

A SPATIO-TEMPORAL, LANDSCAPE PERSPECTIVE ON *ACACIA DEALBATA*
INVASIONS AND BROADER LAND-USE AND COVER CHANGES IN THE NORTHERN
EASTERN CAPE, SOUTH AFRICA



RHODES UNIVERSITY
Where leaders learn

A thesis submitted in fulfilment of the requirements for the degree of

MASTER OF SCIENCE (Environmental Science)

at

RHODES UNIVERSITY

by

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January 2018

ABSTRACT

Biological invasions are a wicked, social-ecological problem, interacting with numerous components within and across a range of spatio-temporal scales, with the potential to disturb broader socio-economic and ecological systems. *Acacia dealbata* is an invasive shrub in South Africa, widely naturalised across the grassland biome. Although the deployment of a biocontrol agent on *A. dealbata* is apparently justified considering its highly invasive and ecologically destructive nature, it should proceed with caution due to the integration of the species into the livelihoods of rural communities. This study sought to understand the nature and extent of the *A. dealbata* invasion in the northern Eastern Cape. Research was conducted in nine villages in rural Matatiele, Mount Fletcher and Maclear, selected for the pervasiveness of *A. dealbata* around these villages. A time-series of aerial photographs were systematically classified according to designated *A. dealbata* and land-use/land cover (LULC) categories in ArcGIS to track changes in the extent and rate of spread of *A. dealbata*, while standard vegetation surveying techniques were used to determine the current abundance and productivity of *A. dealbata* in selected areas. A high degree of spatial variability characterised the extent, density and biomass of *A. dealbata*, as well as the annual rate of spread and biomass production. The growth, productivity and spread of *A. dealbata* were significantly positive, and relatively few biophysical conditions correlated with the invasion. This was indicative of the broad range of invaded and potentially invadable habitats, suggesting that the extent and abundance of *A. dealbata* will likely continue to increase, barring deliberate intervention. Broader changes in LULC were also apparent, multidirectional and spatio-temporally variable. Despite a net increase in *A. dealbata*, the invasion was found to be highly dynamic, with various LULC transitioning to *A. dealbata*, but in turn *A. dealbata* transitioning to other LULC. Indeed, biological invasions are dynamic, context-specific phenomena, shaped by the heterogeneity of landscapes. Management interventions to limit or control *A. dealbata* should therefore consider the spatio-temporal dynamics of invaded landscapes, as well as the local-scale abundance, productivity and biophysical conditions of the area, while taking into consideration the livelihood requirements of the local communities.

DECLARATION

I, Aidan John Gouws, hereby declare that the work described in this thesis was carried out in the Department of Environmental Science, Rhodes University under the supervision of Professor Charlie Shackleton. The thesis has not been submitted to a university other than Rhodes University, Grahamstown, South Africa. The work presented here is that of the author unless otherwise stated.

A handwritten signature in black ink, appearing to read 'Aidan John Gouws', written in a cursive style.

Aidan John Gouws

Date: 30 January 2018

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ACKNOWLEDGEMENTS

The following thesis would not have been possible without the invaluable inputs from the following people, to whom I express my utmost gratitude. To the communities in Matatiele, Mount Fletcher and Maclear, I thank you for your hospitality in welcoming me to conduct this research in and around your villages. I am especially grateful to the chiefs for taking the time to meet with me and to each of my field assistants for their help, company and local expertise.

To my supervisor, Prof Charlie Shackleton, I thank you for affording me the opportunity to work on this project, guiding me, challenging me and urging me to challenge myself. In addition, I express gratitude to Dr Alan Wood and the Agricultural Research Council's Plant Protection Research Institute for facilitating and funding this research. I would also like to thank the rest of the staff and post-graduate students in the Department of Environmental Science at Rhodes University for their continued help and support in various capacities throughout these past two years. To Agripa Ngorima, I thank you for lending your assistance, knowledge and research during the infancy of this project, which continued to be a vital resource throughout this thesis.

To my office and department mates, Nosiseko Mtati, Shannon Herd-Hoare, Afika Njwaxu, Glen Vembo, Yondela Norman and Shayla Tricam, thank you for lending an understanding ear and sharing insightful discussions throughout all the delights and frustrations of this thesis.

Finally, thank you to all my friends and growing family for their unwavering encouragement and support. To my parents, Lauren and Delica Gouws, I am forever grateful for your keen interest in my research and endless support throughout my studies.

CHAPTER ONE: INTRODUCTION

The acceleration of environmental change can be attributed, at least in part, to the invasion of habitats by alien species, impacting on a range of social-ecological systems (SES) across the globe and posing challenges for national and international conservation and governing bodies, as well as for society at large (Vilà *et al.*, 2000; Simberloff *et al.*, 2013; Vaz *et al.*, 2017). This chapter defines invasive alien species (IAS), briefly frames the domain of invasion science and outlines the history of invasion research. The hypotheses of biological invasion are then discussed, highlighting some of the characteristics of invasive alien plants (IAPs). Thereafter, the detrimental and beneficial impacts of IAS are explored, with emphasis on the ecological and socio-economic impacts of IAPs. This is followed by an examination of IAP management in South Africa, which focuses on IAP legislation, management strategies and control options. The penultimate section provides the rationale and motivation for this current study, finally concluding the chapter with the aim, objectives and research questions.

1.1. Invasive alien species

The transport of species across geographical barriers and the subsequent introduction of alien species into new environments are intertwined with the evolution of human civilisation, from early migrations, through the rise and proliferation of agriculture, global trade and military conquest, to colonialism and more recently advanced globalisation (Richardson *et al.*, 2000; McNeely, 2001; Kowarik and Von der Lippe, 2008). Whether alien species are introduced unintentionally or intentionally (e.g. for food or timber production, or ornamental purposes), some species spread beyond the historical control of human management and become invasive (Kowarik and Von der Lippe, 2008).

Invasive alien species are species which have been introduced into habitats outside of their native ranges and have subsequently naturalised (i.e. have overcome local environmental conditions and reproductive constraints), with the ability to disperse and successfully establish self-sustaining, self-proliferating populations at a distance from the site of introduction (Richardson *et al.*, 2000). This definition adopts a purely biogeographic stance on IAS, avoiding the presumption of detrimental impact, as well as any stereotypes or negative connotations associated with the terms *invader* and *alien* (Richardson *et al.*, 2000; Colautti and MacIsaac, 2004; Evans *et al.*, 2008). It is important to note that not all alien species become established in their introduced environments; a relatively small percentage of introduced alien species become naturalised and fewer still subsequently become invasive (Richardson *et al.*, 2000). Moreover, not all invaders are particularly threatening, it is estimated that between a half and three-quarters of invaders pose an actual environmental threat and only a tenth are considered ecosystem *transformers* (Richardson *et al.*, 2000). Native species

may similarly possess invasive traits, which allow for rapid proliferation and long-distance dispersal (Richardson *et al.*, 2000; Naeem *et al.*, 2017). For clarity, these native species are preferably referred to as expansive species (Pyšek *et al.*, 2004), and can be said to be colonising or encroaching, rather than invading (Richardson *et al.*, 2000).

1.1.1. Framing invasion science

There is an inherent wickedness to the problem of biological invasions and IAS, embedded in the complexity of SES and the collective action required to address the problem (Marshall, 2013; McNeely, 2013; Xiang, 2013). Transdisciplinary, problem-orientated research promotes the production and integration of three types of scientific knowledge, namely *systems knowledge*, *target knowledge* and *transformation knowledge* (Kueffer and Hirsch Hadorn, 2008). In the domain of invasion science, these correspond to the understanding of causal relationships (i.e. the drivers, mechanics and process of invasion), the evaluation of impacts, values and conflicts, and the exploration of management options, respectively (Kueffer and Hirsch Hadorn, 2008). Richardson (2011) conceptualises the domain of invasion science as a Venn diagram consisting of two broad overlapping fields of study, namely invasion ecology and biosecurity studies, as illustrated in Fig. 1.1.

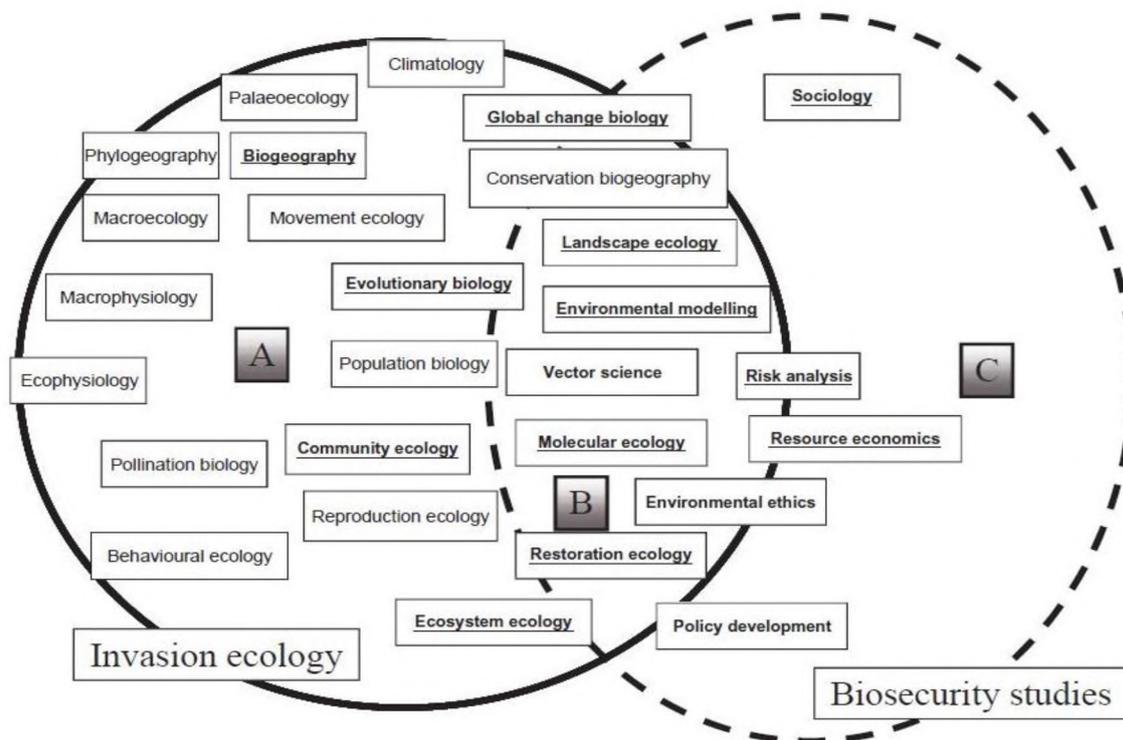


Fig. 1.1: The domain of invasion science (from Richardson, 2011).

The first zone (Fig. 1.1, zone A: systems knowledge) largely includes discipline-based studies housed within, or related to, invasion ecology; for example, studies on the biogeography, population biology or community ecology of IAS (Richardson, 2011). Historically, a succession

of overlapping research approaches have been adopted in invasion research in pursuit of systems knowledge (Kueffer and Hirsch Hadorn, 2008). According to Kueffer and Hirsch Hadorn (2008), these approaches have focused on species invasiveness and habitat invasibility (*classical model*); the phases of the invasion (*phase-transition models*); the broader insights invasions offer to understanding ecological processes and interactions (*natural experiments*); the broader influence of biotic and abiotic factors and change as drivers of invasion (*multifactorial case studies*); the role of spatio-temporal landscape dynamics in shaping biological invasion (*landscape ecology*); the pathways of invasion and the role of human agency (*vector science*); and, the influence of anthropogenic perturbation and land-use in facilitating biological invasions (*land-use science*).

Shifting away from the rigid disciplinary bounds of traditional invasion ecology, the second zone (Fig. 1.1, zone B: target knowledge) occupies the intersecting space between invasion ecology and biosecurity studies, and includes multidisciplinary studies in social, ecological and/or environmental fields; for example, risk analysis, environmental ethics, landscape ecology and environmental modelling (Richardson, 2011). Target knowledge-based invasion research has also shifted focus over time, exploring the biological impact of IAS; the alien/native debate; ecological risk assessment; the economic valuation of IAS impacts; and more recently, the socio-economic valuation of IAS, especially in the context of rural livelihoods (Kueffer and Hirsch Hadorn, 2008).

Finally, the third zone (Fig. 1.1, zone C: transformation knowledge) includes more management-orientated biosecurity studies, reaching into the realms of policy development, resource economics and sociology (Richardson, 2011). These studies either explore IAS management strategies (prevention, eradication and control) and control mechanisms (mechanical, chemical and biological), or attempt to understand the generation and application of knowledge itself in the context of cooperative, collective action in the management of IAS (Kueffer and Hirsch Hadorn, 2008). Invasion science can therefore be viewed as an amalgamation of past and present research trends in the study of biological invasions, encompassing various research approaches, directions of inquiry and hypotheses of invasion.

1.1.2. The study of biological invasions

Although the earliest records of introduced species can be traced back to the colonial period of expansion, a letter from American botanist John Bartram to his contemporaries is the earliest documented record of biological invasion, dating back to 1758 (Mack, 2003; Cadotte, 2006). According to Darlington (1849) and later Mack (2003), Bartram expressed concern for the mounting agricultural impacts of *Linaria vulgaris*, an invasive ornamental plant native to southeastern Europe and southwestern Asia (Meusel *et al.*, 1978; Saner *et al.*, 1995), on

Pennsylvanian farmlands. Later, during the infancy of modern ecology, the work of De Candolle (1855) provided some of the earliest notes on the ecology of IAS. This led Darwin (1859) to formulate one of the first hypotheses of plant invasion, the *naturalisation hypothesis* (Daehler, 2001; Murphy *et al.*, 2006).

The early- to mid-20th century brought a number of important works on biological invasions and IAS (e.g. Thomson, 1922; Allan, 1936; Egler, 1942; Oosting, 1948, 1956; Lindroth, 1957), though none as pivotal as Charles Elton's (1958) book, *The Ecology of Invasions by Animals and Plants*, often credited with setting the foundation for invasion biology and ecology (Richardson and Pyšek, 2008; Simberloff, 2011). For the decade following Elton's (1958) contribution, notable works on the theory, genetics and classification of introduced species (e.g. Sukopp, 1962; Baker and Stebbins, 1965; and, Holub and Jirásek, 1967, respectively) remained on the sidelines of mainstream ecology, while biological invasions and IAS were scarcely mentioned, if at all (Davis, 2006).

It is widely accepted that, despite a steady increase in the number of studies addressing biological invasions from the early 1970s, the discipline of invasion ecology was only explicitly forged as such during the early 1980s with the support of the Scientific Committee on Problems of the Environment (SCOPE; e.g. Drake *et al.*, 1989; Richardson and Pyšek, 2007, 2008; Simberloff, 2011; Heger *et al.*, 2013). In the wake of the International Conference on Mediterranean-type Ecosystems, hosted in Stellenbosch (South Africa) in 1980, SCOPE commenced a global research initiative on biological invasions in 1982 (Drake *et al.*, 1989; Davis, 2006; Richardson and Pyšek, 2007; Simberloff, 2011). Several national-scale SCOPE reports stemmed from this initiative, starting with MacDonald and Jarman's (1984) study on the invasion of South Africa's fynbos biome and culminating in the global SCOPE synthesis on biological invasions by Drake *et al.* (1989). These studies contributed significantly to the development of the budding discipline of invasion ecology (Davis, 2006; Simberloff, 2011) by formulating and testing hypotheses of biological invasion and comparing invasions in different biogeographical zones (Kueffer and Hirsch Hadorn, 2008). However, although a few ecologists opted for developing an autonomous theoretical basis for invasion ecology, the field had become largely intertwined with themes in conservation and restoration ecology, aligning with the ethos of the SCOPE programme (Davis, 2006; Hobbs and Richardson, 2011).

Around the same time, alien-native congeneric and confamilial studies began to receive more attention in IAP research, comparatively analysing the traits of alien-native pairs to identify traits of invasiveness (Kueffer and Hirsch Hadorn, 2008; Pyšek and Richardson, 2008). Although Baker's (1965) description of the 'ideal weed' is considered to be the first attempt at identifying specific characteristics of problematic plants, this description made "no explicit reference to the status of the species as being native or alien", nor did it establish whether

weeds were equivalent to invaders (Pyšek and Richardson, 2008: 97). Since the 1980s, numerous studies have since undertaken the baffling task of identifying characteristics of the 'ideal invader' (Pyšek and Richardson, 2008). These studies have explored a range of differences between alien-native congeners in terms of reproductive traits (e.g. Richardson *et al.*, 1987; Pantone *et al.*, 1995); anatomical and physiological characteristics, contributing to differences in photosynthesis (e.g. Caldwell *et al.*, 1981; Pammenter *et al.*, 1986), growth (e.g. Caldwell *et al.*, 1981; Callaway and Josselyn, 1992) and nutrient uptake (e.g. Black *et al.*, 1994); growth responses to grazing (e.g. Pyke, 1987) and herbivory (e.g. Caldwell *et al.*, 1981; Richards, 1984; Schierenbeck *et al.*, 1994; Schweitzer and Larson, 1999); morphological plasticity and adaptability to introduced habitats (e.g. Schweitzer and Larson, 1999); and, rates of growth and spread (e.g. Perrins *et al.*, 1993). However, identifying ubiquitous traits of invasiveness amongst multiple plant species (across genera) proved to be a challenging frustration (Alpert *et al.*, 2000), fostering despondence during the early 1990s (Pyšek and Richardson, 2008).

It is speculated that Rejmánek's (1996) paper inspired a rejuvenated effort, sparking a rise in comparative multispecies analyses, made possible by advances in data availability and analysis technology (Pyšek and Richardson, 2008). These analyses have varied in "approach, type of comparison, scale, data character, occurrence measures, and analytical methods used" (Pyšek and Richardson, 2008: 104). Despite their contribution, multispecies studies and meta-analyses continue to struggle to find general traits amongst IAPs (Simberloff *et al.*, 2013), and are often better served in conjunction with robust case-by-case examples of congeneric research (Pyšek and Richardson, 2008).

Building on the concepts of habitat invasibility and species invasiveness, studies in invasion ecology began to advocate and develop more process-based understandings of biological invasions during the 1990s and 2000s (e.g. Vermeiji, 1996; Williamson, 1996), exploring the different phases of invasion in more detail (Kueffer and Hirsch Hadorn, 2008). Around the same time, a philosophical debate emerged in invasion ecology, which questioned the 'alien/native' dichotomy (Kueffer and Hirsch Hadorn, 2008; Hattingh, 2011; Hobbs and Richardson, 2011), with a number of authors likening the distinction between alien and native species to biological xenophobia and criticising the use of militaristic metaphors in invasion ecology literature to describe 'invaders', their impacts and how to 'combat' them (e.g. Larson, 2005; Warren, 2007). The concept of 'barriers', although not new to invasion ecology, has since become increasingly more useful for describing and understanding the processes and phases of biological invasion, while simultaneously offering a means of reframing invaders in biogeographical terms to avoid militaristic and xenophobic associations (e.g. Richardson *et al.*, 2000; Colautti and MacIsaac, 2004).

Until fairly recently, biological invasion research was widely considered to be disconnected from mainstream ecology (Simberloff, 2011). During the 2000s, ecologists began to accrue insights from studying biological invasions, which shed new light on traditional ecological principles and the understanding of ecological community structures, functions, processes and interactions (Kueffer and Hirsch Hadorn, 2008). According to Kumschick *et al.* (2015: 55), authors have recently sought to compile meta-analyses, syntheses and reviews on the “magnitude, scope, and variation of the [ecological] impacts of alien species, as well as their geographic and taxonomic distinctions and biases”. These analyses offer a multifactorial understanding of the complexity and context-dependency of biological invasions (Kueffer and Hirsch Hadorn, 2008) and provide a means of comparing the spatially- and temporally-differential ecological effects and risks of IAS (Vilà *et al.*, 2011; Ricciardi *et al.*, 2013; Kumschick *et al.*, 2015).

Consequently, some studies have shifted away from generalised mathematical models of invasion towards more landscape ecological perspectives (e.g. With, 2002; Theoharides and Dukes, 2007), incorporating Geographical Information Systems (GIS) and spatio-temporal modelling into invasion research (Kueffer and Hirsch Hadorn, 2008). Human-centred explanations of invasion have also become increasingly popular in invasion ecology (Kueffer and Hirsch Hadorn, 2008), focusing on the vectors and pathways of invasion (e.g. Kowarik, 2003; Kowarik and Von der Lippe, 2008), as well as the influence of human land-use patterns and practices on biological invasions (e.g. Hobbs, 2000; Pauchard and Alaback, 2004; Von Holle and Motzkin, 2007).

An emphasis on the negative biological and ecological impacts of IAS pervaded much of the impact-orientated literature on biological invasions during the 1990s and early 2000s (e.g. Lodge, 1993; Gordon, 1998; Brooks *et al.*, 2004). Several authors then started to quantify the economic impacts of IAS during the 2000s, focusing particularly on the impacts of IAPs on ecosystem services (e.g. Pimentel *et al.*, 2000; Turpie *et al.*, 2003; Pimentel *et al.*, 2005; Van Wilgen *et al.*, 2008). Since the mid-2000s, a growing body of literature has begun to explore the benefits and detriments of IAS to rural livelihoods and has made strides in understanding the previously neglected socio-economic implications of IAS (e.g. De Neergaard *et al.*, 2005; McGarry *et al.*, 2005; Shackleton *et al.*, 2007; Shackleton *et al.*, 2011; Semanya *et al.*, 2012; Shackleton *et al.*, 2015a, 2015b). These studies have adopted a more people-orientated focus, providing insights for the management of biological invasions and IAS. More recently, an increasing number of researchers have started to explore biological invasions in urban areas (e.g. Gaertner *et al.*, 2016; Shackleton and Shackleton, 2016; Cavin and Kull, 2017).

Although Elton’s (1958) work received little acknowledgement from his contemporaries, it is now regarded as amongst the most consulted literature in invasion biology and ecology,

inspiring a swell of research over the past twenty-five years, ranging from matters of ecosystem stability and the relationship between biodiversity and habitat invasibility, through theories and mechanisms of IAS dispersal, to the impacts of IAS and the role of disturbance and competition in ecological systems (Richardson and Pyšek, 2008; Simberloff, 2011). Authors have often criticised Elton's (1958) work for its bias towards animal ecology and for driving a wedge between invasion studies and mainstream ecology (e.g. Davis *et al.*, 2001; Davis, 2006). Conversely, Elton's supporters have praised his work for its innovative stance in opening the study of biological invasions to multidisciplinary research (e.g. Richardson and Pyšek, 2007, 2008).

In order to confront contemporary wicked problems, environmental management agendas are increasingly shifting towards more holistic understandings of complex SES (Marshall, 2013; Barney, 2016). As a result, the formerly rigid boundaries within and between academic disciplines, and between academia, civil society and governance structures, have become more permeable and conducive to transdisciplinary knowledge flow (Lang *et al.*, 2012; Cundill *et al.*, 2015). In alignment with Elton's vision, invasion science has recently emerged as a transdisciplinary field, melding the traditional ecological focus of invasion ecology with relevant social science theories and methodologies, economic considerations, indigenous knowledge systems, community perspectives and policy directives (Hulme, 2011; Richardson, 2011; Vaz *et al.*, 2017). Invasion science aims to inform sound decision-making in the management of IAS (Hulme, 2011; Richardson, 2011), with efforts for more holistic and collective research expanding the understanding of complex SES (Cundill *et al.*, 2015; Vaz *et al.*, 2017). However, such efforts have also uncovered numerous conflicts of interest (Van Wilgen and Richardson, 2014) contributing to the growing wickedness of IAS analysis and management (McNeely, 2013; Seastedt, 2015).

1.2. Hypotheses of biological invasion

Several hypotheses have been proposed to explain the complexities of biological invasion since Darwin's (1859) *naturalisation hypothesis*. In general, successful invasions proceed from a transportation and introduction phase to a naturalisation (establishment) phase to a proliferation (spread) phase, overcoming a series of barriers (Richardson *et al.*, 2000; Sakai *et al.*, 2001; Heger and Trepl, 2003; Hufbauer and Torchin, 2008). For the purpose of predicting biological invasions, invasion ecologists attempt to understand how and why IAS are able to surmount these barriers to become invasive by identifying the factors contributing to the success of an invasion (Heger and Trepl, 2003; Hufbauer and Torchin, 2008). The success of an invasion is contingent on multiple factors, including the agent (vector) and pathway of transportation; the propagule pressure, a product of the number of individuals released per introduction event (propagule size) and the number of events (propagule

number); the intrinsic characteristics and capabilities of the invader (invasiveness); and the character of the invaded habitat (invasibility) and its response to the invasion (Heger and Trepl, 2003; Hufbauer and Torchin, 2008; Kowarik and Von der Lippe, 2008; Kueffer and Hirsch Hadorn, 2008; Simberloff, 2009; Pyšek *et al.*, 2012b; Simberloff *et al.*, 2013; Hui *et al.*, 2016). Invasiveness can manifest from a specific combination of biological traits (Hamilton *et al.*, 2005; Pyšek and Richardson, 2008); an inherent superiority (Elton, 1958; Sax and Brown, 2000); an enhanced competitive ability (Blossey and Nötzold, 1995; Callaway and Ridenour, 2004; Blair *et al.*, 2005); and/or a preadaptation to particular biophysical conditions (Baker and Stebbins, 1965; Sax and Brown, 2000). Evidently, this may depend on the biophysical conditions during each phase of the invasion (Vermeiji, 1996; Dietz and Edwards, 2006); the ecology, provenance and eco-evolutionary history of the invader (Drake *et al.*, 1989; Hufbauer and Torchin, 2008); and the history of affiliation between humans and the invader (Keane and Crawley, 2002; Kowarik, 2003; Dietz and Edwards, 2006; Kowarik and Von der Lippe, 2008). On the other hand, the susceptibility of a habitat to invasion (invasibility) depends on the structure and composition of the ecological system (Elton, 1958; Shea and Chesson, 2002); natural and human-induced disturbance (Dietz and Edwards, 2006; Didham *et al.*, 2007); local environmental and historical contingencies, including the spatio-temporal dynamics of the landscape (With, 2002; Theoharides and Dukes, 2007; Henriques-Silva *et al.*, 2015) and the patterns of anthropogenic land use (Pauchard and Alaback, 2004; Von Holle and Motzkin, 2007); and global environmental changes (Mooney and Hobbs, 2000).

Hamilton *et al.* (2005) postulate that different comparison pairs and approaches can be used to address key questions regarding the traits of invader plants, given a regional set of species. Alien-alien pairs compare two or more alien species to determine which traits contribute to the relative invasive success of IAPs, while alien-native comparisons can determine which traits contribute to the IAP species becoming more abundant than native species (Hamilton *et al.*, 2005; Pyšek and Richardson, 2008). More specifically, a comparison between expansive species and invasive species can determine if aliens make more successful 'invaders' than natives (Hamilton *et al.*, 2005; Pyšek and Richardson, 2008). Taking these questions into consideration, Pyšek and Richardson's (2008) meta-analysis identifies "height, vigorous vegetative growth, early and extended flowering, and attractiveness to humans, as traits universally associated with invasiveness in vascular plants" (Pyšek and Richardson, 2008: 112). Identifying the trait-based differences between invaders and non-invaders can therefore attest to the inherent superiority or competitive advantage of invaders.

The *inherent superiority hypothesis* argues that invaders possess some intrinsic quality, which contributes to their dominance in an ecosystem (Elton, 1958; Sax and Brown, 2000; Shea and Chesson, 2002; Hufbauer and Torchin, 2008). Whether superiority is inherent or not, the

success of an invader could be attributed to a specific set of traits, which afford the invader an overall competitive advantage. For example, Rejmánek (1996) found that low seed mass, early maturity and animal dispersal are important traits associated with the invasiveness of woody species. Similarly, Ordoñez *et al.* (2010) found that when comparing individual traits, alien species generally have smaller seeds, larger leaves and lower canopies, and tend to grow more rapidly, obtain reproductive maturity earlier and produce more seeds than native species. The competitive advantages afforded by these superior traits are, however, often spatio-temporally contingent (Shea and Chesson, 2002; El-Barougy *et al.*, 2017). As proposed in the *novel weapons* hypothesis, some invaders are armed with allelopathic traits, novel to the habitat to which they are introduced; however, the effects of these novel weapons may vary depending on the tolerance of the local biotic community and ecosystem (Callaway and Ridenour, 2004; Vivanco *et al.*, 2004; Blair *et al.*, 2005; Hufbauer and Torchin, 2008).

Darwin's (1859) *naturalisation hypothesis* asserts that "competition from species in native genera reduces naturalisation by alien congeners" (Daehler, 2001: 327). Similar notions are echoed in more contemporary hypotheses, emphasising the importance of comparative congeneric studies of species traits and species-ecosystem interactions. For example, the *enemy release hypothesis* argues that IAPs escape their natural enemies (competitors, herbivores, pathogens or parasites) when introduced into new environments, which removes key constraints on the introduced invader population, allowing for naturalisation and proliferation to occur more readily (Darwin, 1859; Shea and Chesson, 2002; Hufbauer and Torchin, 2008; Heger and Jeschke, 2014; Correia *et al.*, 2016). This can also explain why the presence of a native congener inhibits IAPs, because congeners often share natural enemies (Darwin, 1859). Furthermore, the energy reserved for defence against natural enemies can be redirected and repurposed, allowing for the *evolution of increased competitive ability* (see EICA hypothesis; Blossey and Nötzold, 1995; Callaway and Ridenour, 2004; Blair *et al.*, 2005; Hufbauer and Torchin, 2008; Siemann *et al.*, 2017).

