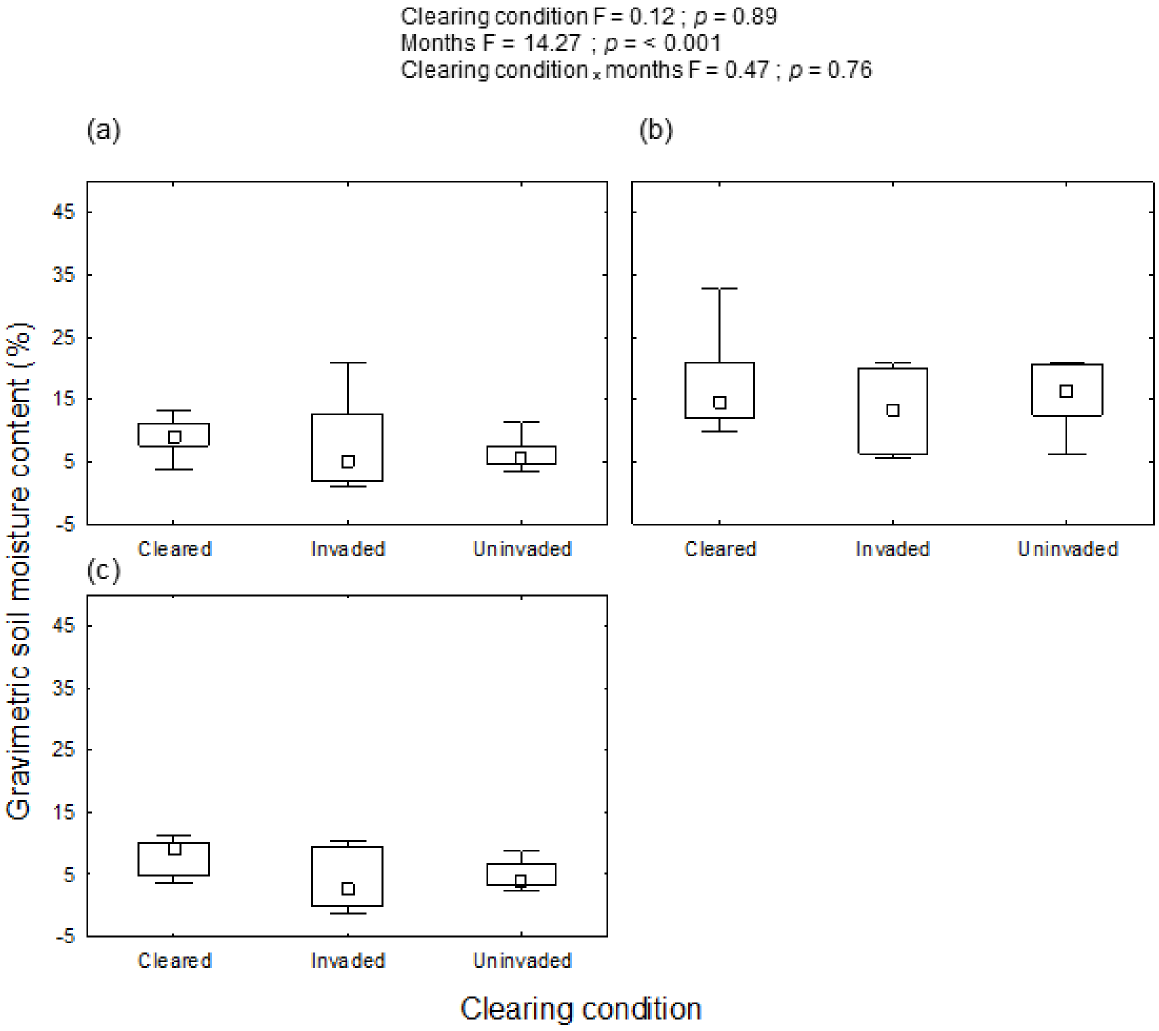

Figure 6.2: Soil gravimetric moisture content (percentage) of soil samples collected under *L. camara* invaded, cleared, and uninvaded conditions in (a) July, (b) September, and (c) November. The findings of the repeated measures ANOVA are also displayed ($p < 0.05$). Bars represent the mean ± SE.

The soil penetration levels ranged from 1.37 to 4.65 kg cm^{-2} across all clearing conditions, and the mean soil penetration resistance levels were 3.03 ± 0.15 kg cm^{-2} in invaded, 3.04± 0.15 kg cm^{-2} in cleared, and 3.79 ± 0.18 kg cm^{-2} in uninvaded conditions. However, no significant ($p > 0.05$) differences were observed in soil penetration resistance among the three clearing conditions (Figure 6.3). For all the months the invaded and cleared conditions had lower soil penetration than the uninvaded condition. Monthly comparisons showed that soils were significantly ($p < 0.001$) less compact in September (2.33 ± 0.12 kg cm^{-2}) than in July (3.61 ±

0.15 kg cm^{-2}) and November (3.92 ± 0.08 kg cm^{-2}). Generally, only monthly changes in soil penetration resistance were observed. Interactions between clearing conditions and months for soil penetration showed no significant ($p > 0.05$) differences.

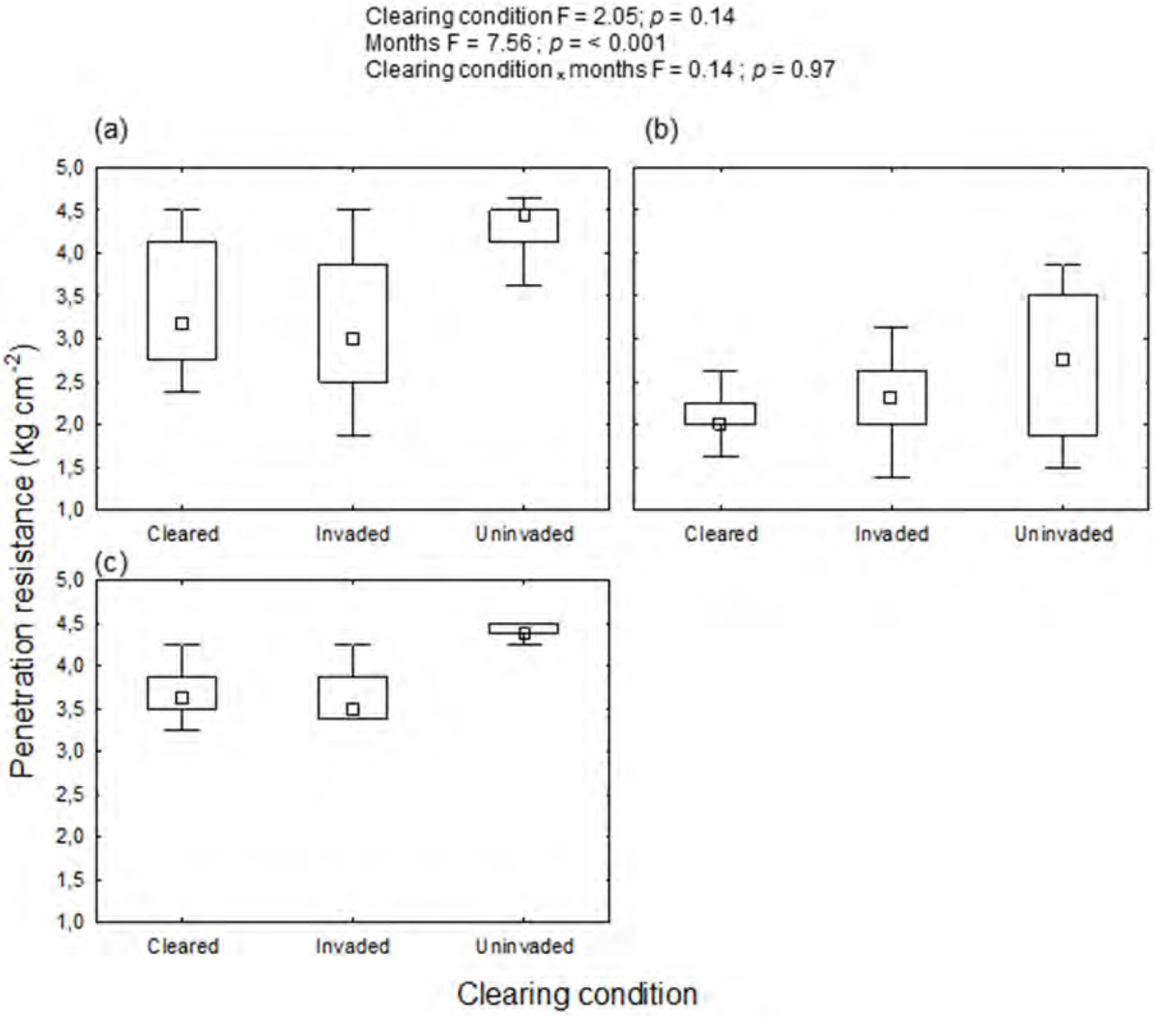

Figure 6.3: The soil penetration resistance levels of soil samples collected under *L. camara* invaded, cleared, uninvaded conditions for the months of (a) July, (b) September, and (c) November. The findings of the repeated measures ANOVA are also displayed ($p < 0.05$). Bars represent the mean ± SE.