Pertaining to the *empty niche hypothesis* (Elton, 1958; Hufbauer and Torchin, 2008), a number of studies have found that IAPs have a competitive advantage because of their ability to discover unutilised (or underutilised) niches by tapping into the resource-base of their invaded habitat more rapidly and effectively than the native species (Bardgett and Wardle, 2010; Simberloff *et al.*, 2013). According to Crawley *et al.* (1996), IAPs occupy and exploit niches at more extreme ends of r- and K-strategies compared to native species. Following the *biotic resistance hypothesis*, ecosystems with higher biodiversity are therefore thought to offer more resistance to invasions than those with lower biodiversity, as more niches are likely to be occupied with increasing levels of species richness (Elton, 1958; Levine *et al.*, 2004; Hufbauer and Torchin, 2008; Yannelli *et al.*, 2017). Consequently, the *maturity concept* suggests that

mature ecosystems are less susceptible to invasion than younger ecosystems, as species richness and community resistance are likely to increase with ecosystem maturity (Shea and Chesson, 2002). On the other hand, the *preadaptation/disturbance hypothesis* posits that some invaders have preadapted to survive and establish in their new habitat (Baker and Stebbins, 1965; Sax and Brown, 2000; Hufbauer and Torchin, 2008), either through an acclimatisation to similar conditions and/or geographical ranges, or through a built-in tolerance (or affinity) for disturbance. Furthermore, areas disturbed by natural processes and/or human activity have lower resistance to invasion and can serve as a nursery for casual invaders to further adapt and acclimatise to local conditions before spreading to less disturbed areas (Dietz and Edwards, 2006).

The hypotheses discussed above are centred on either the invader itself (species-based), the invaded environment (habitat-based) or the relationship between the invader and the invaded environment (Jeschke *et al.*, 2012; Hui *et al.*, 2016), offering predominantly biological, ecological and/or evolutionary explanations (Kowarik, 2003; Hufbauer and Torchin, 2008). Consequently, there remains a scarcity of anthropogenic explanations or human-based hypotheses for biological invasions, with the exception of a few notable studies (e.g. Keane and Crawley, 2002; Kowarik, 2003; Kowarik and Von der Lippe, 2008; Wilson *et al.*, 2009; Tsoar *et al.*, 2011; Horvitz *et al.*, 2017). Kowarik (2003: 293) comments that the “human mediation of biological invasions is still an underestimated phenomenon.” Despite this, humans continue to play a significant role in biological invasions (Richardson *et al.*, 2011).

Humans are widely considered the primary agents or vectors of IAP transportation worldwide, because “. . . species transfer through human agency is much more frequent, efficient and effective than through natural mechanisms and has no parallel in evolutionary history” (Kowarik and Von der Lippe, 2008: 29). Humans play a particularly important role in the dispersal of plant species, overcoming the challenges faced by other vectors during each phase of invasion (Tsoar *et al.*, 2011). Humans facilitate the introduction of species both passively, by strengthening natural dispersal pathways, and actively, by creating and reinforcing new pathways (Wilson *et al.*, 2009).

Following the initial introduction, whether intentional or unintentional, subsequent human-mediated secondary releases have promoted both the naturalisation and proliferation of IAPs by imitating natural population growth processes and by providing effective dispersal pathways for founder populations to escape seclusion, playing a pivotal role in the transition from naturalisation to proliferation (Kowarik, 2003; Kowarik and Von der Lippe, 2008). Moreover, humans facilitate the establishment of introduced plants through cultivation. Mack (2000: 114) dubs cultivation “a *deus ex machina* for plant naturalisation.” In this context, *cultivation* refers to the action of facilitating, nurturing and/or maintaining the conditions

conducive to sustaining the alien plant population, i.e. the care of new arrivals (Mack, 2000; Kowarik, 2003; Wilson *et al.*, 2009).

In alignment with the aforementioned preadaptation/disturbance hypothesis, the *human perturbation hypothesis* suggests that human activity and land use can enhance invasibility by introducing additional disturbances and further weakening the biotic resistance of the habitat (Keane and Crawley, 2002). This gives IAPs with a historical “association with humans and ecosystems modified by humans” (Hufbauer and Torchin, 2008: 83) a particularly significant competitive advantage over native species without these adaptations (Keane and Crawley, 2002). Human-induced global climate change has also become increasingly associated with the exacerbation of biological invasions, influencing the pathways of introduction, facilitating the establishment of emerging invaders and extending the range of existing invaders (Hellmann *et al.*, 2008).

Furthermore, humans unwittingly continue to facilitate invasions through the adoption of poor management practices and inefficient, sometimes counterintuitive, IAP control options. For example, several introduced IAP species in South Africa have escaped from poorly managed and/or abandoned commercial plantations over the past two centuries and have subsequently become invasive in the surrounding grasslands (Carruthers *et al.*, 2011). On the other hand, control measures (mechanical felling and burning) have been found to promote invasions amongst resprouting IAPs (e.g. *Acacia* spp.) when not performed effectively and repeatedly (Lorenzo *et al.*, 2010a; Le Maitre *et al.*, 2011). As a result, management schemes neglecting to rehabilitate and monitor the land post-clearance, usually due to a depletion of economic resources, tend to perpetuate biological invasions by both stimulating the regrowth of IAPs and by disturbing the habitat, leaving it vulnerable to reinvasion (De Neergaard *et al.*, 2005; Witkowski and Garner, 2008; McConnachie *et al.*, 2012). In addition, economic and socio-political constraints continue to preclude the eradication and/or control of some of these species, with the enormous cost of clearance limiting the extent of IAP control (De Neergaard *et al.*, 2005), while conflicting interests hinder the introduction of more radical, more effective control measure, such as biological control (Hoffmann *et al.*, 2011; Dickie *et al.*, 2014).

Although human facilitation is undoubtedly coupled with ecological and evolutionary invasion hypotheses, particularly preadaptation/disturbance, it is more firmly grounded within a social-ecological perspective. It suggests that humans have historically played, and continue to play, a substantial role in facilitating the process of biological invasion (Kowarik, 2003; Kowarik and Von der Lippe, 2008; Richardson *et al.*, 2011). Justifiably, human-related hypotheses of invasion could potentially offer new insights into the process and phenomenon of biological invasion, in turn offering opportunities for the development of more people-orientated control and management strategies.

The fact that the invasiveness, invasion strength and impact of an IAS are species- and context-specific is axiomatic and acknowledged (e.g. Heger and Trepl, 2003; Hufbauer and Torchin, 2008; Heger *et al.*, 2013; Ricciardi *et al.*, 2013; Kumschick *et al.*, 2015). As a result, the identification of ubiquitous traits amongst invaders and the formulation of a universal theory of invasion remain challenging (Alpert *et al.*, 2000; Heger *et al.*, 2013; Simberloff *et al.*, 2013). The lack of standardised terminology in invasion ecology (Richardson *et al.*, 2000; Colautti and MacIsaac, 2004; Shackleton *et al.*, 2007) and inconsistencies in the wording of hypotheses (Heger *et al.*, 2013) introduce additional ambiguity. In response, Jeschke *et al.* (2012) and Heger *et al.* (2013) have recently proposed a dynamic, over-arching *Hierarchy of Hypotheses* framework to integrate and unify current hypotheses, rather than promoting a single universal hypothesis (Heger and Jeschke, 2014). Under this framework, general hypotheses branch into tiered layers of nested and interlinking sub-hypotheses supported by various case-specific empirical examples (Heger *et al.*, 2013).

1.3. Impacts of invasive alien species

The term *impact* has been used rather ambiguously and inconsistently throughout invasion science literature: synonymous with either *change* (*sensu lato*) or detrimental change (*sensu stricto*; Jeschke *et al.*, 2014). In response, a recent paper by Jeschke *et al.* (2014) provides a framework for defining *impact* in terms of four categories, calling for authors to clarify their use of the term within the context of biological invasions.

The first category describes the *directionality* of change within the observed system, i.e. whether the impact represents unidirectional (increasing or decreasing; constructive or destructive; positive or negative; or, beneficial or detrimental) or bidirectional (cost-benefit) change (Jeschke *et al.*, 2014). Consequently, the directionality of change may depend on the next category, which concerns the *classification and measurement* of change. A magnitude-based approach to classification and measurement defines an impact in objective, quantifiable terms, whereas a value-based approach explicitly takes human values and subjectivity into account (Kumschick *et al.*, 2012; Jeschke *et al.*, 2014). For example, a decrease in the abundance of a species is quantifiable (magnitude-based); however, it can be perceived as either beneficial or detrimental, if perceived at all (value-based). Furthermore, the degree of change required to constitute an *impact* should be clarified, whether threshold-dependent or inclusive of any degree of change (Jeschke *et al.*, 2014). In terms of the third category, an impact can be regarded as an *ecological or socio-economic change*, or a combination of the two (Jeschke *et al.*, 2014). Finally, *impact* may be also described in terms of the *scale* category, which encompasses a range of spatio-temporal and taxonomic scales (Jeschke *et al.*, 2014), with different impacts and conflicting perceptions often unearthed at different scales of study (De Wit *et al.*, 2001; Shackleton *et al.*, 2007).

1.3.1. Ecological impacts

Ecologically, the impact of an IAP can be defined as a quantifiable change in the character or functioning of an ecological system, at any ecological and/or biogeographic scale, whether favourable or adverse (Ricciardi *et al.*, 2013). Although the mere introduction of an IAP evokes change (Ricciardi *et al.*, 2013; Malinichi *et al.*, 2017), the frequency and magnitude of change are largely dependent on the degree to which the area has been invaded (Parker *et al.*, 1999; Ricciardi *et al.*, 2013; Kumschick *et al.*, 2015). In an idealised system, barring ecological response and human intervention, Parker *et al.* (1999) postulate that the overall ecological impact (I) of an IAP is equal to the product of its range (R ; in terms of its area of coverage), abundance (A) and per-capita impact (E), i.e. $I = R \times A \times E$. Admittedly, this equation denotes an oversimplified linear relationship, which is most likely not representative of the complexity of biological community interactions found in invaded systems (Parker *et al.*, 1999). While the traits and abundance of the invader are key factors, the character and response of the ecosystem to the invasion also play a significant role in determining the ecological impact (Pyšek *et al.*, 2012b; Simberloff *et al.*, 2013). These in turn depend on the local and historical contingencies of the invaded area (Ricciardi *et al.*, 2013; Kumschick *et al.*, 2015).

It is widely acknowledged that IAS pose one of the greatest threats to ecosystems and biological diversity (e.g. Shackleton *et al.*, 2007; Kannan *et al.*, 2014), cited alongside habitat destruction and fragmentation as a definitive cause of biodiversity decline (Perrings *et al.*, 2005). The invasion of ecosystems by IAPs can contribute to the decrease in local species abundance and richness, altering species composition, community interactions and ecological succession (Reaser *et al.*, 2007; Pyšek *et al.*, 2012b). Some IAPs may even genetically hybridise with related native species at the population level, affecting genetic variation and diversity (Reaser *et al.*, 2007; Vilà *et al.*, 2011; Pyšek *et al.*, 2012b). Furthermore, invasions have been known to fragment habitats, tip trophic balances, alter disturbance regimes and impact on resource availability and flow (Reaser *et al.*, 2007). Disturbance occurs as a natural process and is crucial for moderating community interactions and successional rates and patterns within ecosystems (Meiners and Pickett, 2013), as well as maintaining energy and nutrient flows (Brooks *et al.*, 2004). Invasive alien plants can often capitalise on disturbance, while simultaneously modifying the disturbance regime of the ecosystem (Richardson *et al.*, 2007; Meiners and Pickett, 2013). In this way, disturbance and IAP proliferation can therefore perpetuate in a positive feedback loop (Didham *et al.*, 2005), facilitating subsequent invasions and potentially resulting in an invasional meltdown (Simberloff and Von Holle, 1999).

Fire plays an integral role in shaping many ecosystems and biomes (Pickett and White, 1985; Brooks *et al.*, 2004), while the vegetation structure and abundance of ecosystems reciprocally influences the fire regime, i.e. the extent, frequency and intensity of fire (Mandle *et al.*, 2011).

Many alien plant invasions may alter fire regimes by changing the abundance and composition of the fuel being burnt (Brooks *et al.*, 2004; Keeley *et al.*, 2011). For example, grassy IAPs are relatively low in biomass and promote more frequent fires, whereas woody IAPs are comparatively higher in biomass and tend to promote high intensity fires, though at less frequent intervals (Mandle *et al.*, 2011; Chamier *et al.*, 2012). The fuel properties, such as flammability and moisture content (Brooks *et al.*, 2004), of IAPs also often differ from indigenous plants, therefore impacting on the fire regime (Mandle *et al.*, 2011). While some grassy IAPs are beneficial in the stabilisation of fire regimes (Mack and D'Antonio, 1998), high intensity fires associated with woody IAP invasions may create highly-erodible hydrophobic soil layers (Smith *et al.*, 2011). Following rainfall events, the resulting erosion can be particularly detrimental to riparian environments by increasing the stream sediment load and erosivity, and perpetuating erosion along the watercourse (Chamier *et al.*, 2012).

Globally, riparian ecosystems are increasingly threatened by the accumulation of water-depleting IAPs (Mooney, 2005; Richardson *et al.*, 2007). As a result of the dynamic nature of rivers, coupled with the anthropogenic alterations of watercourses, riparian environments are highly prone to disturbance (Richardson *et al.*, 2007). Although native riparian species tend to be hardy and adapted to such conditions (Richardson *et al.*, 2007), riparian IAP species tend to undergo more rapid growth and evapotranspiration (Malan and Day, 2002; Chamier *et al.*, 2012), consuming larger volumes of water to outcompete and replace the native flora (Chamier *et al.*, 2012). This is because invaders can accumulate more per capita biomass and obtain higher densities faster than native species, contributing to an overall higher consumption of water (Chamier *et al.*, 2012). Streamflow can be significantly reduced as a result of the voluminous consumption of water by IAPs (Enright, 2000; Chamier *et al.*, 2012). This in turn promotes sedimentation and affects the quality of water by decreasing the dilution capacity of the river system, resulting in the concentration of salts, nutrients and other contaminants (Enright, 2000; Chamier *et al.*, 2012). Water quality is further impaired by the accumulation of IAP litter biomass, which not only physically obstructs waterways, but also contributes to the alteration of biochemical and nutrient cycles, which can accelerate eutrophication (Chamier *et al.*, 2012) and impact adversely on both flora and fauna in riparian ecosystems.

The edaphic impacts of IAPs include changes in physical soil structure, soil nutrient and organic matter compositions, soil chemistry, soil ecology (including mycorrhizal interactions), and pedogenic processes (Liao *et al.*, 2008; Fei *et al.*, 2014; Gibbons *et al.*, 2017). These changes vary over space and time and may be constructive or destructive and/or favourable or unfavourable, or bidirectional (Jeschke *et al.*, 2014). Invasive plants can potentially benefit the soil by enhancing aeration and porosity (Raizada *et al.*, 2008); stabilising slopes and

streambanks, reducing soil erosion (Fei *et al.*, 2014); improving nitrogen-fixation, particularly in the case of leguminous invaders (Chamier *et al.*, 2012; Simberloff *et al.*, 2013); increasing nutrient and organic matter levels, therefore increasing soil fertility (Chamier *et al.*, 2012; Simberloff *et al.*, 2013), and enhancing plant performance (Liao *et al.*, 2008; Vilà *et al.*, 2011). On the other hand, these benefits tend to create conditions conducive to the proliferation of the invader and suppression of native species (Chamier *et al.*, 2012). The latter is achieved actively when the invader releases allelochemicals into the soil (Raizada *et al.*, 2008; Gaertner *et al.*, 2014), and passively when mycorrhizal mutualisms weaken as a result of higher concentrations of nutrients (Sanon *et al.*, 2009; Gaertner *et al.*, 2014).

1.3.2. Socio-economic impacts

McNeely (2001) asserts that biological invasions are essentially an anthropogenic issue, arguing that humans are the primary transporters of species across the globe and often facilitate the proliferation of invaders; humans, along with other species in the invaded system, reap the benefits or suffer the consequences of IAS; and, humans have assumed responsibility for mitigating the issue. It can therefore be said that, although biological invasions continue to pose a threat to ecological systems, the previously-mentioned shift towards a more people-orientated understanding of IAS is not unfounded, but rather overdue. According to Kumschick *et al.* (2012: 78), socio-economic impacts are “changes to human health, infrastructure, animal production, agriculture, forestry and human social life . . . negative or positive, depending on whether they decrease or increase human well-being.” The perception of an invasive species and its associated impacts, however, varies over time from person to person, between households, and across different social, economic, cultural and political categorisations (Binimelis *et al.*, 2008; Van Wilgen and Richardson, 2014). Rai *et al.* (2012) found that perceptions and use of invasive plants vary within and between households in rural Nepal, depending on the species, its invasiveness and its usefulness, as well as the proximity of the homestead to the resource and the structure of the household, including the age, gender, education and occupations of household members. For example, women are often the primary collectors and users of these resources, therefore perceive the IAS differently as compared to men (Rai *et al.*, 2012). Although Rai *et al.* (2012) found no significant difference between male and female perceptions of IAS, this was primarily based on the household perceptions as a whole, rather than individual perceptions. The characteristics of the household, particularly the gender of the breadwinner or head of the household, would therefore have a bearing on the overall household perception of the IAS (Rai *et al.*, 2012). Following the broad definition of socio-economic impacts (*sensu* Kumschick *et al.*, 2012) and the categories of impacts (*sensu* Jeschke *et al.*, 2014), the socio-economic impacts of IAS can thus be considered bidirectional, value-based and threshold-dependent,

linked to ecological impacts and variable across different spatial, temporal and taxonomic scales.

Humans are reliant on numerous goods and services provided by ecosystems (Millennium Ecosystem Assessment [MEA], 2003, 2005). As a result, the impacts of IAS (particularly IAPs) on ecological systems often result in, or are coupled with, socio-economic impacts (Vilà *et al.*, 2009; Jeschke *et al.*, 2014). Additional complexity arises when interacting social actors and intertwining social dynamics are also considered, with resource demands and opposing perceptions factoring into the *directionality* and *classification* of impacts when various socio-economic and political agents, stakeholders and institutions clash over the correct management of IAS (Kumschick *et al.*, 2012; Jeschke *et al.*, 2014). Young *et al.* (2010) identifies six types of conflict, including: conflicts over beliefs and values; conflicts over information; and, conflicts over process, as well as structural conflicts; inter-personal conflicts; and, conflicts of interest. Trade-offs are inevitable when dealing with these conflicts (Shackleton *et al.*, 2007; Van Wilgen and Richardson, 2014). In the context of biological invasions, the “extent and density of infestation, availability of alternatives, costs and mechanisms of control, land tenure, current vulnerability, discount rates, and the severity of loss of ecosystem services” will determine the net trade-off (Shackleton *et al.*, 2007: 114).

Ecosystems offer both utilitarian and non-utilitarian value as a range of direct and indirect supporting, provisioning, regulating and cultural goods and services (MEA, 2003, 2005; Charles and Dukes, 2008). *Supporting services* include production and cycling processes (e.g. pedogenesis, primary production, and water and nutrient cycling), which underlie the other ecosystem services (MEA, 2003, 2005). *Provisioning services* are ecosystem goods (food, water, fuel, etc.), whereas *Regulating services*, such as water and climate regulation processes, perform maintenance and quality control to modulate changes within the ecosystem (MEA, 2003, 2005). *Cultural services* are the human-ascribed, nontangible benefits of ecosystems, including the aesthetic, educational, recreational, religious and spiritual values of ecosystems (MEA, 2003, 2005). Invasive plants can either add, enhance, damage or remove many crucial ecosystem goods and services, with resulting ecological and/or socio-economic implications (Shackleton *et al.*, 2007; Binimelis *et al.*, 2008; Van Wilgen *et al.*, 2008). Some of these goods and services are easily quantifiable as a monetary value (Costanza *et al.*, 1997), therefore allowing the impacts of IAPs on these services to be reflected as economic losses or gains (Charles and Dukes, 2008; Jeschke *et al.*, 2014). However, many other services (particularly cultural services) prove to be significantly difficult to quantify accurately and objectively (Charles and Dukes, 2008; Jackson, 2015).

The negative economic impact of biological invasion is reflected in terms of the direct economic losses and damages suffered to ecosystem services and sectors of the economy

on the one hand, and the costs of control, management and mitigation on the other (Pimentel *et al.*, 2000, 2005; Foxcroft *et al.*, 2013). Numerous studies have attempted to quantify the negative economic impact of IAS. Notably, Pimentel *et al.* (2000) estimated the total global economic impact of IAS at US\$ 1.4 trillion per annum (5 % of the global GDP), extrapolated from a total annual cost of US\$ 314 billion across Australia, Brazil, India, South Africa, the United Kingdom and the United States. More than a decade and a half later, attempts at re-examining the global costs have scarcely been made; however, more regional approaches have been attempted. For example, Pimentel *et al.* (2005) estimated that IAS contribute to environmental and economic losses amounting to US\$ 120 billion per annum in the United States. In a recent study, De Lange and Van Wilgen (2010) estimated a total annual economic loss of ZAR 6.5 billion (approximately US\$ 900 million in 2010) in South Africa due to IAPs alone, predicting that this value would approach the ZAR 50 billion mark in the absence of control measures. Despite such efforts to quantify the economic impacts of IAS, it remains challenging to ascribe unbiased monetary values to non-use ecosystem services and losses, which often leads to significantly underestimated valuations of the total economic impact of IAS (Charles and Dukes, 2008; Jackson, 2015).

A few of the impacts of IAPs on supporting, provisioning and regulating ecosystem services have already been discussed in the previous section, including the impacts on soil formation and nutrient cycling (supporting), fresh water supply (provisioning) and water quality (regulating). These impacts have socio-economic implications for agriculture, food security and water security, consequently affecting economies, public health and human well-being (Binimelis *et al.*, 2008).

In South Africa, the impacts of IAPs on national water resources are touted as the most alarming of IAS impacts, because South Africa is a semi-arid country (Van Wilgen and Richardson, 2014). Versfeld *et al.* (1998) and Le Maitre *et al.* (2000) estimated the total volume of water used by IAPs in South Africa (and Lesotho) at 3 300 million m³ per annum, amounting to 6.7 % of the mean annual runoff (MAR), while Van Wilgen *et al.* (2008) estimated that this figure could increase eight-fold if IAPs were to invade to their full extent. Recently, Le Maitre *et al.* (2013) places this measure at 1 444 million m³ per annum, amounting to 2.9 % of the MAR. This apparent decrease is primarily attributed to the use of a more refined model for estimating unit area flow reduction. According to Le Maitre *et al.* (2013), the true reduction volumes are likely to fall between these two estimates. As a country already riddled with water scarcity, IAPs exacerbate the current pressures on water resources, hampering economic development (particularly in the agricultural, industrial and mining sectors) and adversely affecting human well-being by threatening water security, food production and food security

(Chamier *et al.*, 2012; Van Wilgen and Richardson, 2012, 2014; Van Wilgen and Wannenburg, 2016).

Invasive species can also threaten the agricultural and livestock production sectors more directly, with consequences for food production and security. For example, weedy *Chromolaena odorata* and *Lantana camara* invade cultivated lands, reduce soil nutrients and compete with crops or require labour to clear before planting; woody IAPs (e.g. introduced *Acacia* spp.) pose problems for ploughing and impact on grazing resources, reducing carrying capacity and livestock production; and, invasive pests and pathogens attack both crops and livestock (Pimentel *et al.*, 2000; Binggelli, 2001; Shackleton *et al.*, 2007; Van Wilgen *et al.*, 2008; Van Wilgen and Richardson, 2014). Furthermore, some IAP species (e.g. *Lantana camara*, *Leucaena leucocephala* and *Prosopis* spp.) are poisonous to livestock (Binggelli, 2001). As a result, food production suffers losses as an economic sector and livelihood at both the commercial and subsistence scales, compromising both national and local food security, employment and poverty levels, as well as human health (Binimelis *et al.*, 2008).

Coupled with the health impacts resulting from food and water security, as well as from poor water quality and the consumption of poisonous plants, IAPs can further impact on human health by harbouring disease-carrying vectors, such as the *Aedes* and *Anopheles* mosquitos, which transmit the dengue virus and malaria, respectively (Binimelis *et al.*, 2008; Muller *et al.*, 2017). In addition, dense stands of woody IAPs (e.g. *Acacia mearnsii*) have also been reported to restrict access to water, tarnish sacred cultural pools and threaten human safety and security through providing cover for criminals to ambush fuelwood collectors and passers-by in rural communities (Noemdoe, 2001; De Neergaard *et al.*, 2005; Shackleton *et al.*, 2007; Ngorima, 2016).

On the other hand, many introduced alien species (including invaders) have played a historically-instrumental role in the evolution of modern economic sectors and continue to drive commercial industries worldwide, including the agricultural, forestry, ornamental horticulture, livestock production and fishing industries (Pimentel *et al.*, 2000; McNeely, 2001; Pimentel *et al.*, 2005; Van Wilgen and Richardson, 2012, 2014), while rural communities across the developing world continue to rely on IAS as a source of livelihood (Shackleton *et al.*, 2007; Shackleton *et al.*, 2011; Semanya *et al.*, 2012; Richardson *et al.*, 2015; Shackleton *et al.*, 2015b). These species offer key provisioning ecosystem goods and services, namely: food, including major cereals and subsistence crops, wild fruits and vegetables, and livestock and game; timber and fibre for artisanal and construction purposes; tannins for leather tanning; fuelwood, an important energy source for the rural communities of developing countries; livestock fodder; and medicines (Pimentel *et al.*, 2005; Shackleton *et al.*, 2007; Binimelis *et al.*, 2008; Kull *et al.*, 2011; Semanya *et al.*, 2012; Van Wilgen and Richardson, 2012, 2014).

Important regulating and cultural services may also be acquired from these species. For example, carbon sequestration and erosion control in terms of the former, and ornamental and recreational services in terms of the latter (Binimelis *et al.*, 2008; Van Wilgen and Richardson, 2012, 2014). Furthermore, the control of IAS has become an industry in its own right, promoting economic development, providing mass employment opportunities, alleviating poverty and benefiting social well-being; for example, the Working for Water (WFW) programme in South Africa (Van Wilgen and Wannenburg, 2016).

As previously mentioned, the relationship between IAS and the livelihoods of the rural poor is gaining increasingly more attention in biological invasion research, attesting to the utilitarian, cultural and aesthetic significance of IAS in local livelihoods and ethno-ecological value systems (De Neergaard *et al.*, 2005; Shackleton *et al.*, 2007; Shackleton *et al.*, 2011; Semanya *et al.*, 2012; Ngorima, 2016). According to Shackleton *et al.* (2007), IAS can be integrated into the livelihoods of rural communities via one of three possible pathways, either through the community *accepting* the introduced species, with an explicit and defined intent of using it; through the community *switching* from a scarce and/or less favourable native species to a more abundant and/or more favourable IAS; or, through the community merely *tolerating* the IAS, due to either a lack of urgency or agency to control it.

Poor, rural communities adopt a variety of livelihood strategies (Scoones, 1998), often relying directly on a pool of ecosystem goods (including IAS), which offer *daily net* and *safety net* provisions for accommodating day-to-day needs and for cushioning against socio-economic or environmental hardship, respectively (Shackleton and Shackleton, 2004). For example, Semanya *et al.* (2012) found that communities in the Thulamela Municipality (Limpopo) use several IAP species in their daily lives for food (e.g. *Opuntia ficus-indica*, *Psidium guajava* and *Rubus cuneifolius*), fuelwood (*Eucalyptus paniculata* and *Jacaranda mimosifolia*) and medicine (e.g. *Datura stramonium* and *Lantana camara*), as well as for shading, fencing and ornamental purposes. Some of these *daily* and *safety net* provisions can provide security by being sold for additional household income, used as cost-saving alternatives to typical purchases or used in conjunction with purchases to meet rising consumptive demands (Shackleton and Shackleton, 2004). For example, studies on *Opuntia ficus-indica* (prickly pear) in South Africa have found that the fruit is consumed, traded and occasionally sold for additional income generation, or made into a variety of products (including beer, wines, jams and medicines), providing local commercial and subsistence benefits (Shackleton *et al.*, 2007; Shackleton *et al.*, 2011).

However, these livelihood impacts are rarely unequivocally positive, as the costs of an IAS (both ecological and socio-economic) often begin to outweigh its benefits over time (Van Wilgen and Richardson, 2014). Invaders can therefore be categorised according to a

combination of their competitive ability (strongly or weakly competitive) and potential utilitarian value (useful or undesirable), at any time over the course of their presence in their introduced range (Shackleton *et al.*, 2007). Similarly, the impact of an IAS on rural livelihoods can be conceptualised over time in terms of its costs and benefits, the abundance of the species and the vulnerability of the rural community (Shackleton *et al.*, 2007).

For example, several mesquite species (*Prosopis* spp.) offer beneficial commercial and subsistence ecosystem goods (including construction and crafting material, fodder, food, fuelwood, gum, honey and medicines) to rural communities in South Africa (Wise *et al.*, 2012; Shackleton *et al.*, 2015a, 2015b). On the other hand, mesquite species impact negatively on these communities through deleterious impacts on agriculture, biodiversity, infrastructure, and water and grazing resources (Wise *et al.*, 2012; Shackleton *et al.*, 2015a, 2015b). Although Wise *et al.* (2012) found that the overall trade-off between the beneficial and detrimental impacts of mesquite species on the livelihoods of South African farmers is positive, it was posited that this would soon change. More recently, Shackleton *et al.* (2015b) found that this change has in fact transpired and *Prosopis* has become more trouble than it is worth. This can be attributed to the continued rapid proliferation of *Prosopis* despite control efforts, creating ever denser infestations with increasingly detrimental impacts on native vegetation (Shackleton *et al.*, 2015b). Furthermore, Shackleton *et al.* (2015b) notes that the local communities favoured the use of native trees over *Prosopis*, which both contributes to increasing pressures on native trees and diminishes the relative benefits of *Prosopis*. Similarly, the Australian Acacias are a source of significant contention in biological invasion discourse, sparking numerous conflicts in several countries over the management of these invasive trees and shrubs (Kull *et al.*, 2011; Richardson *et al.*, 2011; Zengeya *et al.*, 2017).

1.4. Invasive alien plant management in South Africa

The control and management of IAPs is challenging and riddled with wicked conflicts of interest (Seastedt, 2015). In light of this, sound managerial decisions should be based on informed understanding, which incorporates both scientific and indigenous knowledge, as well as empirical data and social perceptions (Shackleton *et al.*, 2007; Shackleton *et al.*, 2015a). This requires a contextual understanding and pragmatic approach (Heger *et al.*, 2013; Ricciardi *et al.*, 2013), as well as the agency, involvement and cooperation of multiple different stakeholders (Van Wilgen and Richardson, 2014; Shackleton *et al.*, 2015a).

The impacts, use and perceptions of IAPs are context- and species-specific, and should be managed as such (Van Wilgen *et al.*, 2011; Heger *et al.*, 2013; Ricciardi *et al.*, 2013; Latzka *et al.*, 2016). An assessment of the social-ecological interactions at play in the invaded system is therefore crucial and should include a well-versed, context-specific understanding of the

species in question, its biology, ecology, extent and invasiveness; its uses and impacts; the community and different stakeholders afflicted by the infestation; their perceptions of the species, its uses and impacts; the short-, medium- and long-term direct and indirect consequences of potential control measures; and, any potential conflicts of interest (e.g. Shackleton *et al.*, 2007; Pyšek and Richardson, 2008; Young *et al.*, 2010; Castro-Díez *et al.*, 2011; Morris *et al.*, 2011; Van Wilgen *et al.*, 2011; Simberloff *et al.*, 2013; Van Wilgen and Richardson, 2014; Shackleton *et al.*, 2015a; Van Wilgen and Wannenburg, 2016).

Invaders are categorised in terms of their invasiveness and potential usefulness (*sensu* Shackleton *et al.*, 2007). Particularly severe invaders can then be identified, prioritised and targeted for suitable control measures (Van Wilgen and Richardson, 2014). Management objectives should be clearly defined and prioritised accordingly to identify and develop pragmatic control strategies, which in turn, should be prioritised according to their viability, practicality, sustainability and associated trade-offs (Shackleton *et al.*, 2007; Binimelis *et al.*, 2008; Van Wilgen *et al.*, 2011; Van Wilgen and Richardson, 2014)

South Africa is considered a pioneer in the development of proactive, people-orientated programmes and strategies targeted at the control and management of IAPs, and has been praised for melding socio-economic development imperatives with those of conservation agendas (e.g. Hobbs, 2004; Sheppard *et al.*, 2006; Ntshotsho *et al.*, 2015; Van Wilgen and Wannenburg, 2016; Zengeya *et al.*, 2017). However, these initiatives have not been without flaw and have received much criticism (e.g. Van Wilgen *et al.*, 2012a, 2012b; Ntshotsho *et al.*, 2015; Van Wilgen and Wannenburg, 2016). This section provides an overview of IAP management in South Africa by first defining South Africa plant invaders in the context of national legislation, then by outlining general IAP management options and control mechanisms, and finally by homing in on the world-renowned WFW programme and the use of biological control in South Africa.

1.4.1. Legislation

The Conservation of Agricultural Resources Act (CARA), Act No. 43 of 1983 (amended in 2001), served as South Africa's core piece of IAP legislation for just over two decades (Van Wilgen and Richardson, 2012). Under CARA, potentially harmful plant species are categorised into one of three categories (Republic of South Africa [RSA], 1983). Category 1 species are noxious 'declared weeds' with no utilitarian value, which essentially need to be eradicated (RSA, 1983). Category 2 and Category 3 species are defined as 'declared invaders' with potential commercial value and ornamental value, respectively (RSA, 1983). The former may only be planted in managed plantations under permitted conditions, with adventitious populations requiring control or eradication, whereas the latter do not require eradication under

stipulation that no additional individuals are planted and spread is adequately prevented (RSA, 1983). The CARA category of a species may differ according to the geographic location of the population; for example, *A. dealbata* is categorised as a Category 1 species in the Western Cape and a Category 2 species across the rest of the country (RSA, 1983).

In 2004, CARA was replaced by the National Environmental Management: Biodiversity Act (NEMBA), Act No. 10 of 2004 (Van Wilgen and Richardson, 2012). The official *Alien and Invasive Species Regulations* were published a decade later, listing all invasive species, including over 380 IAPs, under four categories (RSA, 2004, 2014a, 2014b). According to the NEMBA classification, Category 1a species are highly invasive and require complete and immediate eradication, whereas Category 1b species are invasive species which require containment and control (RSA, 2014a, 2014b). Category 2 and 3 species largely follow the same classification as CARA, with the stipulation that any Category 2 or 3 species found in riparian zones are treated as Category 1b plants; *A. dealbata* is a Category 2 species under the NEMBA classification (RSA, 2014a, 2014b).

1.4.2. Management options and control mechanisms

In general, IAP management is grounded on three strategies, namely the prevention, eradication and control of biological invasions (Hulme, 2006; Ntshotsho *et al.*, 2015), where prevention involves assessing and minimising the risk of potential emerging invaders; eradication involves the rigorous clearance of all individuals of a IAP population; and control involves curbing the extent and impact of infestation to more manageable levels (Van Wilgen and Richardson, 2014). Although prevention and eradication are the preferred options for early-stage and geographically-restricted IAPs, these options are unfeasible for established invaders and widespread infestations (Van Wilgen *et al.*, 2000). South Africa has adopted several approaches for controlling IAPs, with varying degrees of success depending on the invader species, biogeographical location, degree of infestation and the mechanism of control employed (Van Wilgen *et al.*, 2000, 2012b; Van Wilgen and Richardson, 2014; Ntshotsho *et al.*, 2015). According to Van Wilgen *et al.* (2000), there are three main mechanisms of IAP control, namely: mechanical control, including felling, uprooting and/or burning; chemical control, namely chemical treatment with herbicides or arboricides; and, biological control, the introduction of the invader's natural enemy (e.g. pathogen, parasite or predator).

In South Africa, there is a growing consensus that an integrated approach to IAP management, which combines all three control mechanisms into an adaptive strategy, has the greatest opportunity for success (e.g. Dennill and Donnelly, 1991; Van Wilgen *et al.*, 2000, 2012a, 2012b; Moran *et al.*, 2013; Van Wilgen and Richardson, 2014; Ntshotsho *et al.*, 2015; Van Wilgen and Wannenburg, 2016; Zachariades *et al.*, 2017). This sentiment is echoed and

supported by the Working for Water programme (Moran *et al.*, 2013; Van Wilgen and Wannenburg, 2016).

1.4.3. Working for Water

The Department of Water Affairs and Forestry (DWAFF) introduced the WFW programme in late 1995; however, the management of the WFW programme has since transferred to the Department of Environmental Affairs (DEA; Van Wilgen *et al.*, 2012a). It was launched in response to two wicked problems facing South Africa, namely the ecological impact of IAPs on national water resources and water security, and the staggering prevalence of poverty and unemployment (Turpie *et al.*, 2008; Van Wilgen *et al.*, 2012a; Ntshotsho *et al.*, 2015; Van Wilgen and Wannenburg, 2016). To address these issues, WFW employs poor people in a labour-intensive effort to clear stands of IAPs along densely-invaded waterways, through a combination of mechanical and chemical control mechanisms (De Neergaard *et al.*, 2005). It has been met with significant acclaim worldwide for integrating poverty alleviation with conservation (De Neergaard *et al.*, 2005).

Currently, the majority of WFW's budget is subsidised by the Expanded Public Works Programme (EPWP; Van Wilgen and Wannenburg, 2016). The total annual budget of WFW has grown drastically over two decades of operation, from ZAR 25 million in 1995 to ZAR 1.5 billion in 2015, with most of the funds directed towards paying labourer wages (Van Wilgen and Wannenburg, 2016). Van Wilgen *et al.* (2012a) calculated that approximately a fifth of all WFW funds (1995-2008) were allocated to projects targeting black and silver wattle, amounting to about ZAR 560 million and ZAR 80 million, respectively. The programme has, thus far, cleared over two million hectares of land infested by IAPs, employing about 20 000 rural people per year across 300+ projects nationwide and improving streamflow along infested waterways (De Neergaard *et al.*, 2005; Turpie *et al.*, 2008; Van Wilgen and Wannenburg, 2016). Furthermore, WFW is dedicated to social development through the promotion of gender equality, health and well-being, skills development and education (Turpie *et al.*, 2008). Early successes in job creation have also inspired a number of successful spinoff programmes, namely Working for Ecosystems, Working for Energy, Working on Fire and Working for Wetlands (Van Wilgen *et al.*, 2012a).

For all its successes, WFW is not without its shortcomings and criticisms, as the programme continues to face several challenges. Select species and areas have been prioritised, often without strategic coordination, seemingly on the basis of convenience (Common Ground, 2003; Van Wilgen and Wannenburg, 2016). Van Wilgen *et al.* (2012b) report that WFW projects have often suffered from clearing inefficacy, whereby some wattle sites have required up to nine repeat visits following an initial clearing. In other cases, limited institutional capacity

has constrained the post-clearance monitoring, rehabilitation and follow-up clearance efforts of many WFW projects (De Neergaard *et al.*, 2005). In the absence of rehabilitation, specifically the revegetation of cleared areas with native species, cleared land becomes subject to erosion, degradation and reinvasion, contradicting the aim of the programme (De Neergaard *et al.*, 2005; McConnachie *et al.*, 2012). Coupled with the sheer magnitude of South Africa's IAP problem, ineffective post-clearance maintenance has limited the overall success of the programme, despite exorbitant spending (Van Wilgen and Wannenburg, 2016).

On the socio-economic side, WFW is criticised for its unsustainability and for detracting from other rural livelihoods, creating a community-wide dependence on the programme (De Neergaard *et al.*, 2005). De Neergaard *et al.* (2005) argue that this will inevitably cripple local rural economies when the particular project concludes or debunks due to insufficient funding, ultimately depriving the community of both employment and an important natural resource. Despite the questionable sustainability of WFW projects at the local scale, Turpie *et al.* (2008) contend that WFW is in fact a sustainable national employment initiative due to the magnitude of plant invasions in South Africa. This undoubtedly prioritises maintaining national employment quotas over long-term local well-being and places the two primary directives of WFW at odds with each other, leading critics to speculate that funders have swayed the focus of WFW further away from the goal of IAP eradication and closer towards sustaining employment and alleviating poverty (Turpie *et al.*, 2008; Van Wilgen and Wannenburg, 2016). Biological control is a pertinent example of this.

Working for Water has long advocated the use of biological control to compliment mechanical removal and chemical treatment, investing in the research and deployment of biocontrol agents (Van Wilgen *et al.*, 2012b; Moran *et al.*, 2013; Van Wilgen and Wannenburg, 2016). Despite this, WFW's biocontrol division remains largely underfunded due to assumptions that successful biocontrol will eliminate a vital source of employment for thousands of poor people by rendering labour-intensive mechanical clearance obsolete (Van Wilgen *et al.*, 2012b; Ntshotsho *et al.*, 2015). The full potential of biological control therefore remains unrealised (Impson *et al.*, 2011; Wilson *et al.*, 2011).

1.4.4. Biological control of invasive plants in South Africa

The South African example serves as a comprehensive roadmap for national biological control initiatives worldwide (Sheppard *et al.*, 2006; Wilson *et al.*, 2011; Zachariades *et al.*, 2017). Moran *et al.* (2013) chronicle the long history of weed biological control (WBC) in South Africa, which has been characterised by a farrago of advances, setbacks, successes and failures. Furthermore, throughout its history in South Africa, WBC has been both advocated and opposed by academics, conservationists, forestry industrialists, funders and political

organisations alike (Dennill and Donnelly, 1991; Wilson *et al.*, 2011; Moran *et al.*, 2013; Van Wilgen and Richardson, 2014).

The first biocontrol agent (the cochineal insect: *Dactylopius ceylonicus*) was released in South Africa in 1913, successfully bringing the widespread infestation of invasive *Opuntia monacantha* under control (Moran *et al.*, 2013; Zachariades *et al.*, 2017). During the first half-century of the WBC agenda, South African projects pooled WBC knowledge from research and experiences abroad (Moran *et al.*, 2013). Thereafter, under the auspices of the Department of Agriculture, the Plant Protection Research Institute (PPRI; the precursor to the Agricultural Research Council [ARC]) assembled an in-house team to research, screen, test, deploy and monitor WBC agents (Moran *et al.*, 2013). However, as soon as the PPRI WBC agenda began to gain some apparent momentum in the 1970s and 1980s, preparing to tackle invasive Australian Acacias, it was met with objections from the commercial forestry industry (Dennill and Donnelly, 1991). In response, PPRI proposed the use of host-specific, seed-attacking insects (seed weevils and gall-forming wasps) to reduce the reproductive capacity of commercially-important invasive trees, without damaging the adult plants (Dennill and Donnelly, 1991). Despite this, plantation owners remained wary of the potential impacts of biocontrol, doubting whether consecutive years of tree production could be maintained from a continued reduction in seed production (Dennill and Donnelly, 1991).

After much initial deliberation, the PPRI finally started deploying biocontrol agents (gall wasp *Trichilogaster acaciaeongifoliae* and seed weevil *Melanterius ventralis*) on *Acacia longifolia* during the mid-1980s (Dennill and Donnelly, 1991; Wilson *et al.*, 2011). Subsequent WBC projects were similarly met with conflict, resulting in either the approval of a particular biological agent or the suspension of the project (Dennill and Donnelly, 1991). Biocontrol agents which fail host specificity tests or result in indirect impacts on the adult tree are dismissed for commercially-important species (Hoffmann *et al.*, 2011; Dickie *et al.*, 2014). In spite of the setbacks to WBC in South Africa, 75 biocontrol agents were released on 45 IAP species between 1913 and 2013, of which almost a quarter were completely controlled (Moran *et al.*, 2013). According to Zachariades *et al.* (2017: 2), these numbers have since increased, confirming that “to date, about 93 species of insects, mites and plant pathogens have been established on 59 IAP species”.

Currently, nine taxa have been introduced to control ten of the invasive Australian *Acacia* species in South Africa (Wilson *et al.*, 2011; Zachariades *et al.*, 2017). According to Impson *et al.* (2011), these agents include seed-feeding weevils (*Melanterius* spp.), bud-galling wasps (*Trichilogaster* spp.), flower-galling midges (*Dasineura* spp.) and a pathogenic rust fungus (*Uromycladium tepperianum*). The latter damages or kills the entire plant and is reserved for the commercially-insignificant *A. saligna* species (Impson *et al.*, 2011). Notably, *M. maculatus*

was introduced to control the *A. mearnsii* and *A. dealbata* in 1995 and 1998, respectively; *A. mearnsii* is also attacked by *D. rubiformis*, which was introduced in 2002 (Impson *et al.*, 2011; Wilson *et al.*, 2011). In light of this, South Africa is revered as the first and only country to have successfully planned *and* implemented WBC projects for Australian Acacia species (Impson *et al.*, 2011; Wilson *et al.*, 2013).

Conflicts and setbacks, along with funding deficits and the extra obstacle of bureaucratic red-tape, have limited and slowed the progression of WBC in South Africa ever since the mid-1970s (Dennill and Donnelly, 1991; Van Wilgen *et al.*, 2012b; Moran *et al.*, 2013; Van Wilgen and Richardson, 2014). Despite this, support for biocontrol has grown, especially since the launch of the WFW programme, albeit at an incremental pace (Moran *et al.*, 2013). Although controversial, biological control is arguably the most efficient, effective and sustainable means of IAP control, both financially and practically (Van Wilgen *et al.*, 2012b).

1.5. Rationale

Although much has been learned in the study of biological invasions, it is evident that there are still numerous unexplored avenues for research, with the emergent field of invasion science opening up enticing transdisciplinary opportunities (Hulme, 2011; Richardson, 2011). Research on the biological control of invaders, particularly on highly invasive species such as *A. dealbata*, is especially intriguing and crucial for tackling the wicked problem of biological invasions (Van Wilgen *et al.*, 2012b). Although the deployment of a biocontrol agent on *A. dealbata* is apparently justified considering its highly invasive and ecologically destructive nature, it should proceed with caution due to the integration of the species into the livelihoods of rural communities (De Neergaard *et al.*, 2005; Ngorima, 2016; Zengeya *et al.*, 2017). A better understanding of the social-ecological interactions at play in areas invaded by *A. dealbata* is therefore required to inform decision-making in the management of this contentious species, to synchronise socio-economic development and the needs of rural communities with environmental conservation. This warrants further study and serves as the rationale behind this research thesis.

1.6. Aim, objectives and research questions

This study is the second of two complementary studies contracted by the Agricultural Research Council as part of a broader research endeavour, which sought to understand the effects of IAS invasions on the well-being of poor, rural communities. Ultimately, this will be used to inform policy, which will support or oppose the release of a biological control agent. The first study, conducted by Mr Agripa Ngorima over the 2015/2016 period, consisted of a social survey aimed at gauging the community perceptions of *A. dealbata* invasions in the

Eastern Cape (Ngorima, 2016). This current study sought to understand the nature and extent of the *A. dealbata* invasion through the completion of the following two objectives:

- I. To track the historical changes in the extent and rate of spread of *A. dealbata* invasions.
 - i. Has the extent and distribution of *A. dealbata* changed over time?
 - ii. What is the rate of invasion?
 - iii. How has land-use and cover changed over time?
 - iv. What is the probability of transition between different land cover/use classes?
- II. To determine the growth rate and current abundance of *A. dealbata* in selected locations and landscapes.
 - v. What is the growth and production rate of *A. dealbata*?
 - vi. What is the current density and biomass of the invasion in different landscapes?
 - vii. Is the invasion associated with any specific biophysical conditions?

CHAPTER TWO: RESEARCH APPROACH, STUDY AREAS AND SPECIES

Biological invasions are complex ecological processes and systems, shaped by the spatio-temporal context of the landscape. A spatio-temporal perspective is congruent with the study of systems and landscapes alike. This chapter presents the theoretical and conceptual underpinnings of this thesis, describes the areas and species under study and addresses any potential ethical concerns.

2.1. Concepts and frameworks

This section opens with a definition of the wicked problems concept (introduced in Chapter 1). The SES context is then expanded upon, highlighting the tenets of systems theory and discussing the characteristics of complex adaptive systems (CAS) with reference to the adaptive cycles model, panarchy and the SES framework. Thereafter, the landscape ecological perspective is discussed, highlighting the similarities between landscapes and complex systems, leading to the overall research approach moving forward in this thesis.

2.1.1. Wicked problems

Rittel and Webber (1973) coined the concept of 'wicked problems' to describe a broad set of complex problems, each of which are unique and context-specific, indeterminate in formulation and scope, and symptomatic of other wicked problems (Xiang, 2013). Wicked problems are often value-laden and contentious, provoking conflict between socio-political actors with diverse perspectives and vested interests (Chapin *et al.*, 2008; Seastedt, 2015). Consequently, wicked problems often circumvent resolution, recur and become increasingly tenacious, with each attempted solution temporarily subduing the problem (or sometimes even enhancing it), rather than eliminating it completely (Xiang, 2013). Furthermore, solutions to wicked problem tend to uncover additional concerns and can often become wicked in and of themselves (Seastedt, 2015). This is because the management of wicked problems requires inclusive planning, consensus, adaptive practices and collective action, each of which are riddled with a slew of their own wicked problems and complexities (Rittel and Webber, 1973; Marshall, 2013). Wickedness is therefore inherent in most contemporary social, economic and environmental issues (Chapin *et al.*, 2008; Xiang, 2013); for example, poverty, unemployment, climate change and biological invasions. The systems approach has become increasingly appealing in the analysis and management of wicked problems (Williams and Van't Hof, 2014). Biological invasions are a wicked, social-ecological problem (McNeely, 2013), with the potential to disturb the broader SES (Kannan *et al.*, 2014). In the context of complex SES, "wickedness, the ubiquity of wicked problems, is the norm, and . . . [wickedness] co-evolves with the system" (Xiang, 2013: 2). Accordingly, IAS are increasingly being examined in the

context of CAS and SES to forge a more holistic understanding of the complexities of biological invasions (e.g. Foxcroft, 2004; Sundaram *et al.*, 2012; Kannan *et al.*, 2014).

2.1.2. The social-ecological systems context

A system is an organised, structured assembly of interconnected constituent parts, operating in unison towards a specific objective or function (Meadows, 2008). Systems thinking and the systems approach developed throughout the 20th century in response to the limitations of reductionist science, promoting transdisciplinary research and giving rise to a more holistic understanding of natural and social phenomena (Flood, 2010).

2.1.2.1. Systems theory

Adams *et al.* (2014) recently redefined ‘systems theory’ according to a set of seven interrelated axioms as a means of understanding systems and their properties. The *centrality* axiom deals with the interrelated concepts of emergence (i.e. the manifestation of unique system properties as a result of all system parts and interactions operating together); the hierarchical organisation of elements, interconnections and functions; the communication within and between these hierarchies; and the control of system operation and performance (Adams *et al.*, 2014). This links to the *information* axiom, which asserts that system operation and performance relies on the flow of information within and between parts, subsystems and hierarchies (Adams *et al.*, 2014). The *viability* axiom states that the continued operation and sustainability of the system is largely shaped by a set of constraining parameters and feedback loops, while the *design* axiom argues that systems are often designed as an intentional imbalance of stocks and flows since there are rarely “sufficient resources to satisfy all of the relationships in a systems design” (Adams *et al.*, 2014: 119). The *contextual* axiom focuses on the influence of local external factors on systems, with a holistic view of the system-environment relationship, whereas the *operational* axiom deals with system self-organisation, the context-specific behaviour and *in situ* operation of the system and the equilibrium between systems and their surrounding environments (Adams *et al.*, 2014). Finally, according to the *goal* axiom, system behaviour is intentional and goal-orientated (Adams *et al.*, 2014).

2.1.2.2. Complex adaptive systems and panarchy

Complexity can arise as an emergent property of the self-organisation of relatively simple parts, processes, patterns, interactions or functions within systems (Drake *et al.*, 2007; Meadows, 2008). Drake *et al.* (2007: 162) state that complex systems “self-organise, exhibit nonlinearities, nonequilibrium behaviour, and feedbacks across scales, that, in concert, are expressed in some macroscopic fashion.” Complex systems are dynamic (i.e. evolve over time), progressing along a trajectory contingent on both the local and global environmental context and history of the system and its surroundings (Ingegnoli, 2002, 2011; Adams *et al.*,

2014). Complex systems can therefore evolve from simpler systems via stable intermediaries and construct nested hierarchies of subsystems, while developing higher degrees of self-organisation and self-regulation (Meadows, 2008). Hierarchy theory proposes that these types of systems have a dual structure: a vertical structure of hierarchical levels and a horizontal structure made up of holons (Wu and David, 2002; Farina, 2006). A holon is an assembled unit of interacting parts, which itself forms a part of a greater whole; for example, a subsystem (Wu and David, 2002; Farina, 2006). Consequently, 'intra-hierarchical' interactions and information flows occur within a hierarchical level, while 'inter-hierarchical' interactions and information flows occur between hierarchical levels (Wu and David, 2002; Farina, 2006). Furthermore, complex systems characteristically experience cyclic collapse and renewal, and rely on multiple cross-scale interconnections, feedback loops, delays and oscillations (Foxcroft, 2004; Meadows, 2008; Allen *et al.*, 2014).

A category of complex systems, CAS, are particularly dynamic and highly adaptive to change, with complex interactions and information flows occurring within and between multiple hierarchies and spatio-temporal scales (Rammel *et al.*, 2007). Gunderson and Holling (2002) frame CAS in terms of panarchy, a descriptor of adapting hierarchical systems composed of multiple dynamic, nested subsystems and adaptive cycles. The adaptive cycle model is conceptualised as a stylised Mobius strip composed of four successive system phases (Fig. 2.1), namely exploitation (r), conservation (K), release (Ω) and reorganisation (α), progressing on a continuous rotation (Gunderson and Holling, 2002).

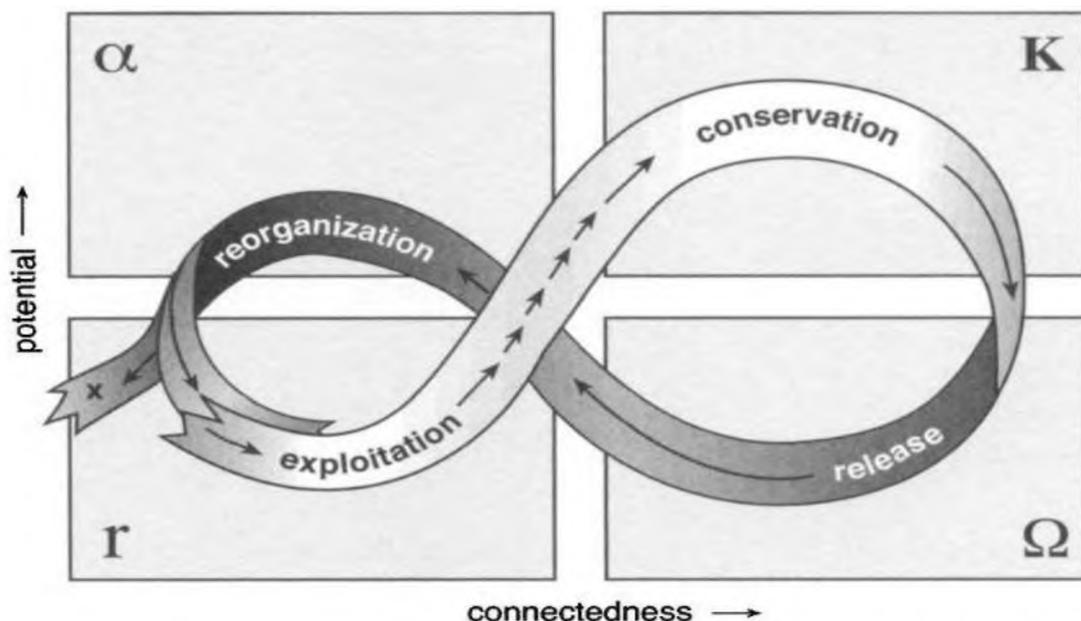


Fig. 2.1: Adaptive cycle of change (from Gunderson and Holling, 2002).

Two-dimensional change is observed along the adaptive cycle (Fig. 2.1), influencing the potential and connectedness of the system (Gunderson and Holling, 2002; Holling, 2004). The

first two phases form the forward loop (logistical growth), where the r phase represents rapid growth or expansion, the K phase represents the more gradual process of accumulation, and both the potential and the connectedness of the system increase (Gunderson and Holling, 2002; Holling, 2004). The next two phases form the back loop (system reorganisation), where the Ω phase, triggered by some disturbance event, relieves accumulated stock and decreases the potential and connectedness of the system, and the α phase regains potential by disconnecting and reorganising the remaining stock to restart the cycle (Gunderson and Holling, 2002; Holling, 2004). A third dimension of change, resilience, builds towards the r phase and declines towards the Ω phase (Gunderson and Holling, 2002; Holling, 2004). Since these adaptive cycles are nested in one another at a multitude of spatio-temporal scales, smaller and faster cycles can affect larger and slower cycles, and *vice versa* (Gunderson and Holling, 2002; Holling, 2004). The former can trigger the initiation of the release phase in the latter (process of revolt), whereas the latter can regulate the renewal of the former (process of remembering), emphasising the role of panarchical (cross-scale, inter-hierarchical) relationships (Fig. 2.2; Gunderson and Holling, 2002; Holling, 2004).

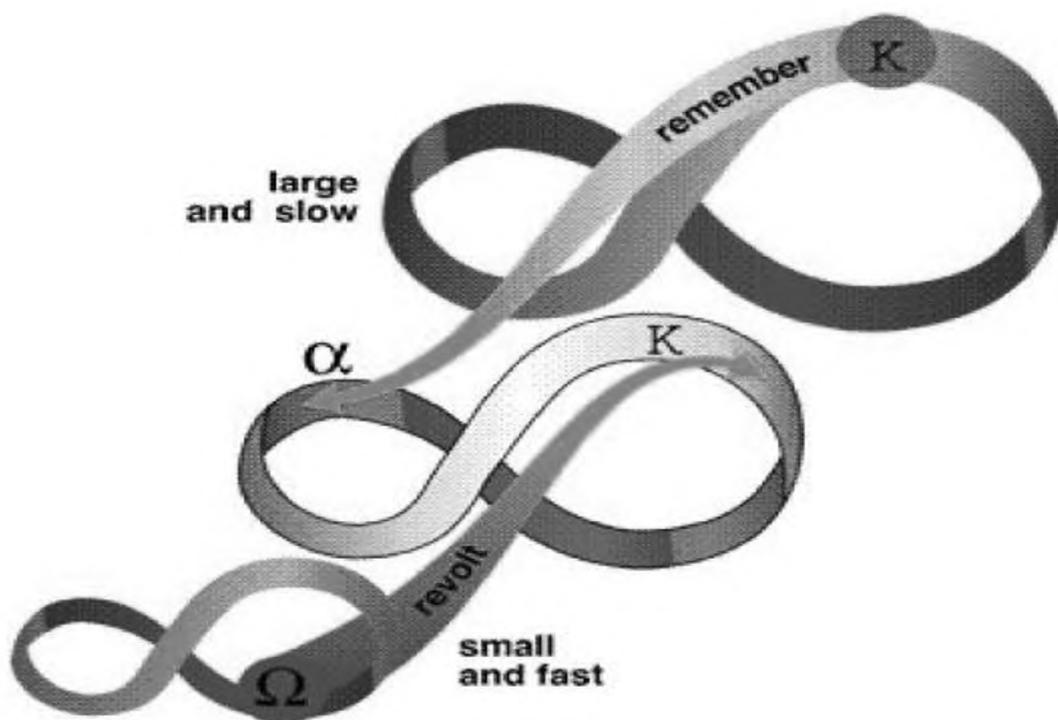


Fig. 2.2: Panarchy (from Gunderson and Holling, 2002).