The average soil infiltration rates ranged between 0.14–1.23 cm for the soil collected at the *L. camara* invaded condition, 0.18–1.94 cm for the soil collected at the cleared condition, and 0.11–1.47 cm for the soil collected at the uninvaded condition. Significant ($p < 0.001$) differences in soil cumulative infiltration rates were found among the clearing conditions (Figure 6.4), with faster infiltration rates recorded in the invaded and uninvaded conditions compared with the cleared condition. When comparing across months, faster soil infiltration rates were observed in July than in September and November, and significant ($p < 0.001$) differences were observed. The mean infiltration rates in September and November for the invaded were faster compared with the cleared and uninvaded conditions. Similarly, interactions between clearing conditions and months for soil cumulative infiltration rates also showed significant ($p < 0.001$) differences (Figure 6.4). Overall, soil infiltration rates were low in the cleared conditions and were influenced by the months and the interaction of the clearing conditions and months.

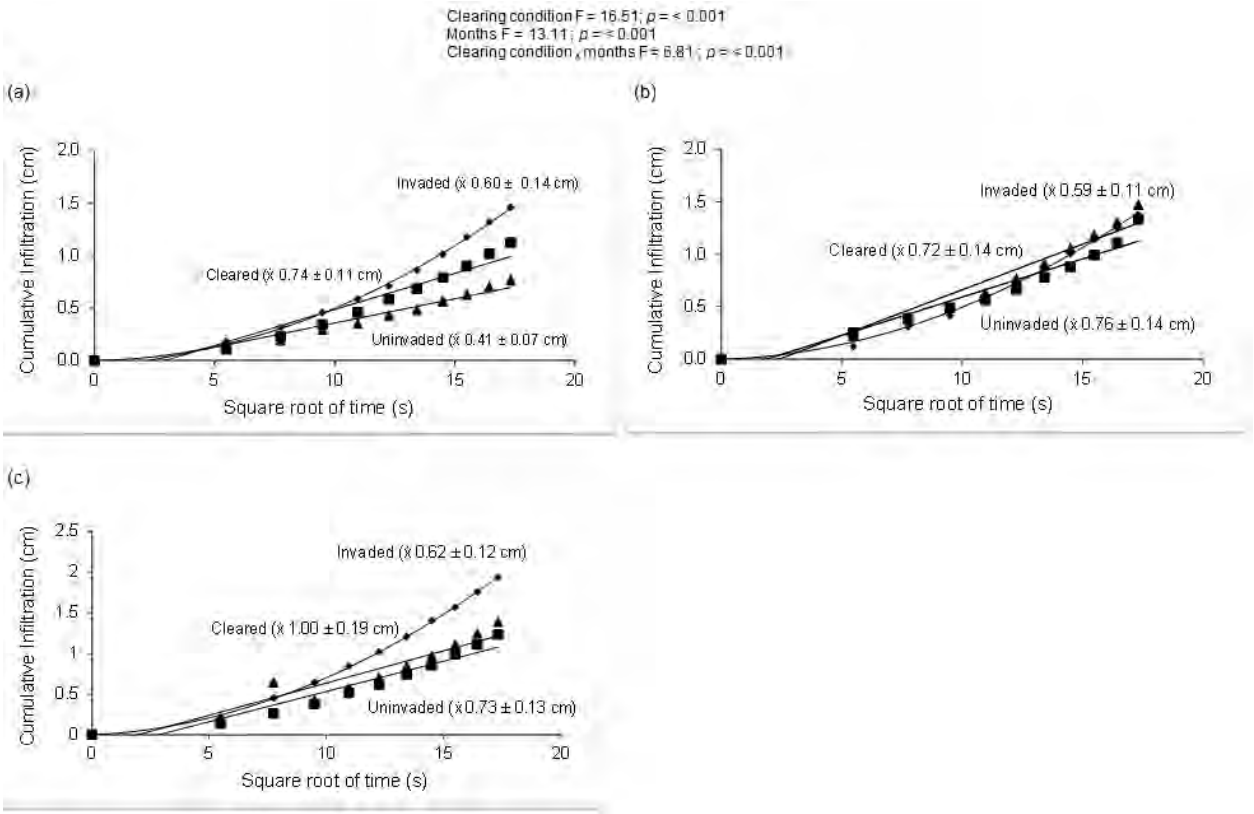

Figure 6.4: Soil infiltration levels of the soil samples collected from three clearing conditions (*L. camara* invaded (■) ,cleared (◆), and uninvaded (▲)) for the months of (a) July, (b) September, and (c) November.

The Chi-squared analysis of WDPT showed no significant ($p > 0.05$) difference among the invaded, cleared, and uninvaded conditions over the three months. All the soil collected from the three clearing conditions were mostly wettable (Figure 6.5). In July, the invaded condition had soils that were wettable (70%) to slightly repellent (30%), the cleared condition had soils that ranged from being wettable (90%) to being slightly repellent (10%), and the uninvaded condition had soils that were wettable (80%), slightly repellent (10%), and severely repellent

(10%). In the cleared condition, the soil became more repellent in September and November, and the severely repellent soil (10%) was only recorded in the uninvaded condition in September (Figure 6.5).

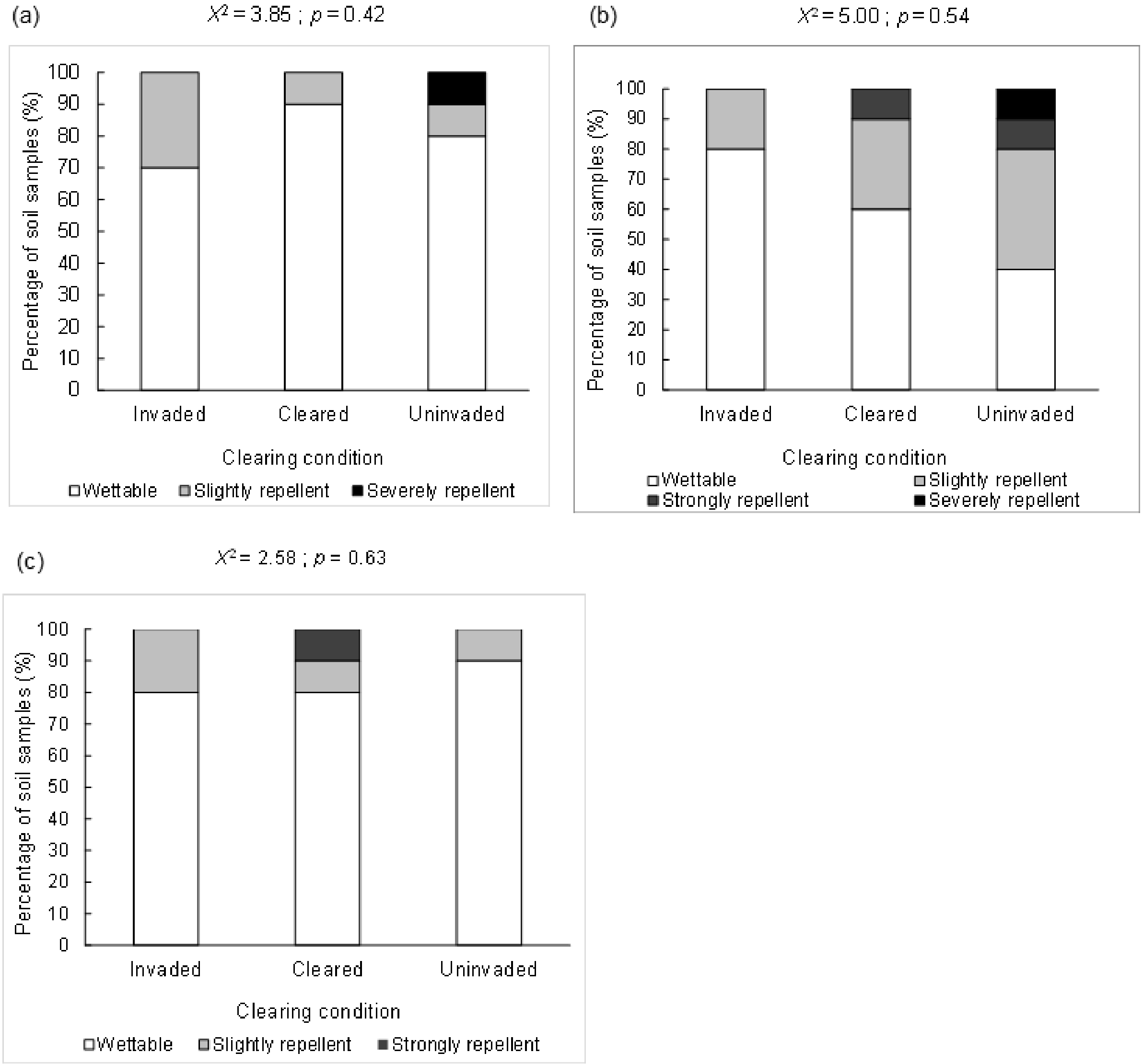

Figure 6.5: Classification of water repellency classes (based upon the Water Droplet Penetration Time method) in the soil samples collected from three clearing conditions (*L. camara* invaded, cleared, and uninvaded) for three months; (a) July, (b) September, and (c) November.

Soil pH ranged between 4.5–7.4 in all the clearing conditions, and the invaded and cleared conditions had significantly ($p < 0.05$) lower soil pH compared to the uninvaded condition. Comparisons of soil nutrients across invaded, cleared, and uninvaded conditions showed no significant ($p > 0.05$) differences in soil nutrient concentration and exchangeable cations. Overall, all measured soil chemical properties showed no significant differences among the three clearing conditions, except for soil pH (Table 6.1).