Although the panarchy framework is derived from the classical model of ecological succession, it has been used more broadly across the analysis and management of complex systems, including SES (Gunderson and Holling, 2002). The social-ecological perspective has become increasingly important in systems thinking (Flood, 2010), playing a particularly important role

in dismantling the human/nature dichotomy (Marcus and Colding, 2011) and building a holistic scientific understanding of human-nature interactions (Glaser *et al.*, 2008).

2.1.2.3. Social-ecological systems

Social-ecological systems are a class of CAS (Marshall, 2013) “. . . in which some of the interdependent relationships among humans are mediated through interactions with biophysical and non-human biological units” (Anderies *et al.*, 2004: 3). These systems are characteristically complex, dynamic, panarchical, nonlinear and unpredictable (Anderies *et al.*, 2004; Folke, 2006; Ostrom, 2009), contributing to the inherent wickedness of these systems (Xiang, 2013). According to McGinnis and Ostrom (2014), a SES consists of multiple nested social and ecological subsystems (holons) and internal variables interacting with one another. McGinnis and Ostrom’s (2014) SES framework (Fig. 2.3) conceptualises the interactions between a set of core subsystem within SES (resource systems, resource units, actors and governance systems) and the outcomes thereof, and identifies key variables for each. This ‘social-ecological’ interface is contextualised in relation to broader social, economic and political settings and related ecosystems (McGinnis and Ostrom, 2014).

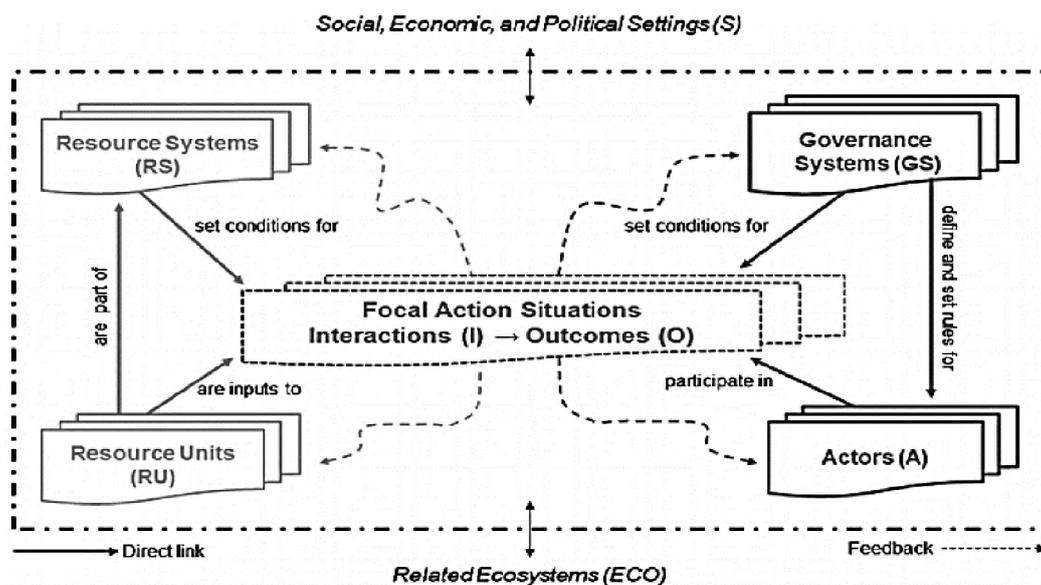


Fig. 2.3: Social-ecological systems framework (from McGinnis and Ostrom, 2014).

The relationship between humans and IAS form a complex and adaptive SES (Foxcroft, 2004; Kannan *et al.*, 2014), exhibiting adaptive cycles of change and panarchy (*sensu* Gunderson and Holling, 2002), as well as various resource-user-governance holons, components, interactions and outcomes (*sensu* McGinnis and Ostrom, 2014). Consider, for instance, a given community dependent on IAPs; for example, rural communities in the Eastern Cape dependent on invasive wattles for several of their livelihood needs (e.g. De Neergaard *et al.*, 2005; Shackleton *et al.*, 2007). Several nested panarchical social, ecological and social-

ecological subsystems (Fig. 2.3), progressing along interdependent adaptive cycles (Fig. 2.1) at various spatio-temporal scales and hierarchies (Fig. 2.2), are nested within the broader SES complex of this system. These may include household-, neighbourhood- and community-level social subsystems, within the broader social, economic and political setting; individual-, population- and community-level ecological subsystems, as well as related ecosystems; and social-ecological subsystems, including resource systems, resource units, users and governance systems.

Previously, the study of biological invasions focused on atomistic, reductionist (predominantly ecological) explanations of invasion systems (Richardson, 2011), resulting in the formulation of largely top-down IAS management strategies (Foxcroft, 2004; Shackleton *et al.*, 2007; Kannan *et al.*, 2014). These ultimately neglected the landscape ecology and social dimensions of these complex SES (Richardson, 2011) and failed to address the problem of IAS. The analysis and management of biological invasions has recently shifted towards more systems-based approaches (including the landscape ecological, CAS and SES approaches), which encourage holistic scientific understanding and emphasise the importance of working with the system, promoting adaptation and integration, improving system memory, building resilience and facilitating self-organisation (Foxcroft, 2004; Richardson, 2011; Kannan *et al.*, 2014).

2.1.3. The landscape ecological perspective

Landscape ecology studies the “relationships between spatial pattern and ecological processes” (Turner and Gardner, 2015: 1). A *landscape* is broadly defined as a spatially heterogeneous area, consisting of an extensive, homogeneous and well-connected background cover (matrix), interspersed with a mosaic of spatial elements (Forman, 1995; Turner and Gardner, 2015). Landscapes are essentially complex systems, appropriately described in terms of the hierarchy theory of system structure (Farina, 2006).

Ingegnoli (2002) frames the complex structure of landscapes in terms of the landscape structural (ecotissue) model (Fig. 2.4). The ecotissue model conceptualises a landscape as a complex, hierarchical structure of layered thematic, spatial and temporal mosaics (Ingegnoli, 2002, 2011). Following the complex systems analogy, a landscape is composed of mosaics (holons), each of which are in turn made up of smaller spatial elements (Ingegnoli, 2002, 2011). According to Ingegnoli (2002, 2011), the smallest (indivisible) element of a landscape is the *tessera*, a relatively homogenous area in terms of a specific attribute (e.g. a specific vegetation, geology, land use type), while a thematic mosaic is a localised assembly of heterogeneous tesserae of a specific theme (e.g. vegetation, geology, land use, etc.). Superimposed thematic mosaics produce a multidimensional mosaic at the local scale, representing a holon of combined biotic and abiotic structural and functional characteristics

(Ingegnoli, 2002, 2011). In this context, an *ecotope* can be described as the smallest multidimensional landscape element, composed of two or more superimposed tesserae of different local thematic layers (Ingegnoli, 2002, 2011). The local-scale multidimensional mosaic is contextualised temporally in relation to past and future local-scale multidimensional mosaics, and contextualised spatio-temporally in relation to the past, present and future of the broader landscape system (or *ecotissue*), as well as the broader regional scale (Ingegnoli, 2002, 2011).

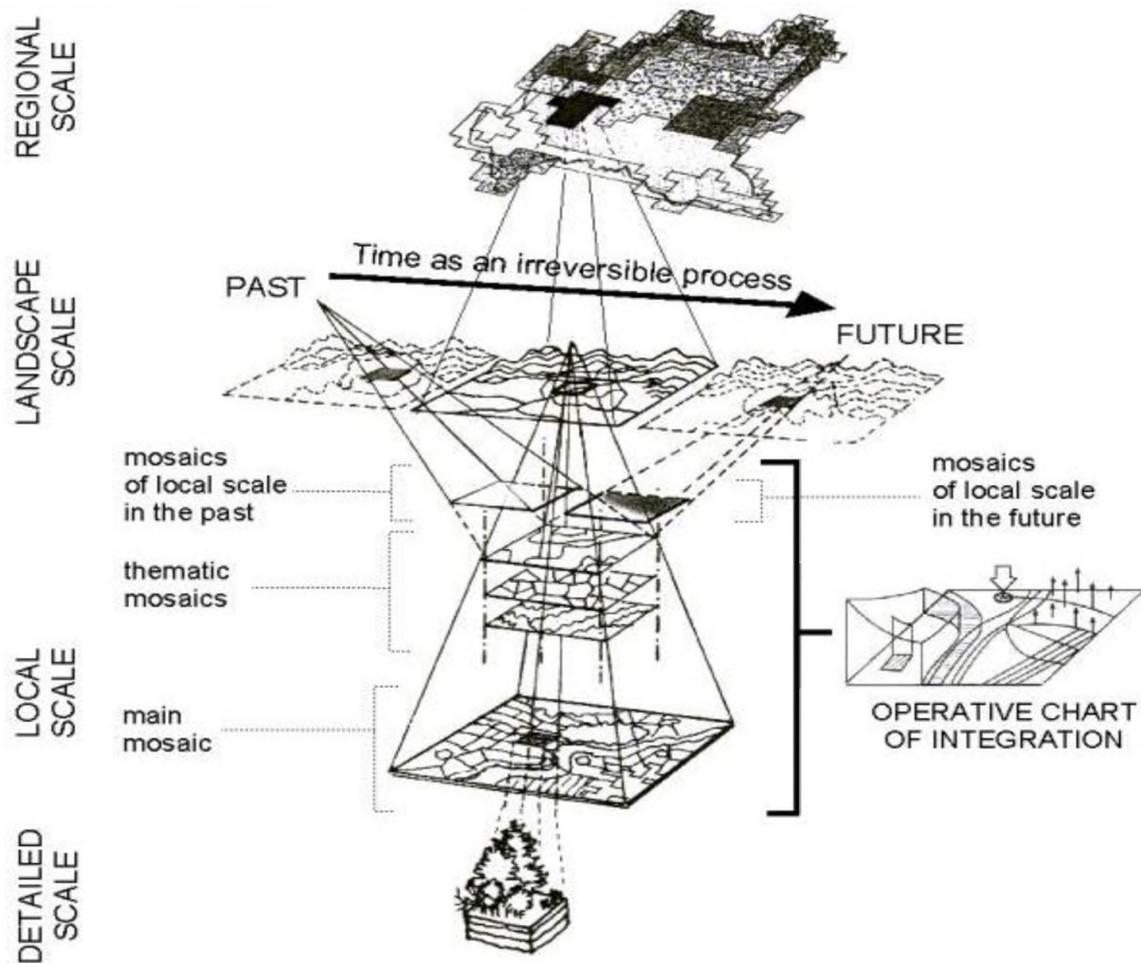


Fig. 2.4: The landscape structural (ecotissue) model (from Ingegnoli, 2002).

Landscape patterns emerge from the composition, configuration and connectivity of spatial elements (and holons) at a range of spatio-temporal scales (Forman, 1995; Turner and Gardner, 2015). The scale of a landscape therefore varies, both spatially and temporally, according to the specific factors, processes or phenomena under study (Turner, 1989; With, 2002; Turner and Gardner, 2015). Consequently, landscapes can consist of a number of nested landscapes of interest to the landscape ecologist (Turner, 1989; Farina, 2006; Turner and Gardner, 2015). Although Ingegnoli's (2002) ecotissue model adopts the traditional view of a landscape as a broad geographical scale and order of ecological hierarchy (an

intermediary between ecosystem and biome), it still proves useful for illustrating the multidimensional, spatio-temporal complexity of landscapes, regardless of an arbitrarily large (and anthropocentric) interpretation of scale. Landscape ecology requires an understanding of the spatio-temporal contingencies of ecological processes within the framework of dynamic, multidimensional landscapes (Turner and Gardner, 2015). According to With (2002: 1194), “a landscape ecological perspective on invasive spread thus involves understanding how the spatial distribution of resources, populations, or habitat at any scale affects various stages of the invasion process.”

2.1.4. Research approach

In terms of the analysis and management of IAS, the paradigm shift from a “classical mindset of eradication to that of adaptation . . . is nested in the social-ecological systems framework of inexorable two-way links between ecological stock and flows and social outcomes and actions, from a landscape governance scale down to household level livelihoods” (Kannan et al., 2014: 663-664). This quote aptly advocates the concepts and frameworks discussed in this chapter and informs the overall research approach moving forward in this thesis. A systems-based, spatio-temporal landscape perspective was adopted throughout the study, acknowledging that human-IAS systems are inherently wicked, complex, adaptive SES, shaped by the spatio-temporal context of the landscape. A spatio-temporal landscape perspective offers a better understanding of the behaviour of systems, in this case providing a means of analysing and managing human-IAS systems in attempt to curtail the wicked problem of biological invasions.

2.2. Study areas

The invasion of *A. dealbata* in the northern Eastern Cape was studied across three broad study areas, namely the Matatiele, Mount Fletcher and Maclear areas. These areas, known to be invaded by *A. dealbata*, were selected based on supporting evidence of the use of *A. dealbata* by local communities (Ngorima, 2016). Three villages were selected for each of the three main study areas, encompassing the villages surveyed by Ngorima (2016) and their surrounding *A. dealbata* harvest zones, determined to be within three kilometres of the village boundaries. This section provides a brief description of the Eastern Cape and then hones in on the areas under study in this thesis.

2.2.1. Eastern Cape

The Eastern Cape was established as a province following the abolition of apartheid in 1994, merging the eastern section of the former Cape Province with the former Transkei and Ciskei homelands (Makiwane and Chimere-Dan, 2010; Hamann and Tuinder, 2012). The Eastern Cape is the third most populated of South Africa’s nine provinces, with a population of approximately 6.5 million (12.7 % of South Africa’s total population), nearly 1.7 million

households, according to the 2011 National Census (Statistics South Africa, 2012, 2014). The majority of the population are IsiXhosa speakers (Makiwane and Chimere-Dan, 2010). Socio-economically, the Eastern Cape is plagued by persistent, widespread, race-based inequality, income disparity, poverty and unemployment, as well as a high household dependency ratio, a prevalence of female-headed households, poor education and inadequate economic growth, owing to the enduring legacy of the apartheid regime (Makiwane and Chimere-Dan, 2010; Hamann and Tuinder, 2012). In addition, infrastructure development and service delivery remain poor in many parts of the Eastern Cape, particularly in the rural areas (Makiwane and Chimere-Dan, 2010).

The Eastern Cape is the second largest of South Africa's nine provinces, occupying an area of 168 966 km², 13.8 % of South Africa's total land area (Statistics South Africa, 2012, 2014). Topographically, the Eastern Cape features the Drakensberg, extending southwards from Lesotho into the northern parts of the province; the Amathole mountains, making up the central interior; the Sneeuberge, found in the west; and the Cape Fold mountains, reaching across the south from the Western Cape to Port Elizabeth (Hamann and Tuinder, 2012). Situated in the southeastern part of the country, the Eastern Cape experiences bimodal rainfall, receiving summer rainfall in the subtropical northern, eastern and coastal belt regions; all year rainfall along the temperate southern coast; and winter rainfall in the semi-arid western and central regions, with snowfall common at high altitudes (Hamann and Tuinder, 2012).

With the exception of the Desert biome, all of the South African vegetation biomes are found in the Eastern Cape (Hamann and Tuinder, 2012). Grassland dominates across most of the north and central interior, while the Savanna occupies a broad belt along the escarpment, with the narrow Indian Ocean Coastal Belt (predominately forest cover, with interspersed grassland) found along the eastern coast (Mucina and Rutherford, 2006). The Nama Karoo makes up most of the western region, separated from the Fynbos biome, occurring along the temperate southern coast, by a narrow band of the Succulent Karoo in the southwest (Mucina and Rutherford, 2006). Albany thickets extend from the southwest interior across to the southeastern coast, while the Forest biome is interspersed between Fynbos and thickets along the south and southeastern coasts, respectively (Mucina and Rutherford, 2006). In addition, the Eastern Cape supports parts of two global biodiversity hotspots, namely the Cape Fynbos hotspot and the Maputaland-Pondoland-Albany hotspot (Hamann and Tuinder, 2012).

According to Hamann and Tuinder (2012), the Eastern Cape only contributes seven percent to South Africa's total GDP (Hamann and Tuinder, 2012). In the absence of a mining industry, the primary sector in the Eastern Cape relies heavily on agriculture and forestry (Hamann and Tuinder, 2012). Subtropical zones are characterised by C4 grasses, suited to cattle and sheep farming, whereas the semi-arid zones are characterised by C3 grasses and shrubs, suited for

sheep and goat farming. The dominant land use in the Eastern Cape is grazing (Hamann and Tuinder, 2012). The Eastern Cape suffers from some of the worst land degradation in the country, with overgrazing and plant invasions common in grasslands and the Albany thickets (Hamann and Tuinder, 2012). Furthermore, riparian ecosystems are becoming increasingly threatened as a result of IAPs (Hamann and Tuinder, 2012).

2.2.2. Study areas and villages

The Matatiele local municipality falls within the broader jurisdiction of the Alfred Nzo district municipality and borders KwaZulu-Natal and Lesotho (Statistics South Africa, 2014). It covers an area of about 4 352 km², with 49 527 households and a total population of 203 843 people (Statistics South Africa, 2012, 2014). The Matatiele study area (30.3453° S, 28.8038° E) is situated approximately 20 km from Lesotho's southern frontier, on the foothills of the Drakensberg (Fig. 2.5; Ngorima, 2016). Nkasela (30.2054° S, 28.7727° E), Outspan (30.2404° S 28.8394° E) and Caba (30.3579° S 28.6622° E) were chosen as the villages for the Matatiele area (Fig. 2.5).

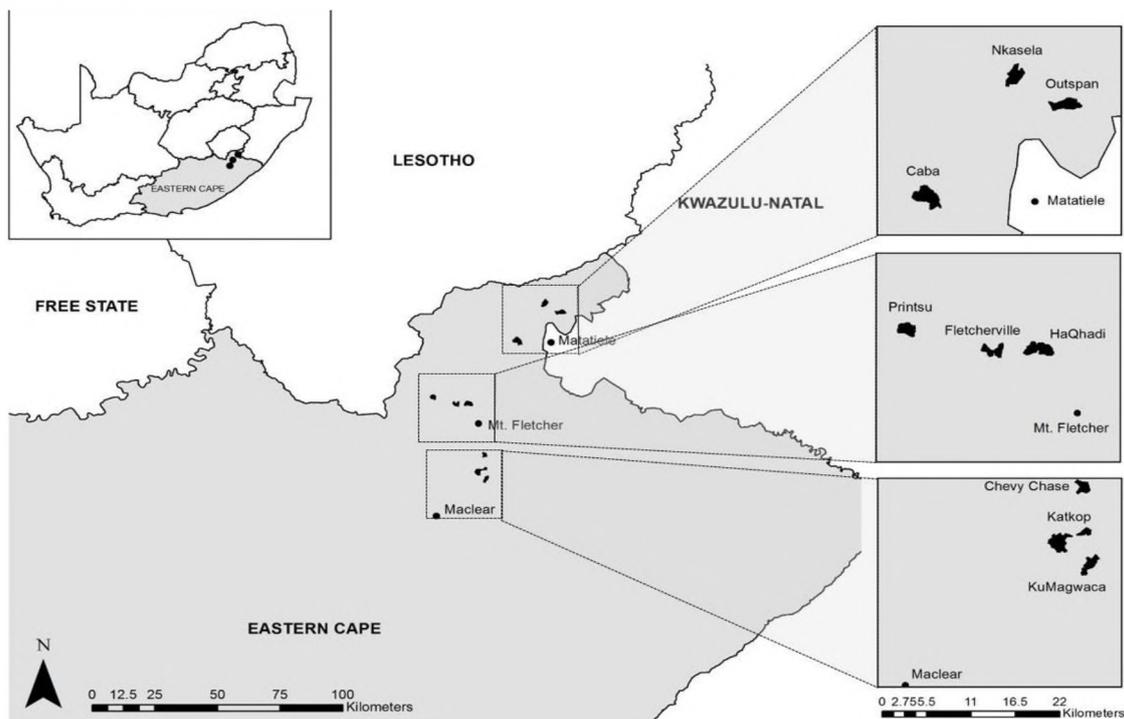


Fig. 2.5: Study areas and villages in the northern Eastern Cape, South Africa.

On the other hand, the Mount Fletcher and Maclear study areas fall within the Elundini local municipality, which in turn falls under the jurisdiction of the Joe Gqabi district municipality (Statistics South Africa, 2014). The Elundini local municipality covers an approximate area of 5 065 km², with 37 854 households and a total population of 138 141 people (Statistics South Africa, 2012, 2014). The Mount Fletcher area (30.6888° S, 28.5062° E) is found around 50 km southwest of Matatiele and around 50 km north-northeast of Maclear, with the following

villages under study: Printsu (30.5873° S, 28.3148° E), Fletcherville (30.6139° S, 28.4116° E) and HaQhadi (30.6121° S, 28.4627° E; Fig. 2.5). The Maclear area (30.8834° S, 28.5116° E) is located south of Mount Fletcher, roughly halfway between Mount Fletcher and Maclear (Fig. 2.5). The villages selected for the Maclear area include Chevy Chase (30.8168° S, 28.5331° E), Katkop (30.8834° S, 28.5116° E) and KuMagwaca (30.9134° S, 28.5404° E; Fig. 2.5). Demographic statistics for the local municipalities and villages are summarised in Table 2.1.

Table 2.1: Demographic statistics for local municipalities and villages: Nkasela (Nka); Outspan (Out); Caba (Cab); Printsu (Pri); Fletcherville (Fle); HaQhadi (HaQ); Chevy Chase (Che); Katkop (Kat); and KuMagwaca (KuM) (compiled from 2011 National Census data: Statistics South Africa, 2011).

Local municipality	Matatiele			Elundini					
Area (km ²)	4 352			5 065					
Total population	203 843			138 141					
Growth rate 2001–2011 (%)	0.46			0.05					
Female (%)	54			53					
Male (%)	46			47					
Number of households	49 527			37 854					
Population density (persons.km ²)	47			27					
Dependency (%)	83			77					
Unemployment (%)	39			44					
Study area	Matatiele			Mount Fletcher			Maclear		
Village	Nka	Out	Cab	Pri	Fle	HaQ	Che	Kat	KuM
Area (km ²)	3.47	3.86	5.67	2.34	1.97	3.65	1.63	4.15	1.94
Total population	997	1 761	3 686	351	443	946	292	577	367
Number of households	237	459	876	105	7	5	77	168	99
Population density (pop.km ⁻²)	287	311	956	150	224	259	180	139	189
Education									
No schooling (%)	5	4	5	5	12	2	12	19	28
Some primary (%)	38	25	18	33	30	20	40	32	23
Primary (%)	9	8	8	5	10	9	10	7	5
Some secondary (%)	35	46	49	40	36	34	30	21	27
Matric (%)	12	12	14	14	8	32	7	13	16
Higher education (%)	2	5	6	3	5	2	2	9	1
Energy									
Cooking									
Electricity (%)	56	45	77	0	0	0	0	0	0
Wood (%)	39	36	6	48	33	100	78	55	74
Other (%)	5	19	17	52	67	0	22	45	26
Heating									
Electricity (%)	61	12	9	0	0	0	0	0	0
Wood (%)	35	61	33	95	67	75	100	54	51
Other (%)	4	27	58	5	33	25	0	46	49
Lighting									
Electricity (%)	61	12	9	0	0	0	0	0	0
Other (%)	39	88	91	100	100	100	100	100	100

The three main study areas fall largely within the East Griqualand Grassland (Gs 12) vegetation unit of the Sub-Escarpment Grassland bioregion (Mucina and Rutherford, 2006).

This type of vegetation is found on hilly terrain, dominated by Highland Sourveld and Dohne Sourveld (Acocks, 1953), at an altitudinal range of 920–1 740 m above sea-level (Mucina and Rutherford, 2006). The geology includes mudstone and sandstone from the Beaufort Group, as well as sedimentary rock from the Molteno, Elliot and Clarens formations (Mucina and Rutherford, 2006). Soils are well-drained, 500–800 mm deep and prone to erosion on steeper slopes (Mucina and Rutherford, 2006). The region receives summer rainfall and winter snowfall (at high altitudes), with approximately 30 days of frost per year (Mucina and Rutherford, 2006). According to Mucina and Rutherford (2006), Gs 12 has a mean annual precipitation (MAP) of 780 mm (ranging between 620 and 816 mm) and a mean annual temperature (MAT) of 14.7 °C (ranging between 12.9 and 15.6 °C). Approximately one-quarter of the East Griqualand Grassland has been transformed for maize production, plantations and urban development, while natural areas are becoming increasingly overgrazed and invaded by *A. mearnsii* and *A. dealbata* (Mucina and Rutherford, 2006). However, despite being considered vulnerable, it remains insufficiently conserved (Mucina and Rutherford, 2006).

2.3. Study species

Acacias are a particularly wicked problem, stirring contention within and between numerous academic, conservation, cultural, political and socio-economic circles. This section presents the case of introduced Australian Acacias (wattles) in South Africa, leading into an in-depth profile of the species under study in this thesis (*A. dealbata*) in terms of its biological characteristics, ecology and range. Thereafter, the significance of *A. dealbata* is briefly described in relation to its status as a highly invasive, yet useful, species in South Africa.

2.3.1. Australian Acacias

Taxonomically, *Acacia* Mill. was first described in *The Gardeners' Dictionary* by Phillip Miller (1754). Recent phylogenetic discoveries have, however, confirmed that the genus *Acacia* (in the traditional sense) is a polyphyletic assemblage; accordingly, the five clades of *Acacia* (*sensu lato*) have been reclassified into five corresponding genera (Murphy *et al.*, 2010; Brown *et al.*, 2011; Miller *et al.*, 2011; Thiele *et al.*, 2011). In increasing species number per genus, these are: *Mariosousa*; *Acaciella*; *Vachellia*; *Senegalia*; and *Acacia* (*sensu stricto*; formerly the subgenus *Phyllodineae*), which was controversially re-typified on *Acacia penninervis* (Miller *et al.*, 2011; Thiele *et al.*, 2011). The genus *Acacia* is a member of the subfamily Mimosoideae (previously the Mimosaceae family), which in turn belongs to the legume family Fabaceae (Leguminosae; Murphy *et al.*, 2010; Miller *et al.*, 2011).

The journal *Diversity and Distributions* recently published an entire issue of multi-authored, multidisciplinary articles dedicated to the Australian Acacias (wattles) as IAS, attesting to the importance of the group in invasion science research (Richardson *et al.*, 2011). The issue

defines the 'Australian Acacias' as a group of about 1 012 *Acacia* (*sensu stricto*) species native to Australia, of which hundreds have been introduced to various parts of the world and 23 are known invaders (Miller *et al.*, 2011; Richardson *et al.*, 2011); 24 according to recent updates (Rejmánek and Richardson, 2013; Richardson *et al.*, 2015; Souza-Alonso *et al.*, 2017). A sizeable and diverse group, the Australian Acacias have an array of context- and species-specific introduction histories, uses and impacts, and have thus been perceived and managed differently worldwide (Kull *et al.*, 2011; Richardson *et al.*, 2011; Souza-Alonso *et al.*, 2017). The opportunity for study is therefore abundant, with numerous potential avenues for inquiry and lessons to be learned for the management of IAPs in general (Kull *et al.*, 2011; Richardson *et al.*, 2011; Richardson *et al.*, 2015). In this regard, the case of Australian Acacias in South Africa is especially enticing, offering ample opportunity for study (Carruthers *et al.*, 2011; Le Roux *et al.*, 2011).

Several studies have chronicled the historical introduction of Australian *Acacia* species into South Africa (Le Roux *et al.*, 2011; Richardson *et al.*, 2011). Since the early 1800s, approximately 80 species of Australian *Acacia* have been intentionally introduced and re-introduced into South Africa (Richardson *et al.*, 2015) for commercial forestry (tannin, timber and pulp production), dune stabilisation and ornamental purposes, as well as for local fuelwood uses by indigenous communities (De Wit *et al.*, 2001; Binimelis *et al.*, 2008; Carruthers *et al.*, 2011; Le Roux *et al.*, 2011; Richardson *et al.*, 2011; Zengeya *et al.*, 2017). Australian Acacias inhabit a broad native range and dominate in several diverse habitat types across Australia, faring relatively well in some of the harshest of settings, including hyper-arid, nutrient-deprived and/or disturbance-prone environments (Morris *et al.*, 2011; Richardson *et al.*, 2011). Biogeographically, southern Africa has the highest concentration of invasive Australian *Acacia* species outside of their native range (15 of the 24 species; Richardson *et al.*, 2011; Richardson and Rejmánek, 2011), a few of which are considered to be some of South Africa's most invasive species by infestation range (Le Roux *et al.*, 2011).

In support of the previously-discussed hypotheses of invasion, Morris *et al.* (2011) attribute the success of Australian Acacias to their overall competitive advantage over native species, afforded by superior traits and novel weapons, as well as by their evolved and preadapted tolerance to harsh conditions and disturbance. Invasive Australian Acacias possess the ability to out-grow and out-compete native species by accumulating height and biomass more rapidly, and by acquiring and consuming resources more efficiently, than the native species (Morris *et al.*, 2011). As a result, Australian Acacias are able to produce large, resilient seedbanks of nutrient-rich, fast-germinating seeds (Morris *et al.*, 2011). Coupled with their long lifespan, this contributes to the persistence of Australian Acacias in invaded environments, while for some, their allelopathic properties inhibit native vegetation growth

(Morris *et al.*, 2011). Bioclimatic parallels between Australia and South Africa are suspected to further facilitate the ease of invasion of Australian Acacias in South Africa (Richardson *et al.*, 2011).

The perceptions surrounding Australian Acacias in South Africa have become particularly polarised, pitting commercial industry and socio-economic development against conservation initiatives and environmental sustainability (Shackleton *et al.*, 2007; Carruthers *et al.*, 2011; Griffin *et al.*, 2011; Kull *et al.*, 2011; Van Wilgen *et al.*, 2011; Van Wilgen and Richardson, 2014). For example, it is estimated that South Africa's major Australian Acacia plantations contribute approximately US\$ 185 million and US\$ 130 per year in pulpwood and tannin production, respectively (Griffin *et al.*, 2011). In contrast, invasive Australian Acacias impact extensively on natural resources in South Africa, costing over ZAR 4 billion per year (over US\$ 500 million in 2010; De Lange and Van Wilgen, 2010; Van Wilgen *et al.*, 2011). At the local-level, the perceptions of rural communities can be similarly divisive, with invasive Australian Acacias providing crucial natural resources and livelihood sources, while simultaneously impacting on the access to and/or quality of other natural resources (Shackleton *et al.*, 2007; Binimelis *et al.*, 2008; Kull *et al.*, 2011; Kumschick *et al.*, 2012).

2.3.2. Study species: *Acacia dealbata* Link. (silver wattle)

Acacia dealbata was first described during the early 19th century by German botanist Heinrich Friedrich Link (1822). Expanding on the work of Murphy *et al.* (2010), Miller *et al.* (2011) identified five clades within the revised genus *Acacia*, namely the *A. victoriae* and *A. pyrifolia* clade; the Puchelloidea clade; the *A. murrayana* clade; the melanoxyton clade; and, the mearnsii clade. The latter of which includes two of South Africa's most invasive plant species, the closely related black and silver wattles, *A. mearnsii* and *A. dealbata*, respectively (Henderson, 2007; Miller *et al.*, 2011). Lorenzo *et al.* (2010a) attribute the invasiveness of *A. dealbata* to propagule pressure, its superior biological traits and an evolved enhanced competitive ability, the product of the following: its introduction life history; its preadaptation to disturbance and adaptability to change; its phenotypic plasticity and geographical range; vegetative reproduction; and, its novel allelopathic weapons.

2.3.2.1. Characteristics, ecology and range

Acacia dealbata is a phanerophyte (Sheppard *et al.*, 2006), woody perennials (trees or shrubs) with above-ground stems (Raunkiær, 1904). According to Souza-Alonso *et al.* (2014a: 1052), the patterns of growth of *A. dealbata* may differ from "separated individuals" in their native range to "intricate mazes" of dense monoculture in their invaded range. *Acacia dealbata* can generally be described as a monoecious, evergreen tree of small to medium size (Van Wyk and Van Wyk, 2013) in terms of its height (2-35 m), crown size (up to 10 m) and trunk diameter

(5-75 cm; Searle, 1997). The bark is smooth in texture and the branchlets are commonly ridged (Searle, 1997; Van Wyk and Van Wyk, 2013). Both the foliage and bark of the tree appear distinctively grey or silver in colour, hence the common name silver wattle (Searle, 1997; Van Wyk and Van Wyk, 2013). Its bipinnately compound leaves (2.5–25 cm x 4–10 cm) consist of 8–25 pinna pairs, with a gland present on the adaxial side of the rachis (2–12 cm in length) at the junction of each pinna pair (Searle, 1997; Van Wyk and Van Wyk, 2013). Each of the pinnae have 17–50 close-set or overlapping pairs of pinnules, which are 2–6 mm long and 0.4–0.7 mm wide (Searle, 1997; Van Wyk and Van Wyk, 2013).

Typical of leguminous species, *A. dealbata* forms a symbiotic relationship with nitrogen-fixing bacteria in its root nodules (De Neergaard *et al.*, 2005). Australian Acacias generally form associations with the genus *Bradyrhizodium* (Rodríguez-Echeverría *et al.*, 2011; Souza-Alonso *et al.*, 2015). This property allows *A. dealbata* to rapidly and efficiently accumulate and fix available nitrogen in the soil (May and Attiwill, 2003; Lorenzo *et al.*, 2010a). Furthermore, *A. dealbata* can increase its own competitive ability while simultaneously deterring the growth of competing vegetation by manipulating the physical properties of the soil, altering the soil nitrogen and carbon levels, and releasing allelopathic chemicals (Lorenzo *et al.*, 2010a). *Acacia dealbata* possess numerous secondary compounds, several of which are potential novel weapons with inhibitory or phytotoxic allelopathic effects (Lorenzo *et al.*, 2010a).

The inflorescence of *A. dealbata* is an axillary raceme or panicle (branched raceme), borne on a short, pubescent peduncle (Searle, 1997; Van Wyk and Van Wyk, 2013). Each raceme bears around 3–10 globose floral heads (5–10 mm in diameter), with each head composed of a dense cluster of about 20–40 small, bright-yellow, 5-partite florets (Searle, 1997; Broadhurst and Young, 2006; Van Wyk and Van Wyk, 2013). These florets release a fragrant scent from their anthers and are equipped with ample pollen and small amounts of nectar to attract and reward pollinators (Lorenzo *et al.*, 2010a). Inflorescences are open and simple in structure to accommodate a variety of pollination syndromes and pollinators, including pollen and flower feeders, nectar feeders, and opportunist foragers (Stone *et al.*, 2003; Lorenzo *et al.*, 2010a). However, it is suspected that *A. dealbata* flowers are primarily pollinated by honey bees, both in its native range (Bernhardt, 1989) and in its invasive range in South Africa (Rodger, 2012; Rodger and Johnson, 2013). In South Africa, *A. dealbata* typically flowers during late winter to early spring, between July and September (Rodger and Johnson, 2013), with pollen released slowly over the course of the flowering season, presumably to maximise the number of potential pollinators (Stone *et al.*, 2003; Lorenzo *et al.*, 2010a). Although the florets of *A. dealbata* are bisexual, protogyny ensures that the gynoecium (female) reaches maturity before the androecium (male) to prevent self-pollination (Kenrick, 2003; Lorenzo *et al.*, 2010a; Rodger and Johnson, 2013).

Only a few florets in the inflorescence give rise to leguminous pods (Rodger and Johnson, 2013). The pods are 48 x 0.8–1.2 cm in size, flat, straight or twisted, greyish to purplish brown, and slightly constricted around the seeds, which are arranged longitudinally in the pod (Searle, 1997; Van Wyk and Van Wyk, 2013). *Acacia dealbata* mass-produces hard-coated seeds, which are characterised by a nutritious, white arillate appendage to reward potential animal dispersers, typically birds or ants (Sheppard *et al.*, 2006; Lorenzo *et al.*, 2010a; Souza-Alonso *et al.*, 2014a). As with other *Acacia* species, the seeds of *A. dealbata* can persist in the environment during unfavourable conditions in a state of seed dormancy (Morris *et al.*, 2011; Correia *et al.*, 2016). Germination is often triggered by fire (Danthu *et al.*, 2003; Correia *et al.*, 2016) or, in some cases, following the scarification of the seed coat in the digestive systems of ruminants (Or and Ward, 2003). In the event of fire or cutting damage, *A. dealbata* trees are also able to resprout and proliferate from persistent rhizomes (Sheppard *et al.*, 2006; Lorenzo *et al.*, 2010a; Le Maitre *et al.*, 2011). In fact, Ferreira *et al.* (2011) notes that the species can become increasingly more invasive after fires. The floral morphology, pollination syndromes, high seed count and seed dispersal syndromes of *A. dealbata*, coupled with the preadaptation of the species to disturbance and its ability to reproduce via vegetative reproduction, are therefore pertinent to its success as an invader (Lorenzo *et al.*, 2010a).

Ecologically, *A. dealbata* is classified as a pioneer species and r-strategist (Hunt *et al.*, 1999; De Neergaard *et al.*, 2005). The species therefore thrives in early-successional or recently-disturbed habitats, grows and matures rapidly after germination, reaches reproductive maturity at a young age (after about five years) and produces an abundance of seeds (Hunt *et al.*, 1999). The reproductive biology and ecology of *A. dealbata* promote rapid and widespread proliferation, contributing to its overall invasiveness (Lorenzo *et al.*, 2010a). Despite this, few studies have attempted to understand the reproductive biology of *A. dealbata* in its invasive range; only one such study is known to have been conducted in South Africa (see Rodger and Johnson, 2013).

Acacia dealbata is indigenous to the southeastern provinces of Australia (Sheppard *et al.*, 2006; Lorenzo *et al.*, 2010a, 2013; Rodger and Johnson, 2013). Here, the species is adapted to a variety of bioclimatic and environmental conditions (Lazzaro *et al.*, 2014), particularly well-suited to cool to warm sub-humid bioclimatic zones (Doran and Turnbull, 1997). This attests to high phenotypic plasticity (adaptability of physiology to external change) of *A. dealbata* in terms of its high photosynthetic capacity, water use efficiency, specific leaf area and leaf nitrogen content (Lorenzo *et al.*, 2010a). According to Doran and Turnbull (1997), *A. dealbata* inhabits latitudes of 29–43 °S; altitudes up to 1 500 m above sea level; and MAP regions of 300–600 mm, with an average number of rain days between 85 and 170, an average number of frost days between 20 and 80, and a mean minimum of -2 °C for the coldest month.

However, *A. dealbata* is most commonly found within latitudes of 33–38 °S and altitudes between 250 and 900 m (Doran and Turnbull, 1997), preferring to inhabit the slopes and riparian zones of Mediterranean-type ecosystems and flourishing amongst sclerophyllous species (Sheppard et al., 2006) in regions with more than 500 mm of annual rainfall (May and Attiwill, 2003; Lorenzo et al., 2010a; Correia et al., 2016). In terms of substrate, *A. dealbata* can be found growing in moderate to well drained soils (including podsoles, clays, brown earths and lateritic krasnozems), on basalt, granite or sandstone geology (Doran and Turnbull, 1997).

Acacia dealbata is considered the third most invasive Australian Acacia worldwide (Richardson and Rejmánek, 2011; Lorenzo and Rodríguez-Echeverría, 2012). The species has become naturalised across many parts of southern Europe, South America and southern Africa, where it has become particularly threatening to Mediterranean-type ecosystems (Richardson and Rejmánek, 2011; González-Muñoz et al., 2012; Lazzaro et al., 2014; Aguilera et al., 2015; Souza-Alonso et al., 2015). This is because these ecosystems mimic the bioclimatic conditions and disturbance-prone nature of its preferred native range (Richardson et al., 2011). It is similarly exploitative in other disturbance-prone environments, including roadsides and other human-altered habitats, riparian zones and fire-prone areas (Ferreira et al., 2011; Van Wyk and Van Wyk, 2013; Aguilera et al., 2015). Notwithstanding, the species can also be found in a number of other habitats in its invaded range; for example, *A. dealbata* is widely naturalised across the South African grassland biome (Fig. 2.6), where it is considered the second most prominent invasive plant after *A. mearnsii* (Henderson, 2007).

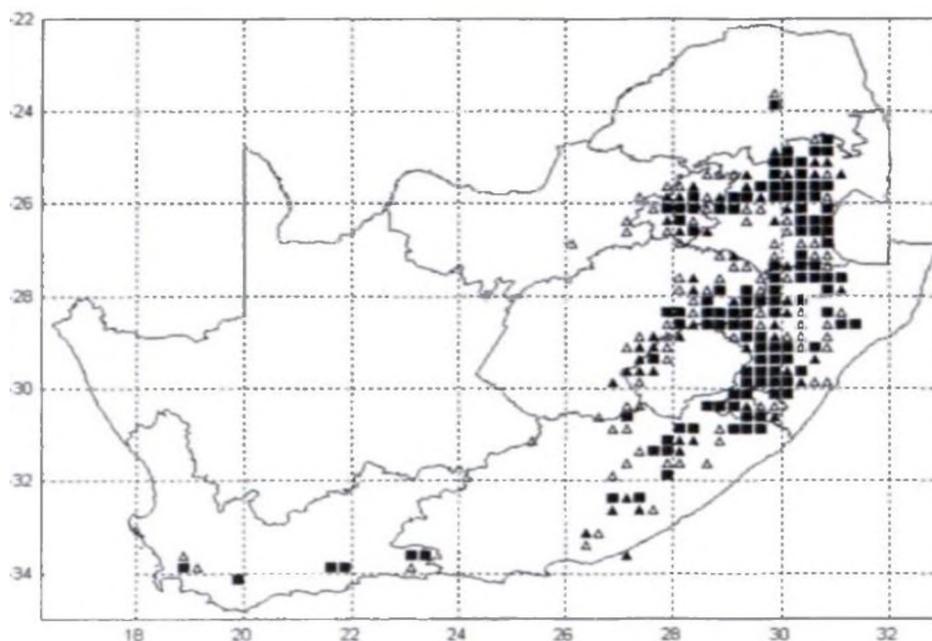


Fig. 2.6: Range of *A. dealbata* in South Africa (from Henderson, 2007).

Acacia dealbata is heterogeneously distributed across its southern African range (Fig. 2.6), which includes: patches in the western parts of Zimbabwe and the eastern parts of

Mozambique; small, sporadic, yet dense, patches along the Cape Fold Mountains; patches along the Drakensberg Escarpment, which become increasingly larger, denser and more widespread towards the northern parts of Eastern Cape, extending far into KwaZulu-Natal, Mpumalanga and Gauteng, as well as the eastern parts of the Free State Highveld; and finally, small stray patches in parts of the North-West and Limpopo provinces (Henderson, 2007; Van Wyk and Van Wyk, 2013).

2.3.2.2. Status of *Acacia dealbata* in South Africa

Acacia dealbata is known to have a number of commercial and subsistence uses worldwide (Kull *et al.*, 2011). For example, the species has been used for reforestation initiatives in Madagascar to reclaim degraded land, as well as for construction purposes, improving soil fertility, fuelwood and charcoal production, which has become a local industry in rural areas (Carruthers *et al.*, 2011; Kull *et al.*, 2011). On the other hand, it is also considered highly invasive and ecologically detrimental (Richardson and Rejmánek, 2011).

Acacia dealbata was first introduced into South Africa around 1850 (Poynton, 2009; Van Wilgen *et al.*, 2011) as a commercial plantation species, specifically for the production of timber and tannins (De Neergaard *et al.*, 2005; Le Roux *et al.*, 2011). However, in contrast to the related *A. mearnsii*, *A. dealbata* experienced very limited commercial success in South Africa, resulting in the widespread abandonment of commercial *A. dealbata* plantations (Dennill and Donnelly, 1991; Poynton, 2009). Consequently, *A. dealbata* began to escape the range of unmanaged plantations, invading surrounding grasslands (Dennill and Donnelly, 1991) and displacing native plant communities. Despite this, *A. dealbata* has long retained a local utilitarian and socio-economic value in the livelihoods of South African rural communities, used primarily for fuelwood and construction materials (De Neergaard *et al.*, 2005; Poynton, 2009). For example, De Neergaard *et al.* (2005) found that almost all households in the Madlanga community of Eastern Cape use a combination of *A. mearnsii* and *A. dealbata* wood for fuelwood and construction, and almost a fifth of the households earn a cash income from selling the firewood. *Acacia dealbata* can also be used for its bark products (e.g. tanbark, medicines, etc.), as a natural fertiliser or as fodder for livestock (De Neergaard *et al.*, 2005; Van Wilgen *et al.*, 2011; Ngorima, 2016).

Nonetheless, *A. dealbata* is a declared invader in South Africa (Van Wyk and Van Wyk, 2013), and is considered widespread and abundant (Nel *et al.*, 2004). Of the most severe IAPs in South Africa, *A. dealbata* is ranked third in terms of water use (Le Maitre *et al.*, 2000); twelfth in terms of infestation area (Le Maitre *et al.*, 2000); ninth in terms of its overall prominence, second and seventh in terms of prominence in grassland and riparian biomes, respectively (Henderson, 2007); and, ninth in terms of total WFW eradication expenditure (Van Wilgen *et*

al., 2012b). Although the species is highly invasive and relatively commercially-insignificant in South Africa, *A. dealbata* is intertwined with the livelihoods of rural communities (Ngorima, 2016), warranting a carefully-constructed, people-orientated approach to the management of the species.

2.4. Ethical considerations

Research was conducted on communal lands under the jurisdiction of local authorities. Permission was therefore sought from the relevant local authorities. A consent letter was drafted, including details of the research aims and objectives, the funders and the potential risks and benefits of the research. Field data for this study were collected through ecological surveying and did not involve any human and/or animal subjects. There were therefore no ethical aspects to this study in terms of the official Rhodes University Ethics Policy. The study was approved by the Rhodes University Department of Environmental Science Ethics Review Committee. Although no participants were involved in this study, the results will be used to inform decision-making by the Agricultural Research Council regarding the potential release, or not, of a biological control agent on *A. dealbata*, a resource used by communities in the surrounding areas. The release of the agent could potentially impact on the livelihoods of the communities in question by reducing their resource base.

CHAPTER THREE: HISTORY OF INVASION AND BROADER LAND COVER CHANGES

Abstract

Biological invasions and human land-use both have the potential to drastically alter the patterns and processes of landscapes, driving habitat fragmentation and altering disturbance regimes. The proliferation of a species across a landscape depends on both the composition and configuration of the landscape. To effectively manage a highly invasive species, such as *Acacia dealbata*, it is crucial to understand the historical progression of the invasion within the landscape. This study sought to track the historical changes in the extent and rate of spread of *A. dealbata* invasions in the northern Eastern Cape. Research was conducted in nine villages in rural Matatiele, Mount Fletcher and Maclear. A time-series of aerial photographs were systematically classified according to designated *A. dealbata* and land-use/land cover (LULC) categories in ArcGIS to track the changes in the extent and rate of spread of *A. dealbata*. Data were analysed using log-linear and regression analyses. The results indicate that invasive spread has undoubtedly occurred in the northern Eastern Cape in the past and will likely continue, barring deliberate intervention. Since the 1950s, *A. dealbata* spread at an overall annual rate of 0.11–0.21 %, occupying approximately 8–18 % of land cover across all sampled sites by 2013. In addition, broader land-use and cover changes were also apparent in the northern Eastern Cape and some LULC classes were more resistant to transition than others. *Acacia dealbata* frequently retained a high proportion of its existing cover across successive timesteps, while most notably invading bare ground, cultivated land and grasslands. Furthermore, both the invasion of *A. dealbata* and the broader changes in LULC were highly variable between regions and landscapes. Any management interventions to limit or control *A. dealbata* should therefore consider the spatio-temporal and LULC nuances of landscapes.

3.1. Introduction

This chapter addresses the first objective of the thesis: to track the changes in the extent and rate of spread of *A. dealbata* invasions in sample sites in the northern Eastern Cape, South Africa. The first section introduces a landscape perspective on biological invasions, exploring the role of landscape composition and configuration in invasive spread and providing a context for mapping biological invasions and broader LULC changes. Following a brief recapitulation of the relevant research questions, the methods and results are described in detail. The discussion then delves into the main findings, setting the stage for the next chapter.

3.1.1. A landscape perspective on biological invasions

Landscapes are spatially heterogenous areas, shaped by the interaction between spatial patterns and ecological processes and are composed of an arrangement of biotic and abiotic

spatial features (Forman, 1995; With, 2002; Turner and Gardner, 2015). The dynamic nature of landscapes can be likened to that of complex adaptive systems, whereby interacting components drive and respond to change at a multitude of spatio-temporal scales (Gunderson and Holling, 2002; Ingegnoli, 2002; Holling, 2004; Pyšek and Hulme, 2005; Farina, 2006; Adams *et al.*, 2014). For example, biological invasions are ecological processes which are both shaped by the landscape and in turn, shape the landscape, i.e. as the components of the landscape (e.g. topography, geology, native ecological communities, etc.) influence the pattern of invasive assemblage, so too can an invasive species alter its surrounding environment to make conditions more conducive to its presence (Hobbs, 2000; With, 2002; Zweig and Newman, 2015). Similarly, the patterns of human land-use have historically been moulded by and engraved into the underlying landscape (Harden *et al.*, 2014). The relationship between landscapes, land-uses and invasions is gaining attention in invasion science research, covering a range of subjects (Vilà and Ibáñez, 2011), including:

- i. conceptual pieces on the influence of landscapes on each stage of the invasion process (e.g. With, 2002; Theoharides and Dukes, 2007); as well as empirical studies on the landscape drivers of invasion, including
- ii. the role of landscape composition, configuration, heterogeneity and fragmentation (e.g. Pauchard and Alaback, 2004; Minor *et al.*, 2009; Henriques-Silva *et al.*, 2015; Ramanantoanina and Hull, 2016; Giometto *et al.*, 2017);
- iii. the land-use drivers of invasion, including the progression of LULC change (e.g. Pauchard and Alaback, 2004; Gavier-Pizarro *et al.*, 2010; Mattingly and Orrock, 2013; Le Maitre *et al.*, 2014);
- iv. the historical progression of invasions, tracking the extent and rate of invasion over time (e.g. Henderson, 1998; Zalba and Villamil, 2002; Foxcroft *et al.*, 2004; De Neergaard *et al.*, 2005; Pauchard and Maheu-Giroux, 2007; Trueman *et al.*, 2014; Zweig and Newman, 2015; Martins *et al.*, 2016); and,
- v. the prediction of future invasive spread and LULC change (e.g. Bradley *et al.*, 2010; Vicente *et al.*, 2011; Chytrý *et al.*, 2012; Bellard *et al.*, 2013).

3.1.1.1. Landscapes and the process of invasion

The landscape plays multiple roles in each stage of invasion, from the transportation and initial introduction of the invader, to its colonisation and establishment, to its eventual spread across the landscape (With, 2002; Theoharides and Dukes, 2007). According to With (2002), the long-distance transportation and subsequent introduction of species can, to some extent, depend on the topography of the landscape, and its association with human land-use, along

the pathway of travel. Moreover, the spatial distribution and configuration of resources, empty niches, refugia and disturbed habitats within the landscape will influence where the introduced species might successfully establish (With, 2002). Similarly, the direction, extent and rate of proliferation will depend on the heterogeneity of the landscape, as well as the residence time of the species in its new habitat and the dispersal strategy of the species (With, 2002; Theoharides and Dukes, 2007; Wilson *et al.*, 2007; Minor *et al.*, 2009). With (2002) postulates that the heterogeneous and dynamic nature of landscapes can result in spatially distributed nascent populations, which promote invasive spread from multiple nodes in the landscape.

3.1.1.2. Landscape and LULC drivers of invasion

Biological invasions and human land-use both have the potential to drastically alter the pattern-process dynamics of landscapes, driving habitat fragmentation and altering disturbance regimes (Hobbs, 2000; With, 2002; Reaser *et al.*, 2007; Vilà and Ibáñez, 2011; Zweig and Newman, 2015). The proliferation of a species across a landscape depends on both the composition and configuration of the landscape (Vilà and Ibáñez, 2011). Landscape composition refers to the biological, biochemical, climatic, ecological, geological, topographic and land-use properties of the habitat patches and surrounding matrix cover in the landscape (With, 2002; Pauchard and Alaback, 2004; Minor *et al.*, 2009; Vilà and Ibáñez, 2011; Malavasi *et al.*, 2014). Correspondingly, landscape configuration refers to the shape, size, edge characteristics and spatial arrangement of habitat patches, including the proximity and connectivity between patches and other landscape elements, as well as the density and distribution of patches within the landscape (With, 2002; Pauchard and Alaback, 2004; Minor *et al.*, 2009; Vilà and Ibáñez, 2011). The invasibility of a landscape is therefore contingent, *inter alia*, on the inextricable attributive (composition) and spatial (configuration) suitability of its constituent habitat patches (Vilà and Ibáñez, 2011).

Many natural habitats have become increasingly disturbed and fragmented because of LULC change, including agricultural, industrial and urban expansion (Hobbs, 2000; Pauchard and Alaback, 2004; Minor *et al.*, 2009; Vilà and Ibáñez, 2011). Consequently, many landscapes have become an archipelago of increasingly fragmented habitat patches, interspersed within a matrix of human-altered areas (Vilà and Ibáñez, 2011). Fragmentation is an effective driver of biological invasions at the landscape scale, increasing the vulnerability of native ecological communities (Vilà and Ibáñez, 2011). The edges of habitat patches are particularly vulnerable to invasion, especially those bordering areas of human land-use, with a higher number and abundance of IAPs typically found along the edge, opposed to the interior, of habitat patches (Vilà and Ibáñez, 2011). In addition, fragmentation shrinks and isolates individual habitat patches, decreasing connectivity, which can decrease the resilience of ecological communities (Vilà and Ibáñez, 2011; Malavasi *et al.*, 2014).

Habitat corridors can serve as conduits for propagule dispersal between habitat patches and prevent the collapse of local populations through exchange (Minor *et al.*, 2009). However, the role of these corridors in invasive spread remains unclear due to the context- and species-specific nature of biological invasions, with habitat corridors increasing the abundance of IAPs in some cases, while having no effect in other cases (Vilà and Ibáñez, 2011). According to Henriques-Silva *et al.* (2015), *ceteris paribus*, landscapes with diverse connective networks will promote a greater variety of dispersal strategies, contributing to range expansion. Although the composition and configuration of habitable range are indicative of the potential spread of a species across a landscape (Vilà and Ibáñez, 2011), the dispersal strategies of a species will determine whether it will be able to capitalise on the availability of these suitable habitats (Henriques-Silva *et al.*, 2015; Ramanantoina and Hull, 2016). Indeed, in landscapes with poorly connected habitat patches, invaders are thought to “spread more easily than native plant species through fragments due to direct or indirect human assistance, and also because wind seed dispersal is a prevalent dispersal mechanism” (Vilà and Ibáñez, 2011: 466).

In terms of landscape and habitat composition, invasibility may depend, *inter alia*, on native biodiversity (biotic resistance hypothesis; Elton, 1958; Levine *et al.*, 2004; Hufbauer and Torchin, 2008); the phase of ecological succession (maturity concept; Shea and Chesson, 2002); the presence of natural enemies (enemy release hypothesis; Darwin, 1859; Shea and Chesson, 2002; Hufbauer and Torchin, 2008; Heger and Jeschke, 2014); the saturation of available niches (empty niche hypothesis; Elton, 1958; Hufbauer and Torchin, 2008); and the type, frequency and intensity of disturbance (preadaptation/disturbance hypothesis; Baker and Stebbins, 1965; Sax and Brown, 2000; Dietz and Edwards, 2006; Hufbauer and Torchin, 2008). Disturbance is a particularly prevalent contributor and earmark of biological invasions in both natural and human-altered habitats (Baker and Stebbins, 1965; Sax and Brown, 2000; Hufbauer and Torchin, 2008). Invasive plants are often found in disturbance-prone areas with fluctuating resource availability (Davis *et al.*, 2000; Chytrý *et al.*, 2008; Pyšek *et al.*, 2012a; Pyšek and Chytrý, 2014). For example, natural and semi-natural riparian habitats tend to be highly susceptible to plant invasions because rivers not only routinely supply and cycle resources and serve as an effective mechanism of propagule dispersal, but also provide frequent and turbulent source of disturbances (Liendo *et al.*, 2015).

Similarly, human activities and land-uses are widely considered to be a major driver of habitat disturbance, promoting IAS spread (e.g. Didham *et al.*, 2007; Theoharides and Dukes, 2007; Von Holle and Motzkin, 2007). The type, intensity and history of land-use can increase the susceptibility of a landscape to invasion (Vilà and Ibáñez, 2011; Mattingly and Orrock, 2013). For example, agricultural, horticultural and silvicultural areas historically served as the point of introduction (source of invasion) for numerous alien cultivars and unintentional stowaways

worldwide (McNeely, 2001), while many, particularly those which have been abandoned, now serve as highly disturbed and invulnerable sinks of invasion (e.g. Pauchard and Alaback, 2004; Vilà and Ibáñez, 2011; Mattingly and Orrock, 2013; Malavasi *et al.*, 2014). On the other hand, the presence of urban land-use may either impede invasive spread by acting as a dispersal barrier or perpetuate it by providing a source of propagules and disturbance, while extensive transport networks with high traffic volumes further promote the dispersal of propagules, accelerating the rate of invasion (Vilà and Ibáñez, 2011).

3.1.1.3. Tracking invasive spread

According to Pyšek and Hulme (2005), invasion ecologists have adopted a range of methods to determine the extent and rate of biological invasions, using a combination of data sources, including herbaria archives, written accounts and distribution records (e.g. Williamson *et al.*, 2005; Kelly *et al.*, 2014; Wilson *et al.*, 2014); field experiments (e.g. Myers and Berube, 1983; Perrins *et al.*, 1993); population densities (e.g. Foxcroft *et al.*, 2004; Strum *et al.*, 2015); population age structures (e.g. Frappier *et al.*, 2003); measured distances from source populations (e.g. Schepker and Kowarik, 1998); permanent field plots (e.g. Wiser *et al.*, 1998; Wang *et al.*, 2016; Malizia *et al.*, 2017); field surveys and maps (e.g. Henderson, 1998; Meyer *et al.*, 1998); and, ecological and statistical models (e.g. Kannan *et al.*, 2013; Hernández *et al.*, 2014; Kelly *et al.*, 2014), as well as remotely-sensed data, including aerial photographs (e.g. De Neergaard *et al.*, 2005; Gorchov *et al.*, 2014; Masocha *et al.*, 2017) and satellite imagery (e.g. Trueman *et al.*, 2014; Martins *et al.*, 2016; Niphadkar and Nagendra, 2016).

A spatio-temporal understanding of landscapes offers insight into the dynamics of environmental change at a scale widely applicable to human activity, shedding light on the systems, drivers and impacts of anthropogenic and ecological processes, such as land-use change and biological invasions, respectively. Mapping the historical progression of biological invasions provides a means of tracking the extent, location and distribution of the invader through time, quantifying the rate of spread, determining the drivers of invasion and projecting potential future distributions, all of which are crucial to the effective management of IAS (Pyšek and Hulme, 2005; Trueman *et al.*, 2014; Zweig and Newman, 2015; Witt *et al.*, 2017).