Table 6.1: Chemical properties of soil samples collected from *L. camara* invaded, cleared, and uninvaded conditions. The data is mean ± standard errors, and the ANOVA results are shown. (*) means significant differences at $p < 0.05$.

Soil properties	**Invaded**	**Cleared**	**Uninvaded**	**ANOVA**	
				F	**P**
pH	5.11 ± 0.12^{b}	5.34 ± 0.12^{b}	5.81 ± 0.23^{a}	4.57	0.019*
Nutrient concentrations					
P Bray II (mg/kg $^{-1}$)	12.42 ± 3.78^{a}	9.83 ± 2.76^{a}	18.32 ± 6.45^{a}	0.83	0.421
Total N (%)	0.26 ± 0.06^{a}	0.34 ± 0.06^{a}	0.33 ± 0.08^{a}	0.39	0.675
Total C (%)	2.81 ± 0.34^{a}	3.42 ± 0.48^{a}	3.29 ± 0.40^{a}	0.62	0.547
Exchangeable cations (cmol/kg $^{-1}$)					
Ca	3.68 ± 0.52^{a}	5.55 ± 0.95^{a}	7.19 ± 1.85^{a}	2.01	0.154
Na	0.16 ± 0.02^{a}	0.21 ± 0.03^{a}	0.25 ± 0.04^{a}	2.25	0.125
K	0.45 ± 0.09^{a}	0.62 ± 0.16^{a}	0.79 ± 0.21^{a}	1.12	0.341
Mg	1.44 ± 0.22^{a}	2.48 ± 0.39^{a}	1.85 ± 0.36^{a}	2.51	0.100

6.3.2. Vegetation characteristics

6.3.2.1. Vegetation composition and structure

A total of 29 plant species were recorded within all the plots, of which 15 were trees and shrubs, nine were forbs, four were graminoids, and one was a fern (see Appendix 6.1). Ten of these species were IAPs, and 19 were natives. The total number of plant families was highest in the uninvaded condition as compared to the *L. camara* invaded and cleared conditions (20 families) (See Appendix 6.1). The high number of families showed the wider spectrum of plant growth forms within these different clearing conditions, with Asteraceae showing the highest number of forb species.

Species from both native and IAPs were recorded, with the Asteraceae, Poaceae, and Fabaceae families being the most dominant. Apart from *L. camara,* other IAPs such as *A. mearnsii*, *Opuntia* spp., *Plantago lanceolata*, and *T. minuta* were also found in the *L. camara* invaded condition, although these were in small occurrences of less than 20% (Appendix 6.1). Native species such as *Gymnosporia* spp., *Panicum maximum*, *Searsia pyroides*, and *S. africanus*, as well as several recruited *L. camara* seedlings dominated the *L. camara* cleared condition. Species such as *A. pungens*, *Digitaria eriantha*, *Diospyros* spp., *S. africanus*, and

V. karroo were the most dominant plant species in the uninvaded condition (see supplementary Table 6.3 as an appendix).

6.3.2.2. Species richness, diversity and abundance

A higher species richness was recorded in the uninvaded condition compared to the cleared and invaded conditions (Table 6.2). The species richness of trees and shrubs, and forbs was significantly ($p < 0.05$) higher in the uninvaded condition compared to the cleared and invaded conditions. However, species richness for graminoids showed no significant ($p > 0.05$) difference among the three clearing conditions (Table 6.2). Native species richness was higher in the uninvaded condition (5.80 ± 0.66) than in the *L. camara* invaded (1.80 ± 0.39) and cleared (2.40 ± 0.48) conditions, and significant ($p < 0.001$) differences were observed among the clearing conditions. Furthermore, we observed higher native species richness in the cleared condition. About 50% of the IAPs were recorded in the cleared condition (as recruiting secondary invaders) and the invaded condition, compared to the uninvaded condition, which was dominated by native species.

For all species, both the Shannon-Wiener index (*H'*) and the Simpson's index (*D'*) were significantly ($p < 0.05$) lower in the invaded and cleared conditions compared to the uninvaded condition. Comparisons between the invaded and cleared conditions showed slightly higher *H'* and *D'* indices in the cleared than invaded conditions (Table 6.2). In contrast, species evenness was similar among the invaded (0.59 ± 0.09), cleared (0.64 ± 0.11), and uninvaded (0.77 ± 0.04) conditions and showed no significant ($p > 0.05$) differences (Table 6.2).

Table 6.2: Results of species richness and diversity indices in the three clearing conditions: *L. camara* invaded, cleared, and uninvaded. The means ± standard errors as well as ANOVA results are shown. (*) means significant differences at $p < 0.05$.

Species richness and diversity indices	**Invaded**	**Cleared**	**Uninvaded**	**ANOVA F**	**ANOVA P**
Species richness and diversity indices for all species					
Species richness	3.40 ± 0.45^{b}	2.90 ± 0.53^{b}	6.40 ± 0.78^{a}	9.90	≤ 0.001*
Shannon-Wiener (*H'*)	0.68 ± 0.12^{b}	0.79 ± 0.16^{b}	1.37 ± 0.13^{a}	7.49	0.002*
Simpson's index (*D'*)	0.39 ± 0.07^{b}	0.40 ± 0.09^{b}	0.68 ± 0.05^{a}	4.97	0.015*
Pielou's evenness (*J'*)	0.59 ± 0.09^{a}	0.64 ± 0.11^{a}	0.77 ± 0.04^{a}	1.09	0.350
Species richness per invasion status					
Richness of natives	1.80 ± 0.39^{b}	2.40 ± 0.48^{b}	5.80 ± 0.66^{a}	17.07	≤ 0.001*
Richness of aliens	1.60 ± 0.16^{a}	0.60 ± 0.22^{b}	0.60 ± 0.16^{b}	9.78	≤ 0.001*

		Species richness per growth form			
Richness of trees and shrubs	1.80 ± 0.33^{b}	1.30 ± 0.26^{b}	3.40 ± 0.3^{a}	13.48	≤ 0.001*
Richness of forbs	0.40 ± 1.63^{b}	0.40 ± 0.22^{b}	1.30 ± 0.33^{a}	4.31	0.024*
Richness of graminoids	1.10 ± 0.23^{a}	0.80 ± 0.25^{a}	1.50 ± 0.34^{a}	1.59	0.223

The mean percentage cover differed among the clearing conditions for all growth forms. The percentage cover for trees and shrubs was significantly ($p < 0.001$) higher in the *L. camara* invaded condition (82.2 ± 25.99%) than in the cleared (5.9 ± 1.9%) and uninvaded conditions (58.9 ± 18.62%) (Figure 6.6). However, the mean percentage cover of forbs and graminoids was similar among the invaded, cleared, and uninvaded conditions, and no significant ($p > 0.05$) differences were observed. In the cleared condition, native species recovery was observed and was more prominent for graminoids and forbs. Comparisons of mean percentage cover based on whether the species are natives or IAPs showed that the invaded condition had significantly higher IAPs cover compared to the other two conditions (cleared and uninvaded), this is likely a result of the high *L. camara* cover. Low cover of both IAPs and native species was observed in the cleared condition (Figure 6.6). Also, as expected, the uninvaded condition had significantly ($p < 0.01$) more native species than the cleared and invaded conditions. Generally, *L. camara* clearing reduced the percentage cover of IAPs, and a small cover increase in native species was observed (Figure 6.6).