3.1.2. Tracking *A. dealbata* in the northern Eastern Cape

The history of *A. dealbata* in South Africa spans approximately 160 years (Poynton, 2009; Van Wilgen *et al.*, 2011), with the species currently inhabiting many parts of the South African Grassland biome, including particularly large, dense populations in the northern parts of the Eastern Cape (Fig. 1.2; Henderson, 2007; Van Wyk and Van Wyk, 2013). To understand the magnitude of the problem, this study sought to track the historical changes in the extent and rate of spread of *A. dealbata* invasions, answering the following questions i) Has the extent of

A. dealbata changed over time?; ii) What is the rate of invasion?; iii) How has land-use and cover changed over time?; and iv) What is the probability of transition between different land-use/land cover (LULC) classes?

3.2. Methods

The spread of *A. dealbata* and changes in LULC were contextualised within the systems knowledge sphere of invasion science (Richardson, 2011), with an emphasis on the landscape ecological perspective (Ingegnoli, 2002). Following Ingegnoli's (2002) Ecotissue model, this chapter deals with landscapes as a set of spatial, temporal and thematic mosaics. In a GIS, these mosaics can be represented as separate, yet overlapping data layers. The range of spatial scales included *regional* scale, represented by each of the three study areas; the *landscape* scale, each village selected for the region (represented by a random sample of landscape units per village); the *local* scale, a single landscape unit, composed of classified cells (tesserae); and the *detailed* scale, each of the classified cells. The temporal scale spanned approximately 60 years, represented by repeated classifications for each of four periods (late 1940s/early 1950s, 1975, 1995 and 2013). Two themes were selected, namely *A. dealbata* cover (ACA) and broader LULC.

3.2.1. Data preparation and capture

The *A. dealbata* invasion and broader LULC changes were tracked through time by the classification, analysis and interpretation of aerial photographs in ArcGIS 10.3 (ESRI, 2011). High resolution digital scans of aerial photographs were acquired from the Chief Directorate of National Geographical Information (Department of Rural Development and Land Reform, Republic of South Africa). For the late 1940s/early 1950s period, 1:18 000 and 1:30 000 photographs were acquired for Maclear (Job 207, 1948–50) and Matatiele/Mount Fletcher (Job 220, 1952–53), respectively. Unfortunately, a section of the Mount Fletcher area was not covered in the flight path of Job 220, leading to fewer classified grids for Printsu village for the 1952–53 period. The remaining photographs, for all study areas, included 1:50 000 images for 1975 (Job 731) and 1995 (Job 983), as well as georeferenced, orthorectified 1:10 000 images for 2013 (Jobs 534, 535 and 536).

All historical images were georeferenced to the 2013 images. A buffer was created for each of the nine villages to represent the harvesting zone. Three kilometres was deemed a suitable distance to represent the harvesting zone as villagers reportedly transport fuelwood as headloads or cattle-drawn bundles and spend 10–90 minutes on collection (Ngorima, 2016). A 500 m x 500 m grid was then generated within each of these buffered areas using the Create Fishnet tool (ArcGIS 10.3; ESRI, 2011). Thereafter, the Subset Feature tool (ArcGIS 10.3; ESRI, 2011) was used to create a template data layer of randomly sampled landscape units

(n = 22–24) for each village, accounting for 5–10 % of the total area within the buffers. These landscape units were then subdivided to create grids, composed of 625 (20 m x 20 m) tesserae. For each of the villages, the template data layer (consisting of 13 750–15 000 cells) was duplicated eight times, with each duplicate given a unique descriptive name corresponding to the name of the village, the period (1950s, 1975, 1995 or 2013) and the theme (ACA or LULC), i.e. Village_Period_Theme, producing a series of superimposed temporal and thematic data layers. The 20 m x 20 m tesserae were then manually classified as follows. Firstly, each ACA data layer was classified according to the categories described in Table 3.1. Fig. 3.1 depicts an example of an ACA themed landscape.

Table 3.1: Description of *A. dealbata* cover (ACA) categories.

Category	Description
No cover	No <i>A. dealbata</i> cover.
Patches	Sporadic, discontinuous patches of <i>A. dealbata</i> , accounting for less than half of the area of the cell.
Edge	Continuous, closed canopy <i>A. dealbata</i> , accounting for less than half of the area of a cell, usually adjacent to other cells of more complete <i>A. dealbata</i> cover.
Half-discontinuous canopy	Discontinuous <i>A. dealbata</i> , accounting for more than half, yet less than 90 %, of the area of the cell.
Half-closed canopy	Continuous, closed canopy <i>A. dealbata</i> , accounting for more than half, yet less than 90 %, of the area of the cell.
Full discontinuous canopy	Discontinuous <i>A. dealbata</i> , accounting for more than 90 % of the area of the cell.
Full closed canopy	Continuous, closed canopy <i>A. dealbata</i> , accounting for more than 90 % of the area of the cell.

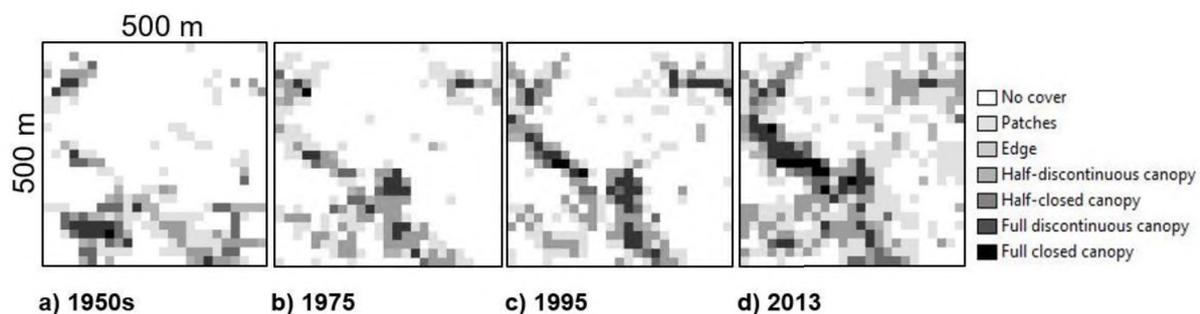


Fig. 3.1: Example of classified ACA landscape units.

Thereafter, LULC was classified according to the categories in Table 3.2. In the event of two or more categories per cell, the dominant category (i.e. covering the most area relative to the other categories) took preference. Fig. 3.2 depicts an example of a LULC themed landscape. Ground truthing focused primarily on verifying the classification of *A. dealbata*, initially

challenging to distinguish from other woody cover, using 148 points sampled for both the growth transects and density plots in Chapter Four to follow. Seventy-seven percent of the sample points were accurately classified as *A. dealbata*, while the remaining 23 % of points were typically plantations and shrublands misclassified as *A. dealbata*. Classifications were amended thereafter.

Table 3.2: Description of land use/land cover (LULC) categories

Category	Description
<i>Acacia dealbata</i>	The aggregation of full and half-closed and discontinuous canopy categories from the ACA thematic mosaic, i.e. <i>A. dealbata</i> dominated cells.
Bare	Bare ground and/or exposed soil, as the result of erosion or deposition.
Cultivated land	Any land apparently used for cultivation at the time of the aerial photograph, typically marked by striations or plough lines, and field boundaries.
Exposed rock	Exposed rock, differing from bare ground by a notably textured appearance. Commonly found in rugged terrain.
Grassland	Grassy cover of any kind, including recovered fields, bare ground, gardens, etc.
Residential/ infrastructure	Including tarred roads, buildings and houses with accompanying gardens (non-striated areas, with a boundary and/or kraal, adjacent or within proximity of a house).
Plantation/woodlot	Blue gum (<i>Eucalyptus</i> sp.) or black/green wattle (<i>A. mearnsii</i> / <i>A. decurrens</i>) plantations, or <i>Populus canescens</i> woodlots
Shrubland	Mild to dense shrubland coverage. Typically, <i>Leucosidea sericea</i> .
Wetland	Any water body (river, dam, lake or vlei) and/or riparian zone (floodplain, marsh, etc.)

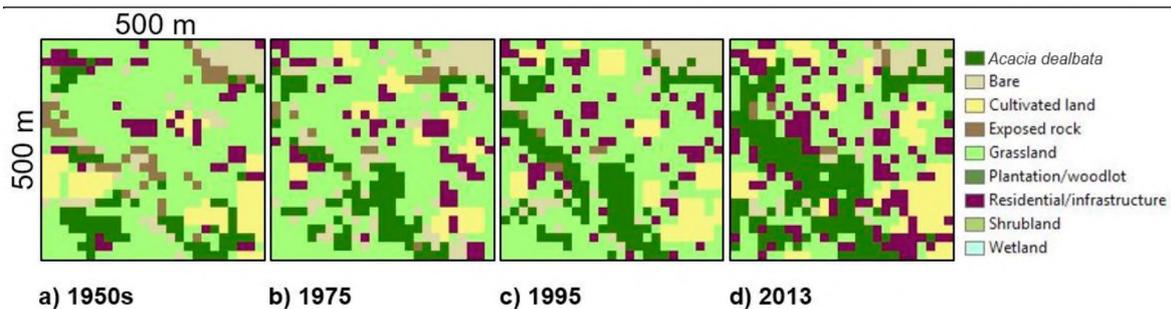


Fig. 3.2: Example of classified LULC landscape units.

3.2.2. Data analysis

Data were analysed in R version 3.4.1 (R Core Team, 2017). The changes in ACA and LULC were determined by comparing the mean percentage cover per category for each period, across all sites, as well as per region and landscape, landscape and region, represented graphically (R package: ggplot; Wickham, 2009). Log-linear modelling was used to compare

spatio-temporal differences in *A. dealbata* cover and broader LULC, while regression analysis was used to determine the rates of invasion (R package: stats; R Core Team, 2017).

Fully-additive, global, log-linear models were fitted to determine whether there were significance differences in cover between ACA and LULC categories across different time intervals, collectively across all sites, as well as at the inter- and intraregional scales (i.e. between and within study areas, respectively). Cell count data were expressed per category as proportions of the total number of cells in a grid (625), which were transformed using an arcsine-square root transformation. For convenience, the '1948' and '1952' categories of the 'Year' variable were merged into a single '1950s' category for these analyses. An additional categorical predictor ('grid number') was included as a non-interaction term to block for repeated measures of landscape units. Initially, the analysis was run on the ACA dataset in its original, disaggregated state. However, since the surrounding 'no cover' matrix was considerably greater than any other single ACA category and the relative proportions of remaining categories were highly variable, 'no cover' was excluded from the analysis and the remaining categories were aggregated. The analysis was then rerun using two aggregated levels of *A. dealbata* cover, namely an upper, more liberal estimate (including all ACA cover categories, apart from the 'no cover' category) and a lower, more conservative estimate (including only the full and half-closed and discontinuous canopy ACA categories, i.e. *A. dealbata* dominated cells).

Independence and conditional independence tests were run and the 'dredge' tool (R package: MuMIN; Barton, 2016) was used to determine and select the most parsimonious models based on Akaike's information criteria (AIC; Logan, 2010). Subset models were ranked based on increasing values of Δ AIC (Δ_i), whereby models with $\Delta_i \leq 2$ are insignificantly different and eligible for model averaging (Burnham and Anderson, 2002, 2004; Mograbi *et al.*, 2017). According to Burnham and Anderson (2004: 271), "the larger the Δ_i , the less plausible is fitted model i as being the best approximating model in the candidate set". Model averaging was considered in a few cases, based on Δ AIC eligibility and the requirements of the model. Pairwise comparison tests based on the Tukey method were run on each model post-hoc using the 'lsmeans' tool (R package: multcomp; Hothorn *et al.*, 2008; R package: lsmeans; Lenth, 2016) to determine which ACA and LULC categories experienced significant changes between each time interval.

The two aggregated ACA estimates were then used to quantify the rate of invasion. Regression models were fitted for the untransformed upper and lower aggregates at each of the spatial scales. In these models, 'year' was left as a continuous variable, with 1948 and 1952 unmerged. Again, the best-fitting models were selected based on AIC and model averaging was considered for subset models with $\Delta_i \leq 2$. The slopes (rates of invasion) were

then determined from the coefficients table and significance levels were examined to detect intra- and interregional differences. The proportion of LULC transitioning from one class to another was then determined using the Tabulate Intersection tool in ArcGIS, which “computes the intersection between two feature classes and cross-tabulates the area . . . of the intersecting features” (ESRI, 2011). For each village and study area, the tool computed the percentage of intersecting LULC classes between each consecutive timestep (i.e. 1950s–1975, 1975–1995 and 1995–2013). These transition probabilities were then represented graphically (R package: ggplot; Wickham, 2009).

3.3. Results

The results of this chapter are presented in three sections, focussing on the extent and rate of spread of *A. dealbata*, land-use and cover change and the proportion of LULC transition. In each section, the findings hone in from a brief broad perspective of the changes occurring across all sites, through an interregional comparison of the three study areas, to intraregional comparisons of the respective villages within the Matatiele, Mount Fletcher and Maclear areas.

3.3.1. Extent and rate of spread of *A. dealbata*

The extent and rate of spread of *A. dealbata* was variable, both spatially within and between regions and temporally between consecutive and non-consecutive timesteps. In the absence of the study area and village variables (i.e. in the overall models), the grid number and year were highly significant ($P < 0.001$) for explaining *A. dealbata* cover in both the upper and lower log-linear and regression models (Table 3.3). Overall, the extent of *A. dealbata* increased significantly between all consecutive and non-consecutive periods for both the upper and lower cover estimates ($P < 0.005$). From the 1950s to 2013, the former ranged 4.35 ± 7.11 % to 18.03 ± 22.65 %, whereas the latter ranged 1.09 ± 2.67 % to 7.73 ± 14.77 % (Fig. 3.3), reflecting an overall annual rate of invasion of 0.11–0.21 % (lower–upper).

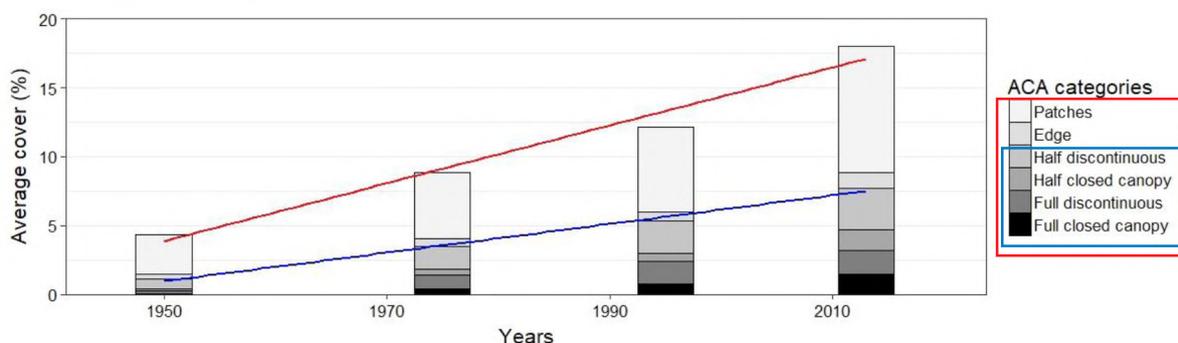


Fig. 3.3: Cumulative mean *A. dealbata* cover change in the northern Eastern Cape across all sites. Upper and lower estimates are indicated by red and blue, respectively.

Table 3.3: Best-fitting subset models for log-linear and regression analyses of *A. dealbata* cover. Only subset models with $\Delta i \leq 2$ were included. Models with two or more subset models with $\Delta i \leq 2$ were eligible for averaging. '+' indicates the presence of the predictor variable in the subset model. Regression models include the best-fitting slope for the continuous 'year' variable.

Region or landscape	Model type	Estimate	Subset(s)	Intercept	Grid	Predictor variables			AICc	Δ	Weight
						Study area or Village	Year	Study area:Year or Village:Year			
Overall	Log-linear	Upper	1	0.56	+		+		-1268	0	1.00
		Lower	1	0.09	+		+		-1479	0	1.00
	Regression	Upper	1	-384.60	+		0.213		6062	0	1.00
		Lower	1	-206.20	+		0.105		5580	0	1.00
Interregional	Log-linear	Upper	1	0.50	+	+	+	+	-1 435	0	1.00
		Lower	1	0.04	+	+	+	+	-1 586	0	1.00
	Regression	Upper	1	-708.53	+	+	0.059	+	5 888	0	1.00
		Lower	1	-423.18	+	+	0.020	+	5 468	0	1.00
Matatiele intraregional	Log-linear	Upper	1	0.50	+		+		-359	0	0.50
			2	0.50	+	+	+		-359	0	0.50
		Lower	1	0.04	+		+		-376	0	0.50
			2	0.04	+	+	+		-376	0	0.50
	Regression	Upper	1	-708.53	+		0.377		2 118	0	0.42
			2	-708.53	+	+	0.377		2 118	0	0.42
			3	-850.37	+	+	0.324	+	2 120	2	0.16
		Lower	1	-423.18	+		0.215		2 024	0	0.42
			2	-423.18	+	+	0.215		2 024	0	0.42
			3	-541.77	+	+	0.168	+	2 026	2	0.16
Mount Fletcher intraregional	Log-linear	Upper	1	-0.14	+		+		-493	0	0.49
			2	-0.14	+	+	+		-493	0	0.49
		Lower	1	-0.08	+		+		-527	0	0.50
			2	-0.08	+	+	+		-527	0	0.50
	Regression	Upper	1	-644.30	+	+	0.204	+	1 944	0	0.95
		Lower	1	-314.10	+	+	0.072	+	1 742	0	0.91
Maclear intraregional	Log-linear	Upper	1	-0.08	+	+	+	+	-660	0	1.00
		Lower	1	-0.03	+		+		-855	0	0.50
			2	-0.03	+	+	+		-855	0	0.50
	Regression	Upper	1	-210.76	+	+	0.106	+	1 533	0	1.00
		Lower	1	-48.14	+	+	0.024	+	1 122	0	0.69

3.3.1.1. Interregional comparison

The fully-additive global models were the best-fitting models for comparing interregional *A. dealbata* cover across the three sampled study areas in the northern Eastern Cape according to the resulting AIC and Δ AIC (Δ i) values (Table 3.3). The grid number, study area and year, as well as the interaction between the study area and year, were all significant variables in these models ($P < 0.001$). Based on the upper estimate (Fig. 3.4.), Matatiele was consistently the most invaded study area, expanding from 7.52 ± 9.11 % in 1952 to 31.28 ± 28.04 % in 2013 at an annual rate of 0.38 %. Mount Fletcher followed with an *A. dealbata* coverage of 4.28 ± 6.30 % in 1952 and 17.81 ± 19.05 % in 2013, an increase of 0.23 % per year. These revealed significant increases ($P < 0.005$) in cover between all consecutive and non-consecutive periods for both Matatiele and Mount Fletcher. Conversely, Maclear had fewer significant increases during timesteps, with an *A. dealbata* coverage ranging from 1.31 ± 3.24 % in 1948 to 5.18 ± 8.44 % in 2013, an annual increase of 0.06 %. Significant increases ($P < 0.05$) occurred in Maclear from 1948–1975, 1948–1995, 1948–2013 and 1975–2013.

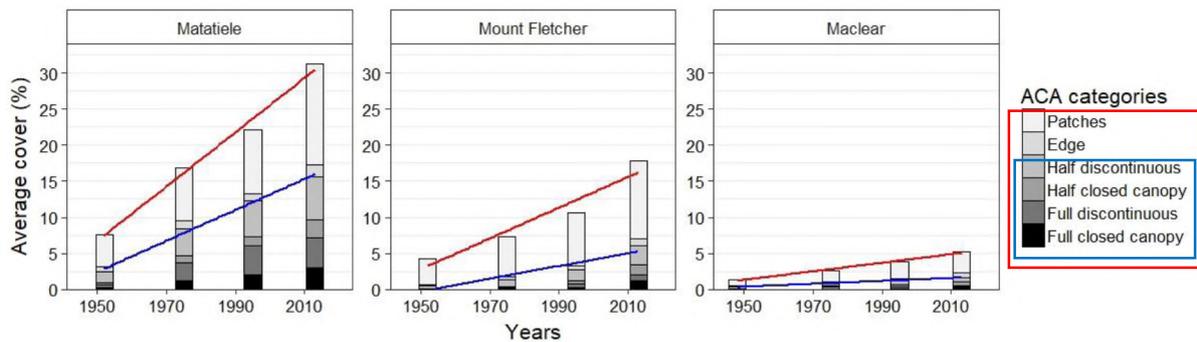


Fig. 3.4: Cumulative mean *A. dealbata* cover change in three regions in the northern Eastern Cape. Upper and lower estimates are indicated by red and blue, respectively.

Conservative estimates suggest (Fig. 3.4) that *A. dealbata* cover increased annually by 0.22 % in Matatiele, 0.09 % in Mount Fletcher; and 0.02 % in Maclear from the late 1940s/early 1950s to 2013. Significant increases occurred across all consecutive and non-consecutive periods in Matatiele ($P < 0.001$) and similarly in Mount Fletcher ($P < 0.05$), apart from the 1952–1975 timestep (z-ratio = 2.06, $P = 0.165$), whereas Maclear only experienced significant increases during the 1948–1995 (z-ratio = 4.27, $P = 0.031$) and 1948–2013 (z-ratio = 3.50, $P = 0.003$) timesteps. There were also significant differences between all study areas during each period, for both the upper and lower estimates ($P < 0.001$).

3.3.1.2. Matatiele

For the Matatiele region, the best-fitting log-linear and regression models were composed of an average of their respective subset models with Δ i ≤ 2 (Table 3.3). Two subset models were averaged for the former, where both subset models included the significant effects of the grid

number and year, and one included the added significant effect of the village, whereas the latter included three subset models, of which all included the significant effects of the grid number and year, two included the added significant effect of the village and one included an insignificant added interaction between the village and the year ($P > 0.1$). The Matatiele area displayed a high degree of intraregional variation in *A. dealbata* cover for both cover estimates (Fig. 3.5), with significant differences between all villages ($P < 0.001$) occurring during each period, as well as significant increases ($P \leq 0.01$) occurring within each village between all consecutive and non-consecutive periods. Nkasela was the most invaded village by a large margin ($P < 0.001$), with conservative and liberal estimates placed at 21.07 ± 22.20 % and 39.49 ± 29.38 % by 2013, respectively (Fig. 3.5). The annual rate of invasion was most rapid in Nkasela (lower–upper: 0.31–0.49 %), followed by Outspan (0.24–0.40 %) and then Caba (0.21–0.37 %).

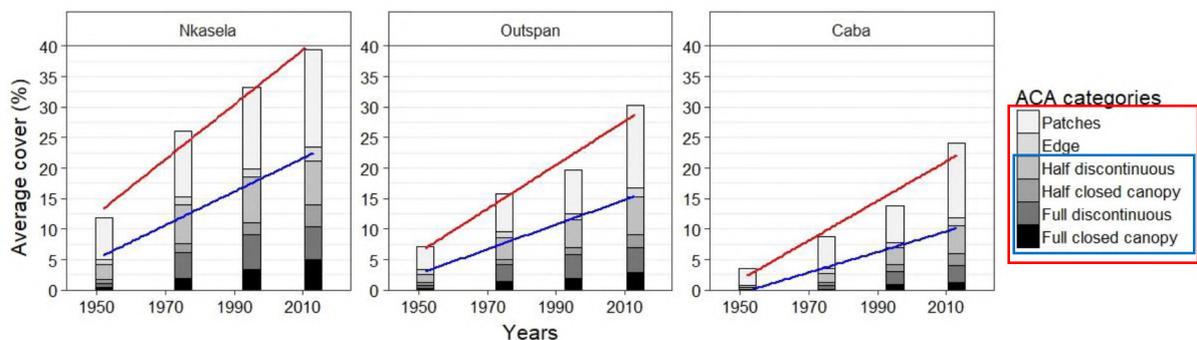


Fig. 3.5: Cumulative mean *A. dealbata* cover change in three villages in Matatiele. Upper and lower estimates are indicated by red and blue, respectively.

3.3.1.3. Mount Fletcher

The best-fitting log-linear models for Mount Fletcher were similarly composed of an average of two subset models with $\Delta i \leq 2$ (Table 3.3). Both subset models included the significant effects of the grid number and year, while one included the added significant effect of the village. However, unlike the regression models for Matatiele, the fully-additive models were the best-fitting for Mount Fletcher, where the grid number, village and year, as well as the interaction between the village and the year, were all significant terms in the models. The Mount Fletcher area displayed less intraregional variation in *A. dealbata* cover (Fig. 3.6) compared to Matatiele. Printsu was significantly more invaded than both Fletcherville and HaQhadi ($P < 0.001$) during all time periods for both upper and lower estimates, reaching between 8.65 ± 15.17 % (lower) and 23.14 ± 23.76 % (upper) by 2013 (Fig. 3.6). Fletcherville was only significantly more invaded than HaQhadi for the upper estimates ($P < 0.001$). There were insignificant changes in both upper and lower estimates during the 1952–1975 and 1952–1995 timesteps in Printsu, as well as during the 1952–1975 and 1975–1995 timesteps

for the lower estimates of both Fletcherville and HaQhadi ($P > 0.05$). Significant increases ($P < 0.05$) occurred during all other timesteps. The annual rate of invasion was most rapid in Printsu (lower–upper: 0.16–0.32 %), followed by Fletcherville (0.07–0.20 %) and then HaQhadi (0.06–0.18 %).

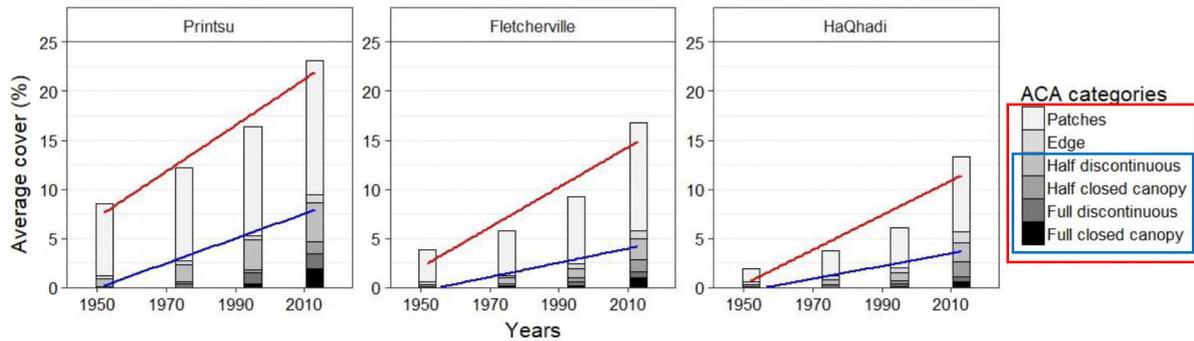


Fig. 3.6: Cumulative mean *A. dealbata* cover change in three villages in Mount Fletcher. Upper and lower estimates are indicated by red and blue, respectively.

3.3.1.4. Maclear

For the lower estimate of *A. dealbata* cover in the Maclear area, the best-fitting log-linear model was composed of an average of two subset models with $\Delta i \leq 2$ (Table 3.3), where both subset models included the significant effects of the grid number and year, and one included the added significant effect of the village. Furthermore, fully-additive models were selected for the upper estimate log-linear model and both upper and lower estimate regression models for Maclear, where the grid number, village and year, as well as the interaction between the village and the year, were all significant terms in the models. The Maclear area displayed the least intraregional variation in *A. dealbata* cover (Fig. 3.7) compared to Matatiele and Mount Fletcher.

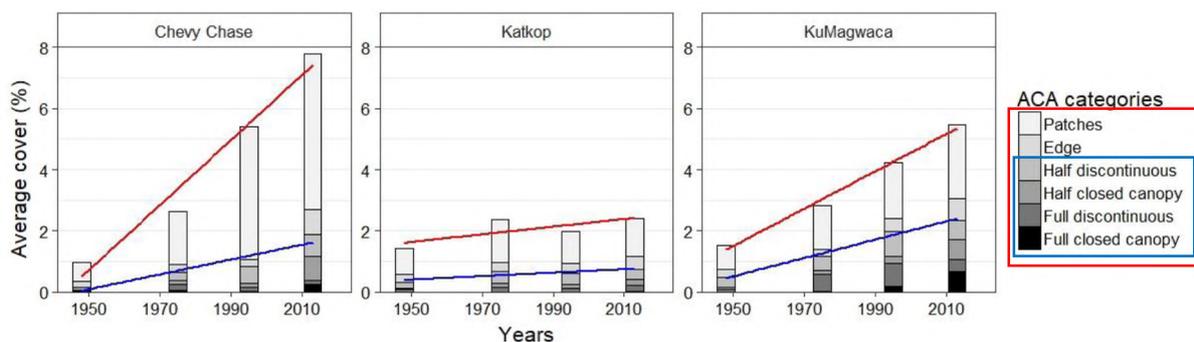


Fig. 3.7: Cumulative mean *A. dealbata* cover change in three villages in Maclear. Upper and lower estimates are indicated by red and blue, respectively.

Chevy Chase was significantly more invaded than Katkop in 1975, 1995 and 2013 in terms of the upper estimate ($P < 0.05$), while KuMagwaca was significantly more invaded than Katkop for both estimates during all periods ($P < 0.05$). KuMagwaca was significantly more invaded

than Chevy Chase in terms of the lower estimate during all periods ($P < 0.001$), however, significantly less than Chevy Chase in terms of the upper estimate during 2013 (z-ratio = -3.17, $P = 0.004$). Significant increases occurred in Chevy Chase during all timesteps, apart from the lower estimate for 1975–1995 and both estimates for 1995–2013 timestep, with cover reaching between 1.89 ± 3.94 % (lower) and 7.80 ± 9.37 % (upper) by 2013 (Fig. 3.7). For Katkop, the only significant increases ($P < 0.005$) occurred during the 1948–1975, 1948–1995, 1948–2013 and 1975–2013 timesteps and only for the lower estimates. Significant increases occurred in KuMagwaca during all timesteps, apart from the upper estimate for 1948–1975 and both estimates for the 1975–1995 and 1995–2013 timesteps. The annual rate of invasion was most rapid in Chevy Chase (lower–upper: 0.02–0.11 %), followed by KuMagwaca (0.03–0.06 %) and then Katkop (0.006–0.013 %).

3.3.2. Land-use and cover change

Each of the fully-additive LULC log-linear models had only one best-fitting subset model, each of which included the following variables: the LULC category, the year, and the interaction between the two (Table 3.4). In addition, the interregional and intraregional models included the study area and village variables, each with an interaction with the LULC categorical variable, respectively (Table 3.4). The LULC category was highly significant ($P < 0.001$) for explaining the percentage cover in all cases. In the absence of the study area and village variables (i.e. in the overall model), the year and associated LULC interaction were highly significant ($P < 0.001$). On the other hand, despite having highly significant interactions ($P < 0.001$), the study area or village and year variables were insignificant in the interregional model ($P = 0.055$ and $P = 0.454$, respectively), as well as in the intraregional model for Matatiele ($P = 0.777$ and $P = 0.830$, respectively); Mount Fletcher ($P = 0.801$ and $P = 0.681$, respectively); and Maclear ($P = 0.907$ and $P = 0.869$, respectively).

Table 3.4: Best-fitting subset models for log-linear analyses of land-use/land cover. Only subset models with $\Delta i \leq 2$ were included. ‘+’ indicates the presence of the predictor variable in the subset model.

Region/ landscape	Intercept	LU LC	St.area or Vill.	Predictor variables			AICc	Δ	Weight
				Yr	LULC:St.area or LULC:Vill.	LULC:Yr			
Overall	0.053	+		+		+	-2247	0	1
Interregional	-0.020	+	+	+	+	+	-2 563	0	1
Matatiele	0.010	+	+	+	+	+	-501	0	1
Mt. Fletcher	0.022	+	+	+	+	+	-1 023	0	1
Maclear	0.019	+	+	+	+	+	-1 472	0	1

Overall, *A. dealbata* cover (Fig. 3.3 and Fig. 3.8), bare ground and to a lesser extent, plantation/woodlot, residential/infrastructure, shrublands and wetlands, increased over time (Fig. 3.8). Conversely, cultivated land and grassland cover tended to decrease, while exposed rock cover generally remained constant (Fig. 3.8). *Acacia dealbata* cover increased

significantly over the following timesteps: 1950s–1995 (z-ratio = 3.90, $P < 0.001$); 1975–2013 (z-ratio = 3.79, $P < 0.001$); and 1950s–2013 (z-ratio = 5.77, $P < 0.001$). Similarly, bare ground increased significantly to 13.50 ± 13.92 % in 2013, from 7.36 ± 9.06 % in the 1950s (z-ratio = 4.72, $P < 0.001$), 8.16 ± 9.30 % in 1975 (z-ratio = 3.88, $P < 0.001$) and 8.34 ± 9.03 % in 1995 (z-ratio = 3.69, $P = 0.001$; Fig. 3.8). Cultivated land decreased significantly during all consecutive and non-consecutive periods ($P < 0.05$), from 29.90 ± 31.02 (1950s) to 13.92 ± 23.54 % (2013; Fig. 3.8).

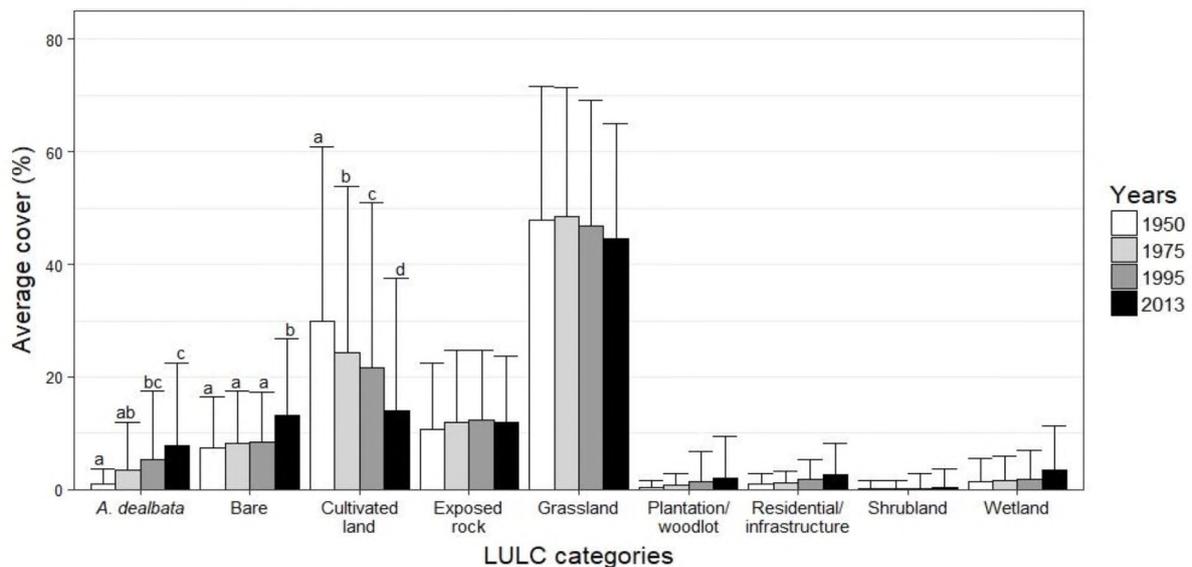


Fig. 3.8: Average LULC change (mean + absolute SD) in the northern Eastern Cape across all sites. Statistically significant differences in cover over time denoted by different letters (a, b, c and d) per LULC class.

The remaining LULC categories remained relatively constant over time, with no significant changes in cover. Grassland cover, though declining, was by far the most abundant, ranging from 47.89 ± 23.80 % in the 1950s to 44.56 ± 20.41 % in 2013 (Fig. 3.8). The following LULC experienced a marginal increase in cover between the 1950s and 2013: exposed rock, ranging from 10.78 ± 11.60 % to 11.98 ± 11.66 %; plantation/woodlots, ranging from 0.35 ± 1.32 % to 2.04 ± 7.52 %; residential/infrastructure, ranging from 1.06 ± 1.74 % to 2.62 ± 5.67 %; shrublands, ranging from 0.12 ± 1.57 % to 5.67 ± 0.39 %; and wetlands, ranging from 1.46 ± 4.14 % to 3.51 ± 7.71 % (Fig. 3.8).

3.3.2.1. Interregional comparison

As previously presented, *A. dealbata* cover increased most significantly in Matatiele, followed by Mount Fletcher and then Maclear (Fig. 3.4 and Fig. 3.9). Bare ground cover, though generally more stable between consecutive periods, increased significantly between 1995 and 2013 in all study areas (Fig. 3.9) from 5.51 ± 5.75 to 15.45 ± 16.02 % in Matatiele (z-ratio = 3.73, $P = 0.001$), 12.08 ± 11.51 to 14.84 ± 13.26 % in Mount Fletcher (z-ratio = 3.76, $P <$

0.001) and 7.28 ± 7.44 to 9.43 ± 9.93 % in Maclear (z -ratio = 3.75, $P = 0.001$). Overall, cultivated land declined significantly in cover ($P < 0.05$) across all study areas between all consecutive and non-consecutive periods (Fig. 3.9). On average, this occurred most drastically in Matatiele, with cover decreasing from 39.35 ± 34.02 % in the 1950s to 13.48 ± 22.47 % in 2013, followed by Mount Fletcher (26.09 ± 32.35 % to 13.92 ± 26.39 %) and then Maclear (24.02 ± 24.17 % to 14.37 ± 21.71 %).

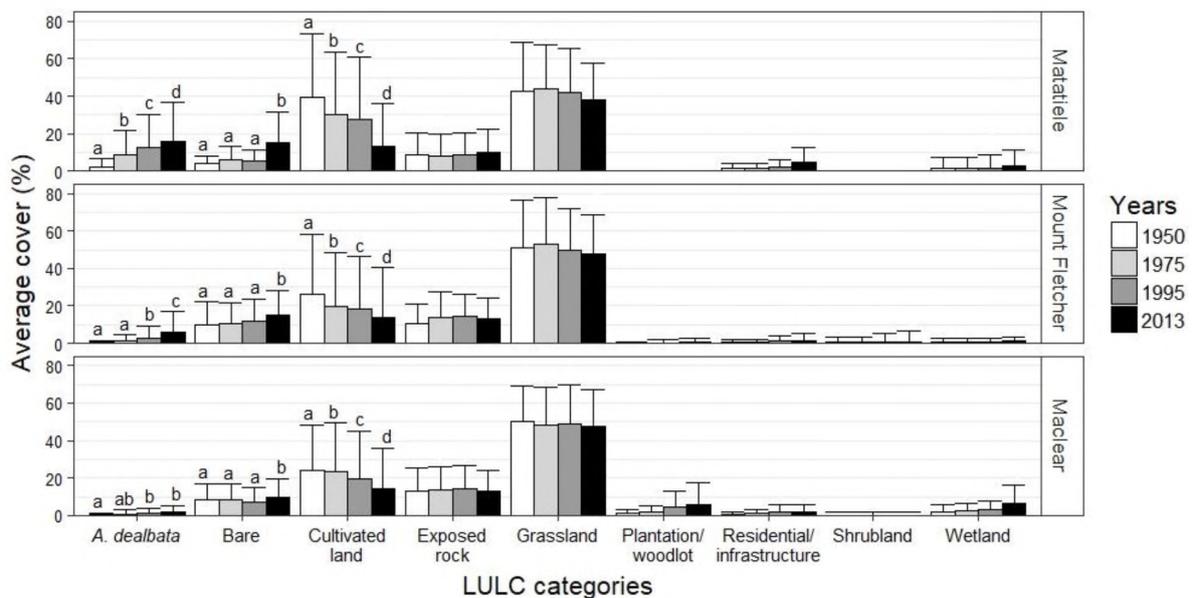


Fig. 3.9: Average LULC change (mean + absolute SD) in three regions in the northern Eastern Cape. Statistically significant differences in cover over time denoted by different letters (a, b, c and d) per LULC class and study area. Significant interregional differences reported in text.

Exposed rock cover experienced insignificant temporal change in all study areas (Fig. 3.9), while significant interregional differences were observed during each period between Matatiele and both Mount Fletcher and Maclear, where the former study area had significantly less exposed rock cover than the latter two (Fig. 3.9). Grassland cover decreased (insignificantly) over time in all study areas. On average, grassland cover was consistently the most abundant in Mount Fletcher (Fig. 3.9), ranging from 51.25 ± 25.51 % (1952) to 47.73 ± 20.81 % (2013), followed by Maclear, ranging from 50.20 ± 18.69 % (1948) to 47.72 ± 19.71 % (2013). During all periods, grassland cover was significantly less in Matatiele, ranging from 42.48 ± 26.11 % (1952) to 38.04 ± 19.41 % (2013), compared to both Mount Fletcher and Maclear ($P < 0.001$). Overall, the plantation/woodlot, residential/infrastructure, shrublands and wetlands LULC categories, where present, experienced insignificant changes in cover over time in all study areas. However, there were significant interregional differences in terms of plantation/woodlot and wetlands, with cover in both categories being significantly higher during all periods in Maclear ($P < 0.001$), compared to both Matatiele and Mount Fletcher (Fig. 3.9).

3.3.2.2. Matatiele

Following the broader scale trends, *A. dealbata* (Fig. 3.5 and Fig. 3.10) and bare ground cover increased, while cultivated land and grassland cover decreased and exposed rock cover remained relatively stable over time in all villages in the Matatiele area (Fig. 3.10). *Acacia dealbata* cover was consistently the highest in Nkasela, followed Outsipan and then Caba (Fig. 3.5 and Fig. 3.10). In terms of bare ground, Caba had a significantly higher cover compared to Nkasela during all periods (Fig. 3.10), with cover reaching 20.93 ± 21.19 % and 10.42 ± 10.97 % by 2013 in each village, respectively. On the other hand, Outsipan, reaching a bare ground cover of 15.04 ± 13.23 % by 2013, did not differ significantly from either Caba or Nkasela (Fig. 3.10). Bare ground increased significantly in all villages ($P < 0.001$) during the 1950s–, 1975– and 1995–2013 timesteps (Fig. 3.10). Except for the 1975–1995 timestep, cultivated land declined significantly in cover ($P < 0.05$) across all villages between consecutive and non-consecutive periods. Both Outsipan and Caba, ranging 44.16 ± 31.88 % to 13.65 ± 15.37 % and 40.56 ± 40.30 to 16.23 ± 31.53 % from 1952 to 2013, respectively, had significantly higher cultivated land cover than Nkasela (ranging 32.90 ± 29.73 % to 10.54 ± 18.47 % from 1952 to 2013) during all time periods.

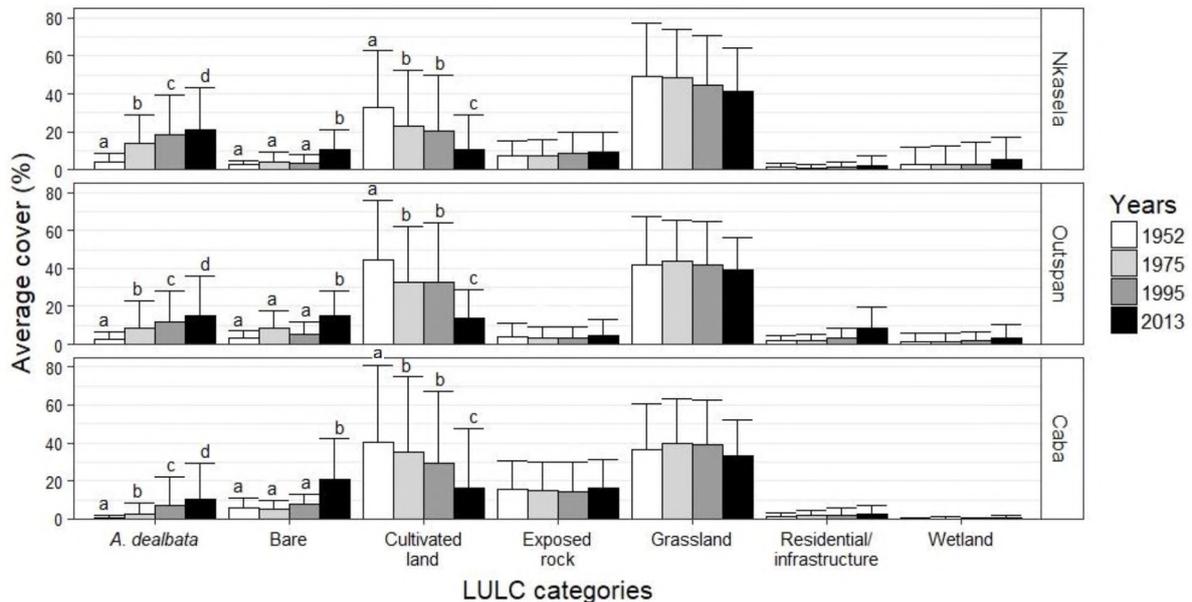


Fig. 3.10: Average LULC change (mean + absolute SD) in three villages in Matatiele. Statistically significant differences in cover over time denoted by different letters (a, b, c and d) per LULC class and study area. Significant intraregional differences in text.

Again, exposed rock and grasslands experienced no significant temporal changes in cover. However, the cover was significantly higher in Caba compared to both Nkasela ($P < 0.01$) and Outsipan ($P < 0.001$) in terms of the former and significantly lower in Caba compared to Nkasela ($P < 0.01$) in terms of the latter during all periods (Fig. 3.10). In the Matatiele area, residential/infrastructure land-use was most extensive in Outsipan (8.69 ± 11.01 %) and

wetlands were most extensive in Nkasela ($5.32 \pm 11.87\%$) by 2013 (Fig. 3.10). Nonetheless, no significant interregional or temporal differences in cover were observed for either of these LULC categories in the region.

3.3.2.3. Mount Fletcher

Acacia dealbata increased gradually across all villages in the Mount Fletcher area, with varying levels of significance over time (Fig. 3.6 and Fig. 3.11). Although consistently higher in Prinstu ($0.89 \pm 1.50\%$ to $8.65 \pm 15.17\%$ from 1952 to 2013), there were no significant intraregional differences in *A. dealbata* cover during any period. Cultivated land experienced significant declines in cover between non-consecutive periods, decreasing significantly over the 1952–1995 ($P < 0.05$), 1975–2013 ($P < 0.05$) and 1952–2013 ($P < 0.001$) timesteps in all villages. HaQhadi, ranging $36.81 \pm 32.42\%$ to $26.78 \pm 33.34\%$ over the latter timestep, was significantly more cultivated than both Fletcherville ($P < 0.001$) and Prinstu ($P < 0.001$) during each period (Fig. 3.11). In turn, Fletcherville, ranging $24.61 \pm 32.90\%$ to $11.32 \pm 25.69\%$ (1952–2013), was significantly more cultivated than Prinstu ($P < 0.005$), which ranged from $12.02 \pm 26.93\%$ to $4.19 \pm 11.19\%$ (1952–2013).

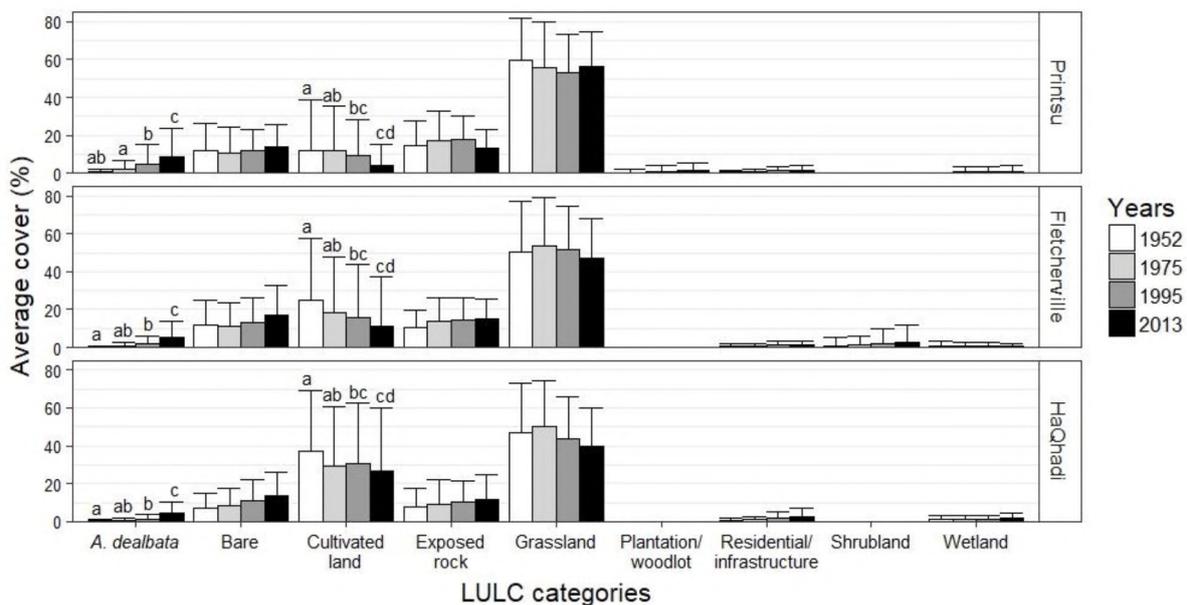


Fig. 3.11: Average LULC change (mean + absolute SD) in three villages in Mount Fletcher. Statistically significant differences in cover over time denoted by different letters (a, b, c and d) per LULC class and study area. Significant intraregional differences in text.

Temporal changes in exposed rock and grassland cover were insignificant across all villages in the region. Exposed rock cover was significantly lower in HaQhadi, compared to both Prinstu and Fletcherville ($P < 0.05$) during all periods, with the mean cover for the three villages in 2013 placed at $11.72 \pm 12.67\%$, $13.22 \pm 10.08\%$ and $15.01 \pm 10.77\%$, respectively. Grassland cover was similarly significantly lower in HaQhadi, compared to both Fletcherville

($P < 0.005$) and Prinstu ($P < 0.001$) during all periods. In 2013, the mean grassland cover for the three villages was 39.58 ± 20.66 %, 47.07 ± 20.66 % and 56.21 ± 18.22 %, respectively. By 2013, Prinstu had the highest plantation/woodlot cover (1.21 ± 4.29 %), Fletcherville had the highest bare ground (17.17 ± 15.48 %) and shrubland (2.80 ± 9.97 %) cover and HaQhadi had the highest residential/infrastructure land-use (2.44 ± 4.43) and wetlands cover (1.66 ± 2.83). However, neither temporal nor intraregional differences in cover were observed for these five LULC categories in the Mount Fletcher area.

3.3.2.4. Maclear

In the Maclear villages, *A. dealbata* cover changed with varying levels of significance over time (Fig. 3.7 and Fig. 3.12). There were insignificant intraregional differences in *A. dealbata* during each period. Although bare ground cover in Katkop, ranging from 5.89 ± 5.34 % in 1948 to 4.42 ± 4.36 % in 2013 (Fig. 3.12), was significantly less ($P < 0.005$) at both Chevy Chase (9.94 ± 10.32 – 12.79 ± 10.59 %) and KuMagwaca (9.20 ± 9.41 – 11.15 ± 11.50 %) during all periods, it did not differ significantly over time in any of the Maclear villages. On the other hand, cultivated land decreased significantly across all villages during the 1950-1995 ($P < 0.05$), 1975–2013 ($P < 0.001$) and 1950-2013 ($P < 0.001$) timesteps, with a significantly higher level of cultivation in Katkop (ranging 27.90 ± 22.84 – 21.47 ± 23.15 % over the latter timestep) compared to Chevy Chase and KuMagwaca ($P < 0.001$) during each period (Fig. 3.12). Similarly, Chevy Chase (24.12 ± 28.75 % to 16.46 ± 24.97 %) was significantly more cultivated than KuMagwaca (20.19 ± 21.07 % to 5.65 ± 13.32 %) during each period (Fig. 3.12).

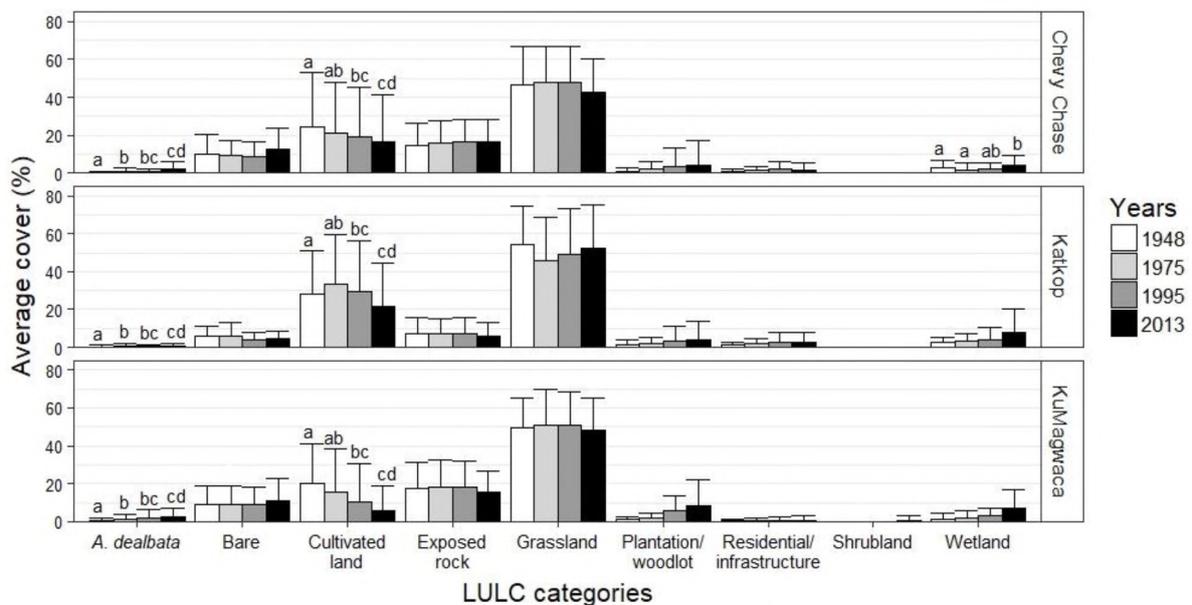


Fig. 3.12: Average LULC change (mean + absolute SD) in three villages in Maclear. Statistically significant differences in cover over time denoted by different letters (a, b, c and d) per LULC class and study area. Significant intraregional differences in text.

The temporal differences in cover for both exposed rock and grasslands were again insignificant for the region (Fig. 3.12). However, interregional differences were observed, as KuMagwaca (17.73 ± 13.81 % to 15.81 ± 10.73 %) and Chevy Chase (14.62 ± 11.51 % to 16.31 ± 12.24 %) both had significantly higher ($P < 0.001$) exposed rock covers than Katkop (7.06 ± 8.39 % to 5.98 ± 7.15 %), whereas Chevy Chase (46.81 ± 19.89 % to 42.57 ± 17.97 %) had a significantly higher ($P = 0.047$) grassland cover than KuMagwaca (49.36 ± 15.89 % to 48.16 ± 17.34 %) during each period. The intraregional differences in cover for the plantation/woodlot, residential/infrastructure, shrubland and wetland LULC categories were insignificant across all villages in the Maclear area (Fig. 3.12). In Chevy Chase, however, there were significant increases in wetland cover over the 1950–2013 (z-ratio = 2.66, $P = 0.039$) and 1975–2013 (z-ratio = 2.64, $P = 0.042$) timesteps (Fig. 3.12).

3.3.3. Proportion of LULC transition

Typically, the proportion of a LULC transitioning from one class to any other class was less than the proportion remaining in the initial class. Furthermore, the proportion of cover remaining in the initial class was often greater than the sum of the cover lost to all other classes. For example, 81.72 % of *A. dealbata* cover at the beginning of the first timestep (1950s) was present at the end of the timestep (1975), while the remaining 18.28 % cover transitioned to one of the other classes, namely: bare (4.74 %); cultivated land (1.18 %); exposed rock (1.55 %); grassland (8.44 %); plantation/woodlots (0.59 %); residential/infrastructure (1.18 %); and wetlands (0.59 %), as illustrated in Fig. 3.13. However, these generalisations were not without their exceptions. For example, only 41.58 % of residential/infrastructure cover in the 1950s remained as residential/infrastructure by 1975, with a substantial proportion (30.24 %) shifting towards cultivated land, whereas none of the shrubland cover present in 1995 remained as such by 2013, with 54.07 % cover shifting to cultivation, 20.06 % to grassland and the remaining 25.87 % to *A. dealbata*, bare, exposed rock and wetlands (Fig. 3.13).

Overall, *A. dealbata* retained an increasingly higher proportion of its existing cover across each successive timestep, with 82.33 % of the *A. dealbata* cover in 1975 remaining in 1995 and in turn, 84.51 % of the cover in 1995 remaining in 2013 (Fig. 3.13). Consequently, a decreasing proportion of *A. dealbata* cover reverted into grasslands, 8.44 % over the first timestep compared to 6.57 % over the third (Fig. 3.13). Bare ground retained approximately 50–60 % of its cover over all timesteps, with a decreasing proportion of bare ground being recovered as grassland, declining from approximately one-third (1950s–1975) to one-quarter recovered (1995–2013), while *A. dealbata* simultaneously invaded an increasing proportion of bare ground with each successive timestep (1950s–1975: 3.51 %; 1975–1995: 4.72 %; 1995–2013: 6.04 %; Fig. 3.13). Cultivated land was more variable in the proportion of cover retained

and lost from one timestep to the next. The proportion of retained cultivated cover increased from 75.47 % (1950–1975) to 81.08 % (1975–1995), and then subsequently decreased to 46.48 % (1995–2013; Fig. 3.13). During each timestep, a higher proportion of cultivated land transitioned to grassland compared to any other LULC class (1950s–1975: 18.76 %; 1975–1995: 15.40 %; 1995–2013: 28.48 %), while the abandonment and subsequent degradation of fields followed with 5.39 %, 3.55 % and 16.05 % of cultivated lands transitioning to bare ground over the first, second and third timesteps, respectively (Fig. 3.13). A comparatively lower proportion of cultivated lands became invaded with *A. dealbata*: 1.51 % during the first timestep, 0.58 % during the second and 2.01 % during the third (Fig. 3.13).

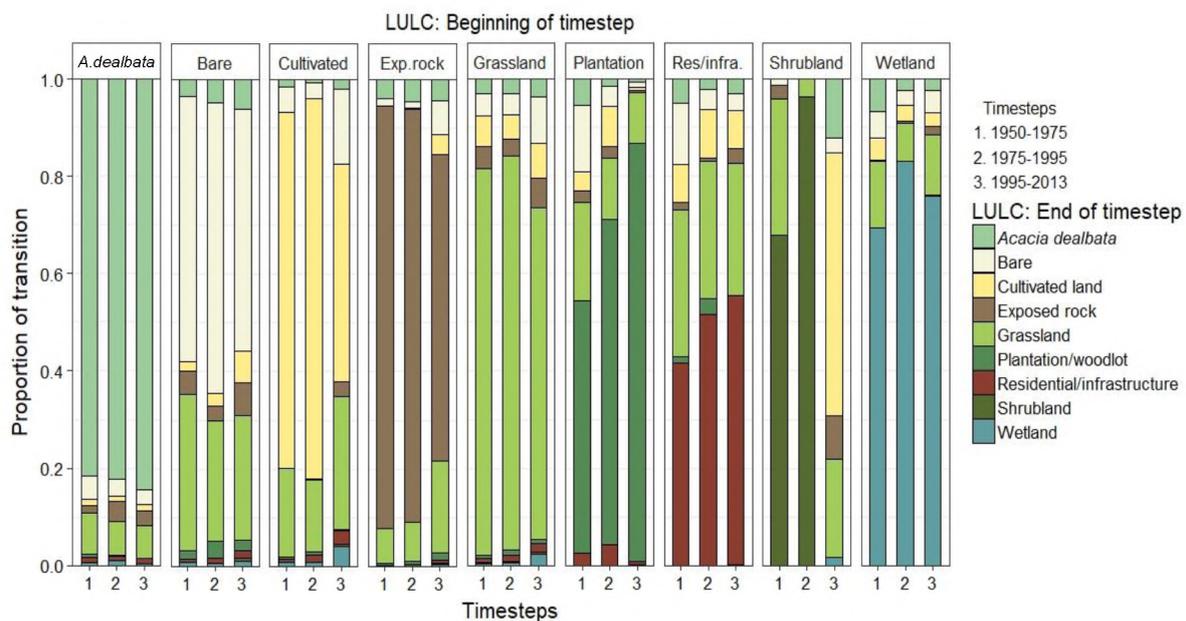


Fig. 3.13: Proportion of LULC transitioning from one class at the beginning of a timestep (top) to another class by the end of the timestep (fill), during each timestep.