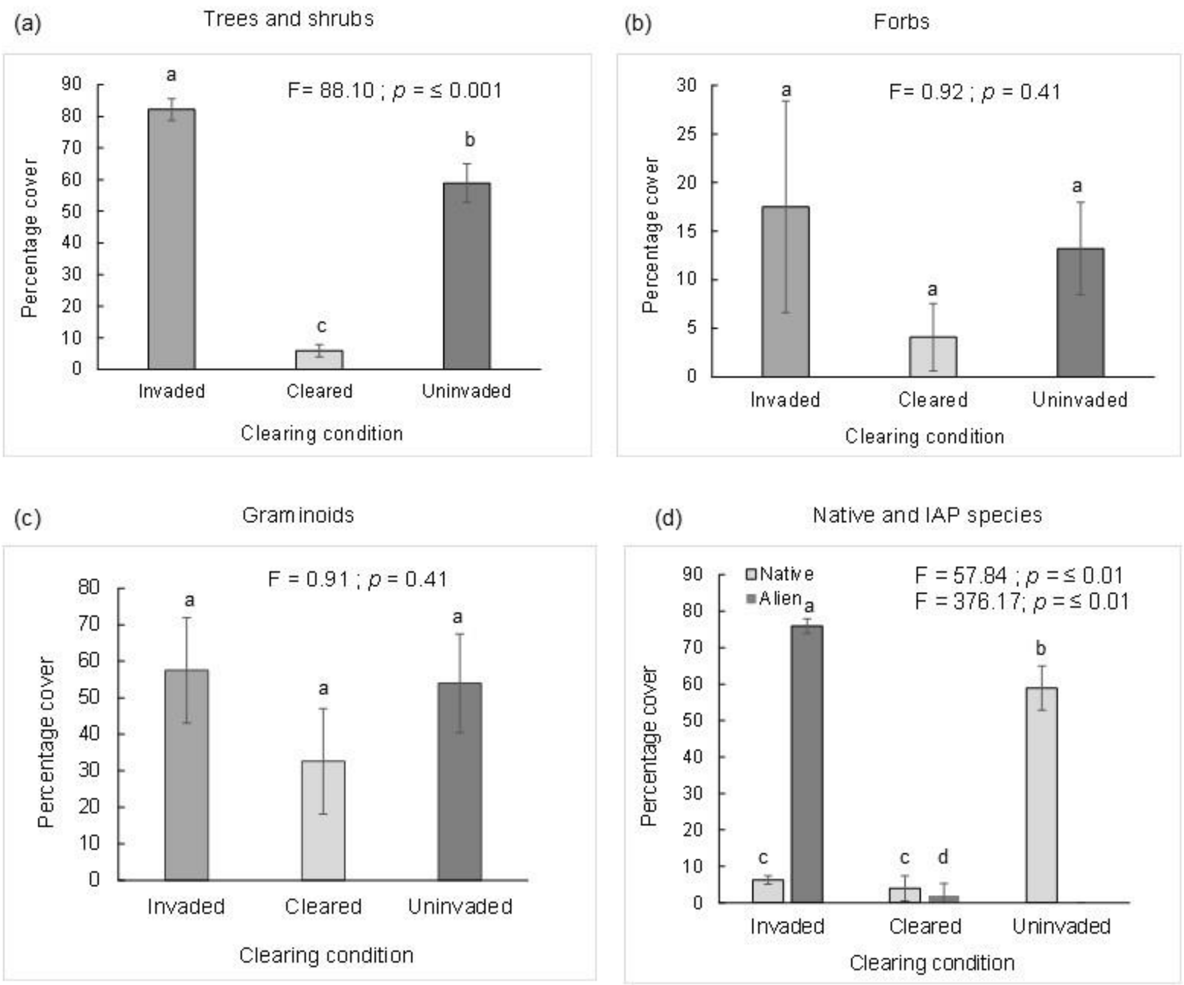

Figure 6.6: Comparisons of plant percentage cover for (a) trees and shrubs, (b) forbs, (c) graminoids, and (d) native and alien vegetation across the three clearing conditions (*L. camara* invaded, cleared, and uninvaded). The bars represent means ± SE, and one-way ANOVAs are displayed.

6.4. Discussion

Invasive alien plant invasion may cause a shift in native vegetation composition and structure as well as in soil properties and functioning across different environments (Ruwanza, 2016; Erckie et al. 2022). This necessitates a greater understanding of plant invasions and their ecological dynamics, as well as the development of effective methods for restoring affected ecosystems. As a result, the objective of this study was to examine changes in soil properties, native vegetation diversity, and composition after *L. camara* removal to better understand the ecological restoration trajectory for both soils and vegetation. In this study, *L. camara* invasion had varied effects on soil properties and vegetation characteristics. For example, soil moisture showed no variations across clearing conditions, but monthly differences were visible. Also, most of the measured soil chemical properties showed no differences across clearing conditions, yet soil penetration and infiltration varied across months but not across clearing conditions. Vegetation diversity was higher in the uninvaded condition than in the cleared and invaded conditions. Moreover, a lot of secondary invaders and re-invasions of the cleared condition were observed. The diverse soil and vegetation recovery described above suggests that the recovery process varied depending on the specific soil property measured and varied over the course of several months.

Although soil moisture did not vary across clearing conditions, the high soil moisture content values recorded in September for all the clearing conditions are likely due to variations in rainfall and temperature patterns during the sampling months. We did not monitor rainfall during the sampling months, but it is likely that rainfall could explain the results since spring (September) in the study area is associated with rain as compared to winter (July). Variations in soil moisture content between clearing conditions have been reported in other studies where increases, decreases, or no change have been reported (Ndou and Ruwanza 2016). For example, Slesak et al. (2022) documented the lack of soil moisture changes after clearing IAPs, whereas Ndou and Ruwanza (2016) recorded a decrease in soil moisture after clearing an IAP. Low soil moisture levels after clearing are mostly associated with the removal of the IAP cover during clearing, which exposes soils to direct sunlight. However, other studies have reported that as a cleared area starts to recover, the regenerating native species produce litter, which helps keep the soil moist (Ruwanza et al. 2013). We observed significant monthly variations in soil compaction. The observed soil compaction results at the monthly level can be associated with the above-mentioned monthly rainfall and temperature variations. During high rainfall months, soils tend to be less compact due to infiltration. Indeed, some studies have shown that wet seasons are associated with wet soil, which can cause soil to be less compact than dry soil in the dry season, which is associated with soil compaction (Bar-Yosef and Lambert, 1981; Quang et al. 2012).

There were differences in soil cumulative infiltration rates among the different clearing conditions and months, as well as interactions between months and invasion conditions. Soil infiltration rates across the months were high in invaded and uninvaded conditions compared to the cleared condition, which reported low infiltration. This could be associated with the fact that the two above-mentioned conditions are dominated by woody species, which would be depositing litter, which, when decomposed, can increase infiltration rates since the soils will be less compact. On the other hand, less infiltration in the cleared condition could be associated with the observed compact soils, which are known to reduce infiltration. It is possible that increased hydrophobic conditions in the cleared condition could reduce the infiltration. The causes of the hydrophobic condition could be linked to the exposure of cleared soils to the direct sun, which can increase chemical compound reactions in the soils to make them compact and reduce infiltration. Indeed, Espinosa-Garcia et al. (2008) and Kerr and Ruwanza (2016) have reported that soil chemical compounds can react with high soil temperatures from direct sunlight to influence soil properties, in this case soil repellency and infiltration rates.

Furthermore, the observed soil infiltration rates under the cleared condition can also be associated with disturbances linked to clearing methods. Ntshuxeko and Ruwanza (2020) discussed how disturbances can lead to low soil infiltration rates. It is predicted that clearing *L. camara* or any other IAPs will make the soil less repellent since *L. camara* invasion has been reported to increase soil repellency (Ruwanza and Shackleton, 2016). However, in this study, the soil in the cleared condition was more repellent in September and November. This could be due to the reported soil compaction; where fire was used during clearing, it could have induced soil repellence. Indeed, WfW clearing is associated with the burning of cleared biomass, and the burning has been shown to cause soils to be repellent through the formation of hydrophobic conditions (Ruwanza et al. 2013; Ruwanza and Tshililo, 2019). However, the dominance of wettable soils in both the cleared and uninvaded conditions suggests that the soils in the cleared condition are looking like the ones in the uninvaded condition. This observation could imply that the cleared soils are recovering towards being similar to the uninvaded soils when it comes to water repellency. Therefore, the removal of *L. camara* facilitates soil to move towards wettable conditions that are similar to uninvaded conditions. Changes in soil repellency after clearing are potentially explained by several factors, e.g., reduced soil legacy, reduced litter release by the invaded plant, and soil type (Ruwanza et al. 2013; Ruwanza, 2017; Kato-Noguchi et al. 2021).

The composition and health of soil properties can significantly impact the growth and survival of native plant species. For instance, low soil infiltration rates in cleared conditions can influence the restoration of these sites in various ways. Firstly, poor soil infiltration rates can limit the availability of water for plant growth, reducing the competitiveness of native species against IAPs. Secondly, reduced infiltration rates can also lead to waterlogging, which may favour the growth of IAPs that are more tolerant of these conditions. Therefore, monitoring soil physical properties over time and between months can help determine when the soil has recovered sufficiently to fully support the recovery of native vegetation.

This study showed no differences in measured soil chemical properties across all clearing conditions except for soil pH. Soil pH was significantly higher in the uninvaded condition as compared to the invaded and cleared conditions. Changes in soil chemical properties after

IAP invasion and clearing have been mixed, and these are potentially determined by the IAP, invasion extent, site characteristics, and litter decomposition. For example, Ndou and Ruwanza (2016) reported no significant differences in some soil properties, such as soil pH, after *Acacia* removal and attributed this to legacy effects, leaf litter changes, and, to some extent, decomposition rates.

Various studies have documented how *L. camara* negatively influences species richness, species diversity, percentage cover, and composition (Gooden et al. 2009; Lone et al. 2021). Moreover, the results of chapter 4 of this thesis showed varied results, with both positive and negative impacts of *L. camara* being observed on vegetation richness, diversity, cover, height, and composition. Based on the passive restoration model, *L. camara* clearing is expected to facilitate the recovery of these vegetation characteristics in the cleared conditions, provided ample time is given. In this study, the *L. camara* condition significantly decreased species richness and diversity compared to the uninvaded condition, an indication that invasion facilitates plant diversity reduction. However, two years post *L. camara* clearing, species richness and diversity remain significantly lower as compared to the uninvaded condition. Besides vegetation diversity, the percentage cover of native species was low in the cleared condition, although variations were noted, with graminoids being more abundant in the cleared condition. Generally, the results indicate that vegetation diversity and cover are low in the cleared condition. The low vegetation diversity and cover in the *L. camara* clear conditions may be associated with the absence of seeds from the expected native plant species.

However, an examination of different species growth forms shows a different pattern. For example, some native trees and shrubs, such as *A. tetracantha*, *Gymnosporia* spp., *S. pyroides*, and *V. karroo*, were observed in the cleared condition. Similarly, graminoids such as *D. eriantha*, *P. maximum*, and *S. africanus* were also frequently occurring in the cleared condition. Ruderal or pioneer plants are often associated with disturbance, which is in this study clearing was a form of disturbance. These species are usually among the first to colonise cleared areas since they are adapted to thrive in disturbed environments. Example of these species include grasses, weeds, and shrubs. Indeed, Vosse et al. (2008) reported on how pioneer species usually dominate after clearing an IAP, and Randelovic and Jovanovic (2023) document how the presence of these plant species serves as a biological signal that the restored area can recover. The presence of these native species in the cleared condition can be beneficial towards ecological restoration, as such species can act as restoration foci. For example, the dispersal of native plant seeds by birds is likely to start from these patches of recruiting native species that are present in the cleared condition. Several studies report on the importance of having a few native species in cleared areas, as they can facilitate vegetation recovery after clearing (Ruwanza et al. 2013; Liu et al. 2014; Ruwanza et al. 2018). These few native species in the cleared condition could be germinating from soil seed banks or could have been dispersed to the cleared areas by birds or animals. For dispersal to happen, native vegetation areas should be close to the cleared areas so that seeds are dispersed. In our case, the native reference site is close to the cleared condition. Regarding soil seed banks, Fourie (2008) reported that soil seed banks of native herbs (from the Asteraceae family) and trees and shrubs (from the Fabaceae family) can persist for a long time and can play a significant role in facilitating native vegetation recovery after clearing. Therefore, our observation seems to imply that passive recovery after IAP clearing relies heavily on the proximity to native reference areas for dispersal purposes and the persistence of native soil seed banks, which can recruit after the IAP has been removed.

In contrast, we observed recruitment of some IAPs in the cleared condition, including *A. mearnsii*, *Opuntia* spp., *P. lanceolata*, *T. minuta*, and *Taraxacum officinale.* Clearing constitutes a major disturbance, and disturbance promotes the recruitment of IAPs, which are adapted to disturbed environments (Parker-Allie et al. 2004; Chabrerie et al. 2008). Consequently, Huebner (2020) refers to IAPs as the passengers of disturbance since they take advantage of the negative effect of disturbance. Some of the factors that enable IAPs to be able to recruit more quickly than native plant species include their ability to adapt to disturbance, their rapid growth and reproduction, and their ability to tolerate a wide range of environmental conditions (Rai and Singh, 2020). The secondary invaders observed in the cleared conditions have the potential to hinder native vegetation recovery. Several studies have reported on secondary invaders after IAP clearing (Ruwanza et al. 2013; Ndou and Ruwanza, 2016; Torres et al. 2018). For example, Galatowitsch and Richardson (2005) reported how clearing can result in the re-emergence of the same IAP and/or cause secondary invasions in which non-target species proliferate and impede the growth of recruiting native species. Several other authors have documented secondary invaders after clearing and how they can complicate ecological restoration (Gooden et al. 2009; Larson and Larson, 2010; Ruwanza et al. 2013; Nsikani et al. 2019). Secondary invasion is caused by several factors, such as (i) the ability to utilise soil nutrients that remain in the soil after clearing, (ii) IAP seed banks in the soils that germinate after removal of the IAP, and (iii) seed dispersal from elsewhere (Ruwanza et al. 2013; Nsikani et al. 2019). We also recorded the re-invasion of the cleared condition by *L. camara*. Since seed production and storage are known to play a substantial role in *L. camara* population dynamics, seedlings re-emerged in the cleared areas. The seed of IAPs can remain dormant in the soil and germinate when conditions are suitable (Gioria and Pysek, 2017). It is possible that the removal of *L. camara* created a suitable condition for its seeds to germinate and re-invade the cleared area. Both secondary invasion and re-invasion of the cleared condition may significantly reduce the likelihood of passive recovery within the study sites, thus resulting in negative effects on biodiversity and ecosystem composition, structure, and functioning (Geerts et al. 2022). The persistent seed banks of *L. camara* and other IAPs may be connected to their re-emergence in cleared areas. Therefore, timeous follow-up clearing is required so that secondary invaders and re-invasion are managed so as to allow native vegetation recovery towards a positive trajectory (Blanchard and Holmes, 2008; Holmes et al. 2008). It is important to acknowledge that soil and vegetation recovery following IAP removal takes time (≥ 10 years) (van der Waal et al. 2012; Ruwanza et al. 2018); thus, the restoration assessment time scale in this study is likely to have been too short to observe significant soil and vegetation recovery. Based on Nerleker and Veldman (2020), the restoration of target plant communities can take decades to centuries, emphasising the importance of analysing successional development in long-term studies.

6.5. Conclusion and restoration implication

A key issue in ecological restoration is whether native species have the capacity to recover and recolonise sites after clearing IAPs. Maclean et al. (2016) document how recovery after clearing is complex and faces challenges such as re-invasion by the same IAP or by secondary invaders. In this study, *L. camara* clearing reduced the invader population. The cleared condition showed varied recovery trends for soil properties. Although species diversity and cover in the cleared conditions seem not to mimic those in the uninvaded conditions, the presence of some native species in the cleared conditions points to a positive vegetation recovery trajectory. However, we also observed the dominance of secondary invasives and the re-invasion of the cleared condition with *L. camara*, which is associated with how these species can respond to disturbance. These findings show that one and two years after clearing, species that are adapted to thrive in disturbed environments establish themselves.

Our findings suggest that clearing alone may not be enough to recover these communities; therefore, other interventions are needed to speed up the soil and vegetation recovery process. Such interventions speak to the need for active restoration to be implemented in the *L. camara* cleared condition. Active restoration interventions that could be implemented include the planting of target native plant seeds, which has the potential to facilitate native vegetation diversity. However, seeds of such native species should be harvested from nearby communities (e.g., native woody species that can grow fast and are drought-resistant). Interventions meant to reduce re-invasion and secondary invasion should be put in place and should include timed follow-up. According to Gaertner et al. (2012), follow-up measures are critical in ecological restoration to prevent re-invasion after clearing. As a result, it is essential that the cleared areas be followed up and monitored at an early stage to deplete the IAP seed bank; this can be done by hand removing re-emerging *L. camara* seedlings and non-target plants or by chemical control methods, e.g., herbicides.

From a future research perspective, it is important to note that ecological restoration is a long-term process, and thus, the time period post-clearing (in this study, it was two years) is insufficient to fully understand the extent of soil and vegetation recovery as it takes much longer. Hence, long-term follow-up studies after *L. camara* clearing should be prioritised to acquire deeper insights into restoration patterns and ecological responses over time. Furthermore, studies on the legacy effects (physicochemical and microbial) of *L. camara* need to be conducted, as it is one of the factors responsible for creating unsuitable conditions for the growth of native species and thus inhibiting the recovery of the invaded sites. Lastly, the efficacy of active management measures after *L. camara* removal needs to be studied and tested before they are implemented.

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Supplementary materials

Appendix 6.1: Frequently occurring plant species observed at the study site.

Plant species name	**Family**	**Clearing conditions**		
		Invaded	**Cleared**	**Uninvaded**
		Trees and shrubs		
**Acacia mearnsii*	Fabaceae	✓	0	0
Azima tetracantha	Salvadoraceae	0	✓	✓✓
Canthium spinosum	Rubiaceae	0	0	✓
Cussonia spicata	Araliaceae	0	0	✓
Diospyros spp.	Ebenaceae	✓	0	✓✓✓
Euclea undulata	Ebenaceae	0	0	✓
Euphorbia triangularis	Euphorbiaceae	0	0	✓
Gymnosporia spp.	Celastraceae	0	✓	✓
**Lantana camara*	Verbenaceae	✓✓✓✓✓	✓	0
Leonotis leonurus	Lamiaceae	0	0	✓✓
**Opuntia* spp.	Cactaceae	✓	0	0
Scutia myrtina	Rhamnaceae	0	0	✓✓
Searsia pyroides	Anacardiaceae	✓✓	✓✓	✓✓
Stoebe spp.	Asteraceae	0	0	✓✓
Vachellia karroo	Fabaceae	✓	✓✓	✓✓✓
		Forbs		
**Alternanthera pungens*	Amaranthaceae	0	0	✓✓✓
Centella asiatica	Apiaceae	0	0	✓
**Plantago lanceolata*	Plantaginaceae	✓	✓	✓
Senecio spp.	Asteraceae	0	0	✓
Sida cordifolia	Malvaceae	✓	0	✓
**Solanum linnaeanum*	Solanaceae	0	✓	✓
**Sonchus asper*	Asteraceae	0	✓	0
**Tagetes minuta*	Asteraceae	✓✓	✓	0
**Taraxacum officinale*	Asteraceae	0	0	✓✓
		Graminoids		
**Cynodon dactylon*	Poaceae	✓	0	✓✓
Digitaria eriantha	Poaceae	✓✓✓✓	✓✓✓	✓✓✓✓

Panicum maximum	Poaceae	0	✓	✓
Sporobolus africanus	Poaceae	✓	✓	✓✓✓
		Other		
Pteridium spp.	Dennstaedtiaceae	0	✓✓✓	✓

✓ Indicates the presence of plant species based on the calculated occupancy frequency that is categorised as follows: ✓(1-20%);✓✓(21-40%);✓✓✓(41-60%); ✓✓✓✓ (61-80%);✓✓✓✓✓ (81-100%); 0 indicated that the species was not present and ***** indicates non-native species (Bromilow, 2010).

Chapter 7: Synthesis, conclusions, and recommendations

7.1. Introduction

Invasive alien plants (IAPs) have both significant positive and negative impacts on native vegetation, community dynamics, and ecosystem processes (Ehrenfeld, 2010; Vila et al. 2011; Rai, 2020). In South Africa, they cover approximately 8% of the country (van Wilgen, 2018; Richardson et al. 2020). This chapter synthesises the main findings of this research and discusses their relevance to the discipline of invasion biology in general. To date, various research questions have been examined, while at the same time, many experiments have been conducted to assess how IAPs have a profound impact on the survival and growth of native species, and efforts have been made to manage and control them. Gioria et al. (2014) document how the long-term impacts of IAPs depend on factors such as the persistence of the IAP, the magnitude and time scale of the impact, and the ability of native vegetation to buffer against their displacement. There are, however, a restricted number of studies that address the different aspects of *L. camara* invasion in South Africa, specifically studies that attempt to examine impacts at various scales, such as species-specific impacts and impacts at the community level. Besides that, no study in South Africa has ever assessed soil and vegetation restoration potential after *L. camara* removal. This thesis attempted that, and it is motivated by the need to address research questions linked to (i) *L. camara* impacts directly linked to the species, (ii) *L. camara* impacts at a community level, and (iii) the need to understand the possibilities for passive restoration after *L. camara* removal. Besides generating novel scientific information to understand impacts and restoration potential, the thesis results provide baseline information that can be used in future studies.

Traits associated with IAPs often undermine the adequacy of restoration strategies (Rai, 2022). Hence, it is important to study these aspects so that restoration can be properly planned and relevant strategies can be adopted. Several studies have advocated the importance of understanding these aspects; for example, Rodrigues et al. (2019) reported how soil properties can influence the distribution of plant species. Ruwanza and Dondofema (2020) also reported how changes in soil properties such as soil infiltration rate, soil moisture, and soil water repellency can enhance plant invasion and leave a soil legacy effect that could persist and affect restoration success once the IAP has been removed. Gioria et al. (2014) discussed the impacts of IAP seed banks, their long-term implications, and how they can interfere with the management process. Holmes et al. (2008) documented the importance of addressing and understanding factors that may hinder restoration efforts. Therefore, before restoration planning, it is crucial to untangle the relationship between ecological factors and the IAP. This thesis adopted that approach and tried to understand the potential for restoration post-clearing *L. camara* from both a soil and vegetation standpoint, since the interaction between soil and vegetation could explain observed changes after IAP removal.

Earlier studies have quantified some of the dynamics of *L.* camara in South Africa, with a focus on biological control (Cilliers and Neser, 1991; Mukwevho et al. 2018; Katembo et al. 2020), its distribution (Taylor and Kumar, 2014), and impacts (Jevon and Shackleton, 2015; Ruwanza and Shackleton, 2016; Ruwanza, 2016; Ruwanza, 2020; Ruwanza and Mhlongo, 2020; Ntalo et al. 2022; Raphela and Duffy, 2023). Aspects such as the impacts of *L. camara* on vegetation and soil seed banks and its restoration are hardly examined, yet they can inform *L. camara* management interventions. For example, an understanding of soil seed banks can assist in understanding vegetation recruitment potential after IAP removal, and in cases where secondary invaders dominate soil seed banks, interventions beyond just the removal of the IAP will need to be considered. Given the need to understand most aspects of the invasion process in order to develop effective management tools, the objectives of this thesis were therefore to investigate the impacts of *L. camara* on soil and vegetation at the plant and community scales. Hence, the thesis examined the impacts of *L. camara* invasion on soil physicochemical properties at the plant level, native vegetation (aboveground impact) and seed banks (belowground impact) at the community level, and lastly, vegetation and soil response post *L. camara* clearing.

This thesis yielded the following key findings: Firstly, *L. camara* invasion altered some soil physical properties, and these changes are likely to create conditions conducive to its growth and promote its invasion. The alterations in soil physical properties can contribute to its competitive advantage. The study also noted that the effects of *L. camara* on soil physicochemical properties, especially certain physical properties, exhibited seasonal variations. Secondly, *L. camara* invasion did not have significant negative impacts on several aboveground vegetations. These results contradict the commonly reported narrative that *L. camara* invasion negatively impacts aboveground vegetation (Ruwanza, 2020). The areas that provided suitable habitat for *L. camara* did not favour some of the species that were absent in the *L. camara* invaded condition. *Lantana camara* co-occurred with species that are adapted to disturbed conditions, moreover, it created favourable conditions for some species that can co-occur with it; thus, it can act as a refugia for some native species. Thirdly, *L. camara* influenced the abundance of forbs and grasses, and the presence of alien forbs and grasses in the soil seed bank has the potential to influence future restoration initiatives. It is important to note that the results of aboveground and belowground impacts showed various impacts, which could be explained by several factors such as seed dormancy and seed recruitment conditions. Lastly, *L. camara* clearing confirmed the possibility of reducing its population, and the presence of native species in the cleared areas points to a positive recovery trajectory where the cleared areas are recruiting towards the uninvaded areas. However, secondary invasions and re-invasions by *L. camara* can hinder the restoration process. These results, their implications, and future research needs are discussed in detail below.

7.2. Main conclusion

Lantana camara is an invasive alien plant that is widely distributed around the world (Bhagwat et al. 2012; Negi et al. 2019). Day et al. (2003), Sharma and Raghubanshi (2009), Simba et al. (2013), Singh et al. (2014), Ruwanza and Shackleton (2016), and Kumar et al. (2021) have all provided evidence of the negative impacts of *L. camara* on ecosystems. In this thesis, the third chapter investigated how *L. camara* invasion affected soil physical and chemical properties in three different sampling positions over four seasons. The study design facilitated the examination of soil impacts caused specifically by *L. camara* plants. This chapter observed how *L. camara* influences and alters some soil physical properties rather than chemical properties. The results of this chapter showed that *L. camara* invasion modified soil physical properties such as soil penetration resistance, infiltration rate, and soil repellency where it invaded. Results also showed that the magnitude and direction of these changes differed based on seasonality and sampling location. This chapter concluded that the observed modifications in these soil physical properties can have important implications for ecosystem processes and the success of restoration efforts. The changes induced by *L. camara* can create an environment that favours its growth and survival of other IAPs, thereby hindering the recovery of native vegetation during restoration. Indeed, Lone et al. (2021) reported on how *L. camara* can alter soil properties, thus favouring its growth. They further discuss how this could lead to changes in ecosystem functioning. This chapter, therefore, accepted the hypothesis that *L. camara* invasion influenced some soil physical properties under different sampling positions but rejected the suggestion that it negatively affected soil chemical properties since no statistically significant changes were observed. Moreover, I also accepted the hypothesis that there were variations in soil properties across the different seasons. It is important to note, however, that the mechanism of invasion does not only include the traits of the IAP but also the characteristics of the receiving community or site. Therefore, since the sites were used for agricultural activities (specifically grazing), disturbances linked to agricultural practices could have influenced these results; however, this was not tested in this study as this aspect is outside the scope of the thesis. Given the observed changes in some soil physical properties due to *L. camara* invasion, the study recommends that the species be cleared to restore soil physical properties, even though it is not clear how long plant-mediated changes in soil properties persist after clearing.

In Chapter 4, I assessed how *L. camara* influenced the aboveground vegetation at a community level. This chapter showed varied results, with both positive and negative impacts being observed. This observation contradicts the general perception that *L. camara* invasion displaces native vegetation, resulting in a decrease in species diversity, richness, and cover. The study also noted that the effects of *L. camara* on some vegetation variables were growth form-dependent, with some differences being noted for trees and shrubs compared to forbs and graminoids. The areas that provided suitable habitat for *L. camara* did not favour the species that were absent in the *L. camara* invaded condition. A key observation was that some native species co-occurred with *L. camara*, an indication that the species acts as a refugia for some species. Based on results from previous studies on *L. camara* invasion impacts (Ruwanza, 2020), one would expect to have recorded negative aboveground vegetation impacts; however, that was not the case. Besides the issues of species co-occurrence, these results also demonstrated that the impact of *L. camara* cannot be generalised, given that *L. camara* is a complex species since it possesses various characteristics or features that contribute to its complexity. Its effects are varied and do not have a predictable pattern, depending on the measured vegetation variables and potentially among vegetation types. Thus, for effective management and control of *L. camara*, planning should be done accordingly, and in this case, consideration should be put in place to protect existing co-occurring species when *L. camara* is removed. This chapter rejected the generalised hypothesis that *L. camara* invasion results in a decline in native species diversity and cover.

In Chapter 5, I examined how *L. camara* invasion affects soil seed banks. The difference in species composition, density, richness, and diversity of soil seed banks was assessed between *L. camara* invaded and uninvaded areas. The findings demonstrated how *L. camara* influences only the abundance and composition of some species in the soil seed bank but not diversity and richness. This was shown by a decrease in seedling abundance of forbs and graminoids in the *L. camara* invaded condition. This chapter also revealed how *L. camara* does not entirely eliminate less competitive plant species but acts as a refugia for them, thus facilitating co-occurrence. This is shown by the presence of native seedlings such as *A. cordifolia*, *C. prostrata*, and *Oxalis* spp. These findings tend to agree with Schmerbeck and Gupta (2022), who reported that *L. camara* does not entirely exclude native plants. The implications of these soil seed bank results are twofold: (i) the native species that germinated from the seed banks collected from *L. camara* areas can serve as a focal point of vegetation recovery once *L. camara* is removed; (ii) the emerging seedlings of secondary invaders such as *B. pilosa*, *C. bonariensis*, and *T. officinale* could complicate vegetation recovery.

In the soil seed bank study, I also observed that certain common native seedlings were not present in the seed bank. This is likely to be explained by the non-availability of seeds in the soil, seed dormancy, or poor seedling recruitment conditions. Vosse et al. (2008) acknowledged how native species can be poorly represented in a soil seed bank. From a restoration point of view, active restoration (such as sowing native target plants) may be required to restore these communities once *L. camara* is removed. In general, *L. camara* invasion negatively influenced the soil seed bank seedling abundance of forbs and grasses. *Lantana camara* also displaced some native seed banks, and at the same time, it also acted as a refuge for some native and alien species. As recommended in the previous research chapter, *L. camara* clearing should be done in a manner that does not adversely affect the existing soil seed bank. This speaks to the issue of clearing methods, and in this case, machinery that can compact and disturb soils as well as affect soil seed banks should be avoided when removing *L. camara*. Therefore, in these areas, an effective clearing method that will be less destructive is mechanical control, i.e., the use of simple handheld tools, not heavy vehicles. Furthermore, the seedlings that recruit after *L. camara* removal should be closely monitored, and measures to eradicate secondary invaders and recruiting *L. camara* should be put in place. Lastly, the uninvaded areas also need to be monitored for seedlings of IAPs, as these were observed in these sites and can take advantage of ecosystem disturbances such as fire (Richardson and Kluge, 2008; Priyanka and Joshi, 2013). Fire is a known driver of alien plant invasion (Zouhar et al. 2008; Davies et al. 2012). This chapter, therefore, accepted the hypothesis that there were differences in soil seed bank species abundance, composition, and density under *L. camara* invaded and uninvaded conditions but not in species richness and diversity.

Generally, Chapters 4 and 5 conveyed some aspects of the invasion meltdown hypothesis, where *L. camara* showed facilitative relationships with both native species and other IAPs. This is shown by its ability to co-occur with other species, particularly those that can mutually benefit from *L. camara*. Furthermore, the observed variations in aboveground vegetation and soil seed banks results in Chapters 4 and 5 could be the result of several factors, including: (1) seeds of most species germinate within the year they are dropped; therefore, it is possible that some seeds were not viable in the soil at the time of soil collection (Thompson et al. 1997). Another possible explanation of the observed differences is linked to (2) a lack of germination or a reduction in emergence capacity in the soil seed bank, which is how some species can be dormant for a long period of time and only germinate when appropriate conditions occur

(Davy, 2002). Indeed, Maskova and Poschlod (2022) report how soil seed banks of different species tend to differ in their persistence, depending on the longevity of the seeds in the soil and their tendency to germinate. The differences in results between the aboveground vegetation and soil seed bank studies may also be associated with (3) differences in greenhouse and natural conditions. That is, natural environmental conditions may be more favourable for seed germination and seedling survival of some species as compared to greenhouse conditions (Bai et al. 2010). Touzards et al. (2002) reported that soil seed banks that are composed primarily of perennial plant species often differ from the aboveground vegetation, and the difference was attributed to differences between field/natural conditions and greenhouse conditions. The above-mentioned three reasons suggested by Guo et al. (2022) and Jedrzejczak et al. (2022) could explain the differences between Chapters 4 and 5 results.

Chapter 6 evaluated soil and vegetation responses following *L. camara* clearing. Even though *L. camara* has been documented as an ecological problem in multiple provinces in South Africa (Vardien et al. 2012), there are no studies on restoration trajectories after clearing *L. camara.* For that reason, in Chapter 6, I examined native vegetation and soil recovery following *L. camara* clearing and found that *L. camara* clearing reduced the *L. camara* population and had varied effects on soil physicochemical properties and vegetation. For example, soil moisture, soil penetration, and infiltration showed no variations between clearing conditions; only monthly variations were visible. The cleared conditions also showed recovery trends in some soil properties, i.e., soil repellency, that were leaning towards being similar to the uninvaded condition. This chapter also demonstrated that during restoration, vegetation reacts faster than soil properties, as shown by the observed changes in vegetation after clearing *L. camara* as compared to some soil properties, viz., soil nutrients, exchangeable cations, soil moisture, and soil penetration, which showed no significant differences. This chapter observed some native vegetation on the cleared areas, an indication of a positive vegetation recovery trajectory, as this can be beneficial for restoration. These existing native species in the cleared condition have the potential to accelerate recovery in the future as they can act as restoration foci. The absence of some species in the *L. camara* cleared conditions may be associated with the absence of seeds from the expected native plant species.

Despite the above-mentioned positive clearing results, *L. camara* re-emergence after clearing was observed. This indicated that *L. camara* has a soil seed bank that persists after clearing, which can become a source of re-invasion if not taken care of. Seeds of *L. camara,* however, can also be introduced from external sources, not just from the soil seed bank. This then means that, apart from the seeds already present in the soil, new seeds can be dispersed and contribute to the spread and establishment of this IAP. In this study, Chapter 5 on the soil seed bank also confirmed that seedlings of *L. camara* germinated in the greenhouse, and the re-invasion has the potential to hinder or slow down vegetation restoration efforts. In the cleared areas, secondary invaders were enumerated, and these were also present in the soil seed bank, as shown in Chapter 5. Secondary invaders have the potential to slow down native vegetation recovery after IAP removal. This chapter also showed how some IAPs, such as *L. camara*, are resilient to removal and how ecological restoration is not a once-off process, thus requiring post-clearance restoration, funding, and frequent monitoring. Indeed, Pretorius et al. (2008) documented that for effective native vegetation recovery to occur, post-clearance restoration is crucial. Generally, the hypothesis that some soil physicochemical properties and vegetation characteristics were recovering in the cleared conditions was supported. However, some re-invasion and secondary invasion could slow down this recovery.

Given that the effects of soil and vegetation recovery following IAP removal have been reported to take time (van der Waal et al. 2012; Ruwanza et al. 2018), the restoration assessment time scale in this study is likely to have been too short to observe significant soil and vegetation recovery. Some studies have documented how the effects of clearing IAPs can only be seen after over 10 years (van der Waal et al. 2012). Ruwanza et al. (2018) reported some changes in vegetation close to 10 years after the initial clearing. Thus, it is essential that long-term studies on soil and vegetation recovery be done to better understand their response after clearing. This chapter has set baseline information on which future projects on soil and vegetation recovery after clearing *L. camara* can be continuously monitored. Based on the data collected in this study, *L. camara* clearing alone might not be sufficient for passive restoration; therefore, active ecological restoration methods should be considered if soil and vegetation recovery is to be accelerated. The benefits of adopting active restoration strategies are that they can fast-track soil and plant recovery and reduce secondary invasion (Wubs et al. 2016; Bulot et al. 2017; Ruwanza, 2017). However, active restoration methods still need to be tested, as some are costly.

It is also important to note that in Chapter 4, higher native plant richness, diversity, and cover of some growth forms were recorded in the *L. camara* invaded areas than in uninvaded areas. Whereas Chapter 6 recorded contrasting results. These findings confirm and illustrate that the impacts of *L. camara* vary and do not only depend on the invader attributes but also on factors such as site characteristics and land use types. Indeed, Dong et al. (2015) documented how *Solidago canadensis* influenced native plant species richness in three contrasting ways, i.e., positive, neutral, and negative impacts. Chapters 4 and 6 were conducted on different sites; thus, the contrasting results between these chapters may be linked to site characteristics. The key results of this study are summarised below as bullet points, and an attempt was made to link these to the conceptual framework of this study (see below, Figure 7.1).

Research aim (i) – invasion impacts and mechanisms at the species level

- *Lantana camara* altered and modified some soil physical properties, and these impacts varied according to sampling location, site, and seasonality.
- *Lantana camara* invasion significantly altered the soil physical properties, which can likely create an environment that favours its own growth and survival by influencing factors such as soil moisture, penetration, and water repellency.
- No effects on soil chemical properties were observed.

Research aim (ii and iii) – invasion impacts (above-and-belowground) at the community level

- The impact of *L. camara* on vegetation varied, with both positive and negative impacts observed on species richness, diversity, cover, height, and composition.
- *Lantana camara* invasion did not negatively affect species richness, diversity, and cover of native species; rather, high species richness and diversity indices were observed in the *L. camara* invaded condition.
- The effect of *L. camara* on vegetation cover was growth form dependent.
- *Lantana camara* also co-occurred with other species and provided refuge for native vegetation.
- The effects of *L. camara* on vegetation are not uniform and thus cannot be generalised; they are largely influenced by site-specific factors.
- *Lantana camara* invasion also negatively influenced the soil seed bank abundance and composition.
- *L. camara* invasion also resulted in the displacement of some native seed banks, but at the same time, it co-occurred with other species, both native and exotic. This shows that *L. camara* does not eliminate less competitive species.
- The co-occurrence of *L. camara* with both native and other IAPs can have positive and negative management and restoration implications following *L. camara* removal.

Research aim (iv) – invasion management and restoration

- *Lantana camara* invasion had a variety of effects on some of the soil physicochemical properties, while *L. camara* removal resulted in changes to some soil properties.
- *Lantana camara* clearing reduced the invader population.
- The cleared condition showed mixed soil and vegetation recovery trends.

- Most of the soil physical properties showed no variation across clearing conditions, but monthly differences were observed.
- Also, most of the soil chemical properties showed no variation among the clearing conditions. Only the soil pH increased after clearing *L. camara*, and it was also leaning towards uninvaded conditions.
- *Lantana camara* invasion influenced the diversity of native plants, i.e., changes in native species richness, species diversity, percentage cover, and composition.
- Native woody species were present in the cleared conditions, and this is significant because these species can serve as restoration focal points.
- *Lantana camara* re-invasion and secondary invaders were observed in the cleared areas, which could obstruct native vegetation recovery.
- Clearing alone may not be enough to restore these communities; therefore, other active restoration interventions may be required to fast-track soil and vegetation recovery.

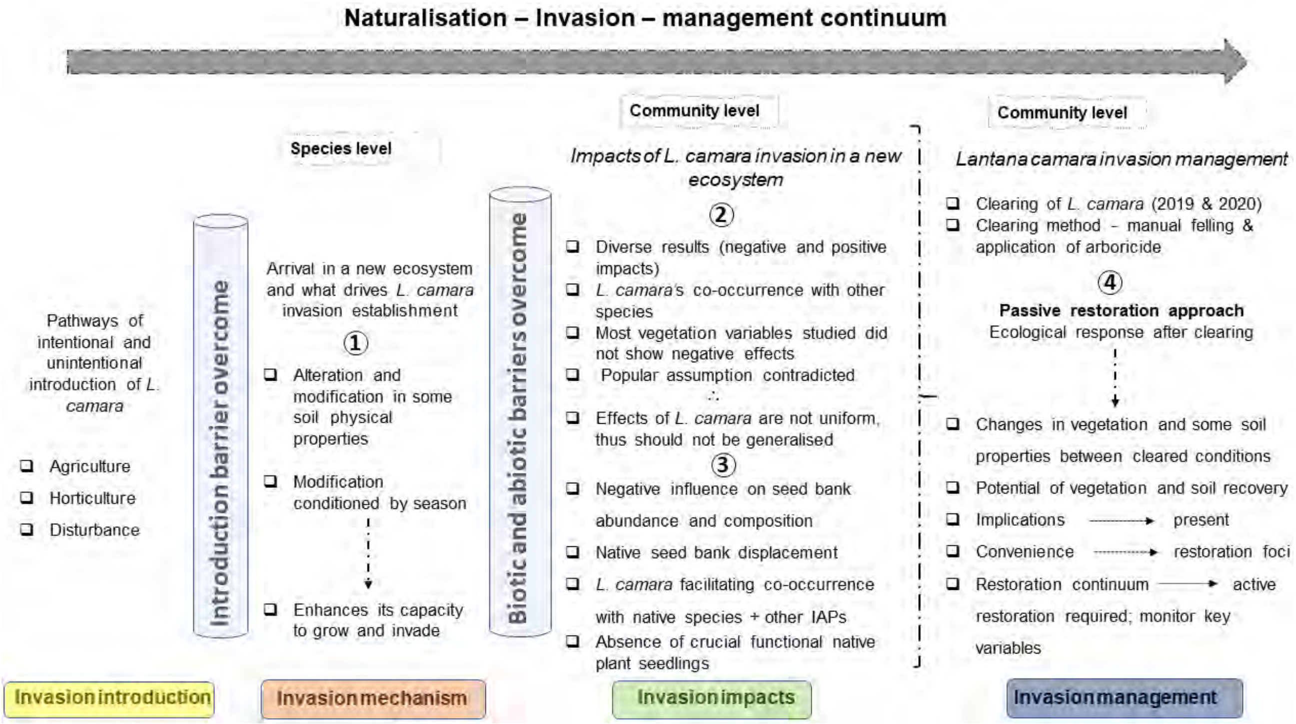

Figure 7.1: A schematic representation and summary of the thesis concepts. Number 1–4 (in black circles) are the research questions addressed in this thesis are numbers.

7.3. Recommendations

This thesis has produced crucial information about *L. camara* and the ecological consequences of its invasion in the Eastern Cape province of South Africa. Additionally, it highlights several important key elements that need to be considered during the management of *L. camara* given that it is a category 1b invasive species in South Africa, so management is compulsory. Most of the research being conducted on IAPs is on aboveground vegetation changes at a community level, and a few studies have been done on belowground soil and vegetation communities as well as how soil impacts are directly linked to a particular species. In addition, ecosystem monitoring following *L. camara* removal has never been done in South Africa, particularly monitoring both soils and vegetation. The results of this thesis contribute to the limited knowledge of *L. camara* effects on soil physicochemical properties, above-and-belowground impacts, and restoration potential after its removal. The results will also enhance our understanding of how *L. camara* behaves once it invades natural areas. It also enables us to comprehend how it can restrict soil and vegetation restoration where attempts to clear it are being put in place. Based on the results of this study, the following overall management recommendations are suggested:

- *Lantana camara removal*: It is imperative that *L. camara* plants be removed/cleared in areas where they have invaded. Removal of *L. camara* is meant to reduce the negative effects on soil and native vegetation, although in this study we found these impacts to vary.
- *Removal methods*: The study recommends that an appropriate removal/clearing method be used when managing *L. camara*. This is because *L. camara* acts as a nurse plant for some native understory species that grow beneath it. Therefore, removal/clearing methods that protect these species are needed since these co-occurring species play a key role during ecological restoration. In fact, Ruwanza (2012) highlights the importance of using an appropriate clearing method and how this method should be based on facilitating vegetation recovery. Therefore, throughout the clearing operations, it is essential to protect the remnant native species (Holmes et al. 2008). Apart from the removal method being non-destructive, it should also protect the soils, given that the soil seed bank of some native species exists beneath *L. camara*. Therefore, where *L. camara* is removed/cleared, heavy machinery that destroys remnant native vegetation and soils should be avoided.
- *Monitoring after removal*: Three aspects are important to consider once *L. camara* has been removed. *(i) monitoring recovery opportunities*: the study recommends that soil and vegetation monitoring after *L. camara* removal should be timeous and continuous. Both soil and vegetation should be monitored, given that the two can influence each other. For example, changes in soil recovery after IAP removal can influence vegetation recruitment,

while on the other hand, vegetation recruitment in cleared areas can affect soils through litter deposition. Therefore, monitoring of both soil and vegetation after the removal of IAPs should be done promptly and over a long period of time. *(ii) monitoring recovery constraints*: in the soil seed bank and restoration chapters, results identified re-invasion and secondary invaders as two processes that can slow down soil and vegetation recovery. The study, therefore, recommends that these two constraints be managed during the restoration process. Both re-invasion and secondary invasion can be managed through proper and effective follow-up control to remove recruiting invaders. Currently, the South African Working for Water programme conducts follow-up twice a year for three years after IAP removal. It is recommended that follow-up be done until re-invasion and secondary invaders are completely managed, even if the follow-up would take more than three years. However, this recommendation has funding implications and might need to be clearly evaluated, including motivating the Working for Water programme to budget follow-up programmes over a long-time scale. *(iii) Active restoration*: Seemingly, unassisted recovery at these sites is challenging; therefore, active restoration should be considered. It is recommended that active restoration methods such as seeding be considered if soil and vegetation recovery is to be fast-tracked to counter re-invasion and secondary invasion constraints.

7.4. Future research

- There seems to be limited knowledge on the response of soil physicochemical properties after clearing *L. camara*, and a lack of these studies may hinder the management and control of IAPs. Thus, it is recommended that more long-term studies on soil physicochemical properties be conducted to better understand how they change over time.
- Little is known about how *L. camara* influences soil microbial activities, yet research in this area can aid understanding of both invasion impacts and recovery after removal. Therefore, research on the invasion impact on soil microbial activities and the recovery of soil microbial communities after clearing is urgently needed. Few studies have attempted this; e.g., Wang et al. (2015) demonstrated how *L. camara* modifies the functional diversity of soil microbes and how this in turn improves its ability to compete with native vegetation and successfully invade. However, no study has been conducted in South Africa on soil microbial activity after invasion or after IAP removal.
- Additional research on the soil seed bank should be conducted since *L. camara* and other IAPs are known to produce a significant number of persistent seeds, as shown in the soil seed bank chapter. This makes it difficult to control and manage *L. camara* or other IAPs that have persistent soil seed banks. Research on soil seed banks after clearing *L. camara*

is also crucial to better understand the plant assemblages that are likely to occur after clearing. This information will assist in ecosystem restoration and diversity conservation. Mndela et al. (2020) discussed the significance of the soil seed bank during restoration and how it can facilitate passive restoration. They concluded that restoration after clearing would likely be initiated by early successional species that exist in the soil seed bank.

- Lastly, since there is no single standard clearing method for the effective management of IAPs, further studies should explore the efficacy of various clearing techniques. The issue to be researched should include which clearing method is effective at reducing the invader and at the same time facilitating soil and vegetation recovery, e.g., limiting the chances of re-invasion and secondary invaders, preserving native vegetation on site, and restoring soils and native plant communities.

7.5. References

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