Approximately 20 % of grasslands were transformed between the 1950s and 1975, predominantly replaced by cultivated land (6.41 %), followed by bare ground (4.57 %), exposed rock (4.37 %) and *A. dealbata* (2.99 %; Fig. 3.13). Despite a marginal decrease in each of these proportions during the second timestep, 31.58 % of grassland cover transitioned to a different LULC class during the final timestep (Fig. 3.13). Notably, 9.68 % of grassland cover degraded to bare ground, while 7.05 % accommodated cultivation, 6.10 % opened to reveal underlying exposed rock and 3.60 % was invaded by *A. dealbata* (Fig. 3.13).

With each successive timestep, less and less plantation/woodlot cover transitioned to grasslands (1950s–1975: 20.23 %; 1975–1995: 12.73 %; 1995–2013: 10.50 %), bare ground (1950s–1975: 13.72 %; 1975–1995: 4.03 %; 1995–2013: 1.04 %) and *A. dealbata* (1950s–1975: 5.35 %; 1975–1995: 1.52 %; 1995–2013: 0.73 %; Fig. 3.13). Respectively, the proportion of plantation/woodlot cover transitioning to agricultural and residential land-uses

increased from 3.95 % and 2.56 % during the 1950s–1975 timestep to 8.38 % and 4.35 % during the 1975–1995 timestep, then decreased to 0.52 % and 0.63 % during the 1995–2013 timestep (Fig. 3.13). An increasing proportion of cover was retained in the residential/ infrastructure class (41.58–55.25 %) from the first to third timestep, while the proportion of cover transitioning to grasslands, cultivated lands and *A. dealbata* averaged 28.52 ± 1.60 %, 8.62 ± 1.27 % and 3.35 ± 1.48 across the three timesteps, respectively (Fig. 3.13).

Although, most of the shrubland cover was retained across both the 1950s–1975 and 1975–1995 timesteps (67.79 % and 96.41 %, respectively), as previously stated, all shrubland cover present during 1995 was replaced by other LULC classes by 2013 (Fig. 3.13). Wetlands retained 69.35 %, 83.09 % and 75.87 % of their initial cover from the beginning to the end of the timestep for the first, second and third timesteps, respectively (Fig. 3.13). During each timestep, a higher proportion of wetland cover transitioned to grasslands compared to any other LULC class (1950s–1975: 13.64 %; 1975–1995: 7.73 %; 1995–2013: 12.33 %; Fig. 3.13). Notably, 6.74 % of wetland cover was invaded by *A. dealbata* over the first timestep, 2.29 % over the second and 2.35 % over the third. In addition, a fair proportion of wetland cover transitioned to the bare ground class (1950s–1975: 5.36 %; 1975–1995: 3.04 %; 1995–2013: 4.62 %), as well as to the cultivated land class (1950s–1975: 4.69 %; 1975–1995: 3.36%; 1995–2013: 2.87 %; Fig. 3.13).

The remainder of this section will focus on key transitions affecting the *A. dealbata* class at the regional and landscape scales, including null transitions, whereby cover is retained within the *A. dealbata* class over the span of the timestep; negative transitions, resulting in the transition of cover from *A. dealbata* to one or more of the other LULC classes over the timestep; and positive transitions, resulting in the transition of cover from one or more of the other classes to the *A. dealbata* class over the timestep.

3.3.3.1. Interregional comparison

The cover retained, lost and gained by the *A. dealbata* class varied between regions and timesteps. Regionally, Matatiele consistently had the highest proportion of retained *A. dealbata* cover (> 80 %), losing a small proportion of cover to other classes such as grasslands (< 10 %) and bare ground (< 5 %), while simultaneously gaining approximately 6–8 % and 10–15 % of cover from the former and latter classes over time, respectively (Fig. 3.14). Conversely, the proportion of retained *A. dealbata* cover decreased over each successive timestep in Mount Fletcher, from over three-quarters during the first timestep to just over a half during the third, with more than a quarter of *A. dealbata* cover lost to grasslands (21.87 %) and cultivated lands (6.15 %) between 1995 and 2013 (Fig. 3.14). Moreover, an increasing proportion of bare ground, cultivated land and grasslands were invaded in Mount Fletcher,

from approximately one to five percent per class from the first to third timestep (Fig. 3.14). In Maclear, a net increase in the proportion of retained *A. dealbata* cover was observed over time, from almost two-thirds (62.86 %) between 1948 and 1975 to over three-quarters (82.12 %) between 1995 and 2013, as a decreasing proportion transitioned, *inter alia*, to grasslands, bare ground and plantations (Fig. 3.14). In addition, *A. dealbata* decreasingly invaded cultivated lands and increasingly invaded bare ground and grasslands over successive timesteps in Maclear (Fig. 3.14). The differences between *A. dealbata* transitions became more pronounced at the landscape level.

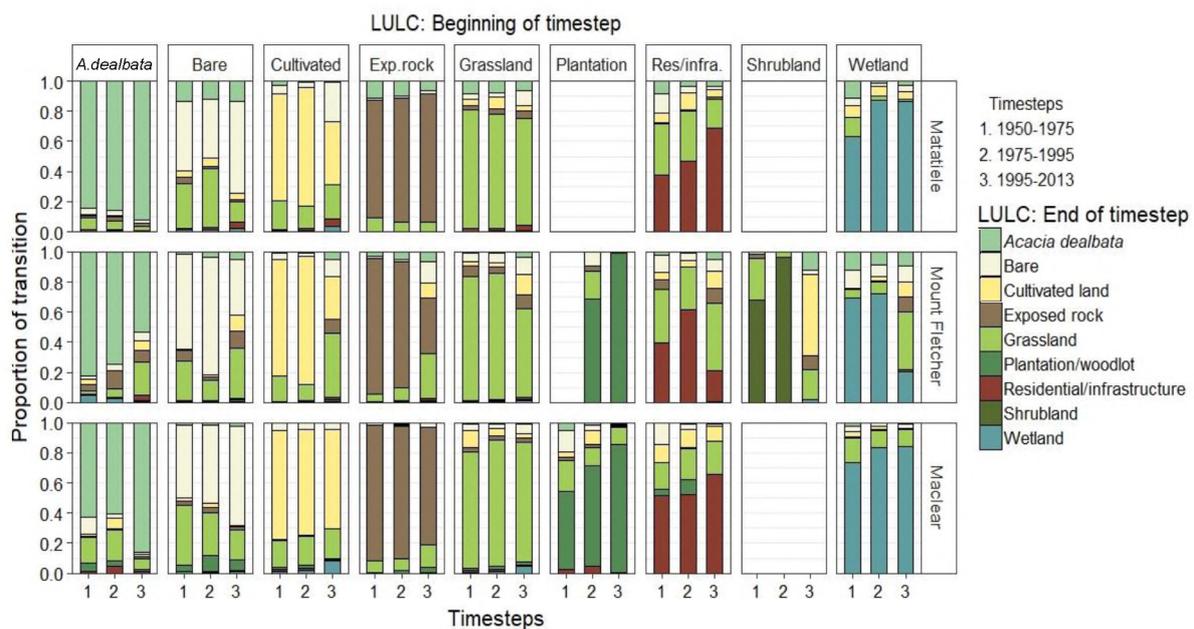


Fig. 3.14: Proportion of LULC transitioning in three northern Eastern Cape from one class at the beginning of a timestep (top) to another class by the end of the timestep (fill), during each timestep.

3.3.3.2. Matatiele

Of the villages in the Matatiele region, Nkasela maintained a consistently high proportion of cover within the *A. dealbata* class over all timesteps (> 85 %), with approximately 3–6 % and 2–3 % transitioning per timestep to grasslands and bare ground, respectively (Fig. 3.15). In addition, *A. dealbata* consistently invaded a high proportion of bare ground in Nkasela, invading between a quarter and a third of bare ground per timestep, while invading a decreasing proportion of grasslands and bare ground over successive timesteps (Fig. 3.15). In Outspan, the proportion of retained *A. dealbata* cover increased (76.29–91.20 %) as a decreasing proportion of cover reverted to grasslands (10.57 % to 3.65 %) from the first to third timestep (Fig. 3.16). Approximately 5–13 % percent of bare ground and 7–9 % of grasslands were invaded per timestep (Fig. 3.15). Similarly, an increasing proportion of *A. dealbata* cover was retained in Caba (71.64–94.53 %) as a decreasing proportion transitioned

to grasslands and bare ground between the first and third timesteps (Fig. 3.15). Approximately 4–12 % of bare ground and 3–6 % of grasslands were invaded per timestep in Caba (Fig. 3.15). Furthermore, almost half of wetlands (47.62 %) in Caba were invaded by *A. dealbata* between 1995 and 2013 (Fig. 3.15).

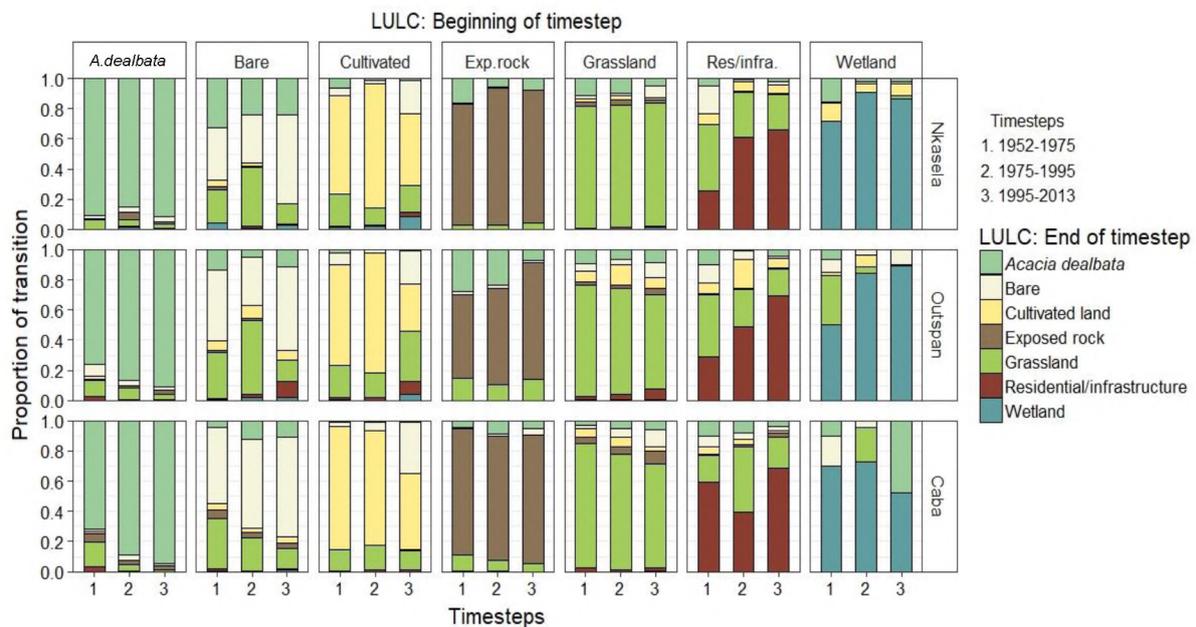


Fig. 3.15: Proportion of LULC transitioning in Matatiele from one class at the beginning of a timestep (top) to another class by the end of the timestep (fill), during each timestep.

3.3.3.3. Mount Fletcher

In the Mount Fletcher region, the highest proportion of *A. dealbata* cover retained between 1952 and 1975 was observed in Printsu (89.16 %), which subsequently decreased to less than three-quarters (73.57 %) between 1975 and 1995, before increasing to 85.56 % between 1995 and 2013 (Fig. 3.16). *Acacia dealbata* most notably transitioned to exposed rock, bare ground and grasslands during each timestep, while increasingly invading bare ground (1.42–6.24 %) and grasslands (2.18–5.05 %; Fig. 3.16). More than 85 % of *A. dealbata* cover was retained over the first timestep in Fletcherville, with cover transitioning, *inter alia*, to bare ground (2.27 %), cultivated land (4.55 %) and wetlands (6.82 %; Fig. 3.16). This decreased to less than three-quarters over the second timestep, with an increasing proportion of cover degrading to bare ground (8.84 %) or reverting to grasslands (6.12 %; Fig. 3.16). However, *A. dealbata* retained almost all its cover (95.85 %) over the third timestep, primarily losing cover to grasslands and wetlands (Fig. 3.16). An increasing proportion of bare ground (0.22–4.91 %) and grasslands (0.38–2.78 %) were invaded by *A. dealbata* over time (Fig. 3.16). In HaQhadi, an increasing proportion of *A. dealbata* was retained over time, from under two-thirds between 1952 and 1975 to over three-quarters between 1995 and 2013 (Fig. 3.16). Simultaneously, an

increasing proportion of bare ground (2.56–8.01 %), cultivated land (0.04–0.75 %) and grasslands (0.27–3.50 %) were invaded over time (Fig. 3.16).

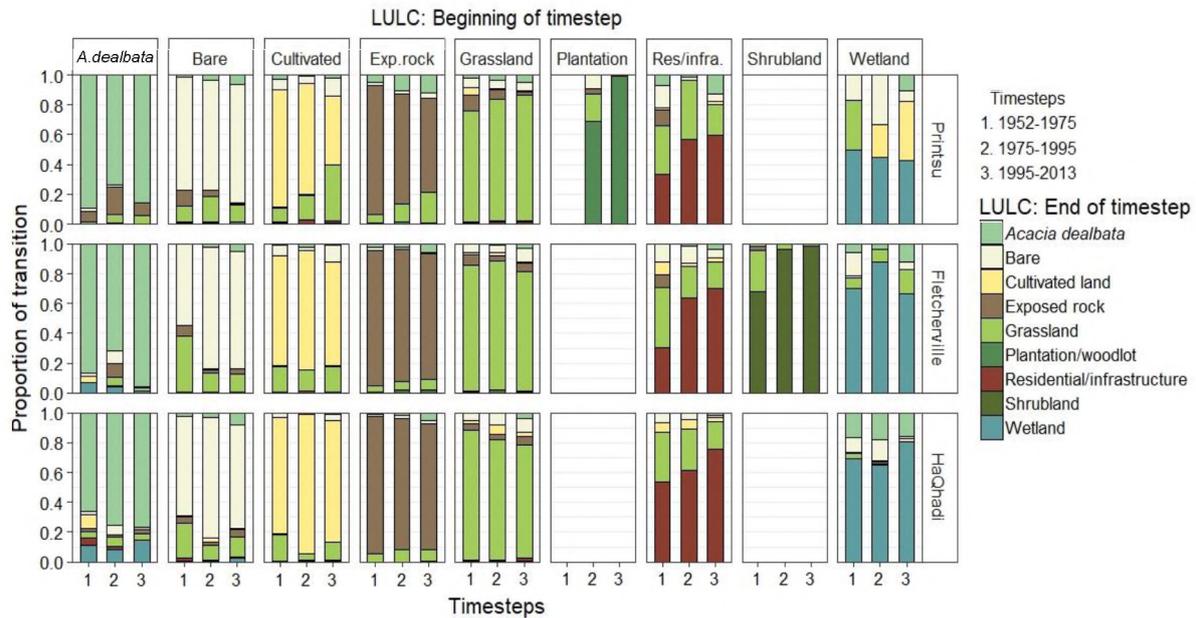


Fig. 3.16: Proportion of LULC transitioning in Mount Fletcher from one class at the beginning of a timestep (top) to another class by the end of the timestep (fill), during each timestep.

3.3.3.4. Maclear

The villages in the Maclear region showed the greatest variation in the proportion of *A. dealbata* cover retained over successive timesteps, compared to both those within the Matatiele and Mount Fletcher regions (Fig. 3.17). In Chevy Chase, the proportion of retained *A. dealbata* cover decreased dramatically from 77.27 % (1948–1975) to 42.22 % (1975–1995), then increased sharply to 81.42 % (1995–2013; Fig. 3.17). The remaining cover primarily transitioned to grasslands (approximately 8–28 %), while a decreasing proportion of cultivated lands and an increasing proportion of bare ground, grasslands and wetlands were invaded by *A. dealbata* over time (Fig. 3.17). Of the villages in the Maclear region, the proportion of retained *A. dealbata* cover was consistently the lowest in Katkop (Fig. 3.17). Over the first timestep, 55.89 % of *A. dealbata* remained intact, with a high proportion transitioning to bare ground (> 20 %) and grasslands (> 10 %; Fig. 3.17). A mere 37.89 % of *A. dealbata* cover was retained over the second timestep, as the remaining cover transitioned, *inter alia*, to grasslands (> 25 %), cultivated lands (> 15 %) and bare ground (> 5 %; Fig. 3.17). The third timestep showed a major increase in the proportion of retained *A. dealbata* cover (79.31 %), with the remaining cover most notably transitioning to grasslands and cultivated lands (Fig. 3.17). Less than three percent of bare ground, cultivated lands and grasslands were invaded per timestep (Fig. 3.17). An increasing proportion of *A. dealbata* was retained in KuMagwaca

from the first to the third timestep (63.38–89.90 %) as less cover transitioned to grasslands, bare ground and plantations (Fig. 3.17). A decreasing proportion of grasslands and plantations were invaded over successive timesteps (Fig. 3.17).

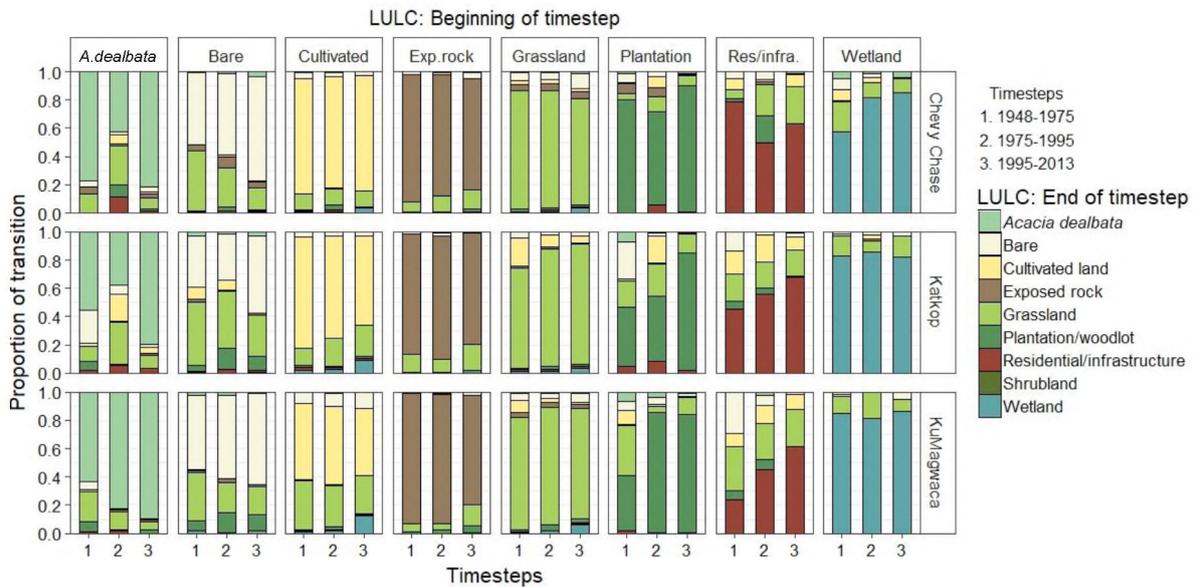


Fig. 3.17: Proportion of LULC transitioning in Maclear from one class at the beginning of a timestep (top) to another class by the end of the timestep (fill), during each timestep.

3.4. Discussion

The results provide evidence supporting three broad conclusions regarding the invasion of *A. dealbata* and broader land cover changes in the northern Eastern Cape. Firstly, invasive spread has undoubtedly occurred in the northern Eastern Cape in the past and will likely continue, barring deliberate intervention. Secondly, broader land-use and cover changes were also apparent in the northern Eastern Cape and, although some LULC classes were more resistant to transition than others and retained a high proportion of cover over time, there was a high degree of variation between regions and landscapes. Thirdly, although there was a net increase in *A. dealbata*, the invasion is highly dynamic, with various LULC transitioning to *A. dealbata*, but in turn *A. dealbata* transitioning to other LULC.

3.4.1. Invasive spread

Acacia dealbata spread at an overall annual rate of 0.11–0.21 % since the 1950s, occupying approximately 8–18 % of land cover across all sampled sites in the northern Eastern Cape by 2013. Although the aerial cover of *A. dealbata* cover increased at all sites, the extent and rate of spread revealed a high degree of spatial variation, both across regions and landscapes. Regional annual spread rates ranged from 0.02–0.06 % in Maclear to 0.22–0.38 % in

Matatiele, whereas landscape-level spread rates ranged from 0.006–0.013 % in Katkop to 0.31–0.49 % in Nkasela.

While any comparison of invasive spread rates should certainly acknowledge the “limitations involved in comparing the spread rates associated with the differing sized areas and populations monitored of previous studies” (Hernández *et al.*, 2014: 211), the rates of invasive spread quantified in this study are within a comparable range of spread rates reported in similar studies. Most notably, Hernández *et al.* (2014) found that forested areas in northwestern Spain were invaded by *A. dealbata* and *A. melanoxylon* at annual rates of 0.083 % and 0.10 % (1998–2008), respectively. On the other hand, De Neergaard *et al.* (2005) tracked the extent of *Acacia* through time in two areas in Madlangala, a village approximately 50 km northwest of Matatiele, where cover increased from 7–48 % in one plot (0.87 % annually) and 20–58 % in the other (0.81 % annually) between 1953 and 2000. However, unlike Hernández *et al.* (2014), De Neergaard *et al.* (2005) did not differentiate between *Acacia* species and instead measured the combined cover of *A. dealbata* and *A. mearnsii*. Far to the southwest, Seath (2017) reported an annual rate of *A. dealbata* spread of 0.03 % between 1938 and 2017 on Glenfinlas farm (near Cathcart, Eastern Cape), despite the implementation of control efforts. This supports the general trend of a decreasing rate of annual *A. dealbata* spread from the northern to more southern parts of the Eastern Cape.

Currently, the invasion of *A. dealbata* in northern Eastern Cape is characteristic of a late stage biological invasion, supported by three broad pieces of evidence corresponding to themes discussed in the first chapter of this thesis, namely the invasion process, the impacts of biological invasion and the management of IAPs. Firstly, *A. dealbata* has passed through each phase of invasion (*sensu* Richardson *et al.*, 2000). Starting with its introduction, through its establishment and naturalisation, to its eventual proliferation across the landscape, *A. dealbata* surmounted geographical, environmental, reproductive and dispersal barriers (Richardson *et al.*, 2000) to become widespread and abundant across the northern Eastern Cape (Nel *et al.*, 2004). Despite its prevalence in the landscape, *A. dealbata* continues to spread rapidly and will likely continue to do so. Assuming the entire landscape were suitable for invasion, *A. dealbata* could theoretically invade between 12 % and 26 % of northern Eastern Cape by 2050, based on the overall annual increase of 0.11–0.21 %. This would undoubtedly have severe implications, compounding the social, economic and ecological impacts of the invasion, as well as posing further challenges for management.

Secondly, the impacts and shifting perceptions surrounding *A. dealbata* also illustrate the stage of invasion in the northern Eastern Cape. The extent and rate of biological invasion influences the magnitude of impact, the perceptions regarding the invader and the strategies adopted to manage the species (Parker *et al.*, 1999; Pyšek and Hulme, 2005; Shackleton *et*

al., 2007; Ricciardi *et al.*, 2013; Trueman *et al.*, 2014; Kumschick *et al.*, 2015). During the early, low abundance stage of invasion, the potential benefits of species have yet to be fully realised and enjoyed by most of the community (Shackleton *et al.*, 2007). As the abundance increases and the species becomes more readily accessible and more widely utilised by local communities, the costs gradually increase and, at some stage, may exceed the benefits (Shackleton *et al.*, 2007). Although an extensive cost-benefit study would be required to unequivocally determine whether the costs of *A. dealbata* have indeed exceeded its benefits in the northern Eastern Cape, Ngorima (2016) provides evidence suggesting that *A. dealbata* is currently in a later phase of invasion (*sensu* Shackleton *et al.*, 2007).

According to Ngorima (2016), the presence of *A. dealbata* at the sampled study sites predates 1930 since the eldest villager reports that it was present, though not yet abundant, at the time of their birth. Notwithstanding the low abundance at the time, *A. dealbata* was already a valued resource to locals such that restrictions were put in place to control access (Ngorima, 2016). The abundance of *A. dealbata* continued to slowly increase in the northern Eastern Cape between 1930 and 1994 in spite of land clearances for human settlement and an increased harvest rate, which coincided with local human population growth area (Ngorima, 2016). Following the dismantlement of apartheid and the subsequent rural-urban migration of many young people searching for work in the cities, the use of *A. dealbata* decreased at the sampled sites (Ngorima, 2016). Moreover, the status of *A. dealbata* as a valuable source of energy has waned as more households have been supplied with electricity (Ngorima, 2016). Reportedly, locals' perceptions surrounding *A. dealbata* have also become increasingly negative since the launch of WFW clearing programmes in the area, which have raised local awareness regarding the impacts of *A. dealbata* and other IAPs (Ngorima, 2016). Additionally, many locals admitted that the species often grows in undesirable areas (near homesteads, in and around fields and gardens, along watercourses and at cultural sites) and locals have become increasingly fearful of criminals hiding in dense *A. dealbata* patches (De Neergaard *et al.*, 2005; Ngorima, 2016).

Finally, the management and control options available to tackle the invasion of *A. dealbata* in the northern Eastern Cape allude to the fact that the species is currently in a late stage of invasion. As previously discussed, the strategy of IAP management depends on the stage and extent of the invasion (Hulme, 2006; Ntshotsho *et al.*, 2015; Witt *et al.*, 2017). Prevention and eradication are typically preferred for early-stage and geographically-restricted IAPs and often are unfeasible for abundant and widespread invaders (Van Wilgen *et al.*, 2000) as in the case of *A. dealbata* in the northern Eastern Cape. *Acacia dealbata* is listed as a Category 2 species, (declared invader with potential commercial value) under the official *Alien and Invasive Species Regulations* of NEMBA and may only be planted in managed plantations under

permitted conditions, with adventitious populations requiring control or eradication, particularly those growing in riparian zones (RSA, 2004, 2014a, 2014b).

Historically, the implementation of control initiatives to address *A. dealbata* invasions in South Africa further suggest and support the notion that the species is currently in a late stage of invasion. For example, since its inception in 1995, the WFW initiative has largely targeted IAP control measures at invasive Australian Acacias, including *A. dealbata* (Van Wilgen *et al.*, 2011; Van Wilgen and Wannenburg, 2016). The limited success of the WFW initiative to control *A. dealbata* and other IAPs over the long-term through purely mechanical and chemical methods has since spurred the exploration of alternative control options, namely the inclusion and integration of biological control into existing management strategies (Moran *et al.*, 2013; Van Wilgen and Richardson, 2014; Van Wilgen and Wannenburg, 2016).

For widespread and late-stage invaders such as *A. dealbata*, biological control is arguably the most efficient, effective and sustainable means of control (Van Wilgen *et al.*, 2012b). The impetus of this current study to determine the necessity of introducing a biological control substantiates the claim that the *A. dealbata* invasion in the northern Eastern Cape is a growing concern. Furthermore, a precedent for deploying a biocontrol agent on *A. dealbata* was already set in South Africa, almost two decades ago, when seed-feeding weevils (*Melanterius maculatus*) were introduced in 1998 in attempt to control *A. dealbata* (Impson *et al.*, 2011). This speaks to the long-standing social-ecological interaction between *A. dealbata* and local communities, as well as the management imperatives aimed at controlling the invasion.

3.4.2. Broader land-use and cover changes

Acacia dealbata cover increased in the northern Eastern Cape over time along with bare ground and to a lesser extent plantation/woodlot, residential/infrastructure, shrubland and wetland cover. On the other hand, cultivated land and grassland cover tended to decrease over time. The overarching trends in LULC change in the northern Eastern Cape echo those in other LULC studies in the province. For example, Manjoro *et al.* (2012) found an increase in soil erosion and woody *Pteronia incana* encroachment in a catchment near Peddie town in the Ngqushwa district of the Eastern Cape, reporting a 3.23 % increase in severely eroded cover and an 11.51 % increase in slightly eroded, dense bush cover between 1998 and 2008. In the Willowvale area, Shackleton *et al.* (2013) found an increase in deagrarianisation along the Wild Coast in the Eastern Cape over the last 50 years, with a distinct decrease in field cover from 12.5 % to 2.7 % and increase in abandoned field cover from 1.5 % to 6.9 % (1961–2009). In addition, simultaneous woody encroachment was evident as forests and woodlands increased by five percent and 14.9 %, respectively, while grasslands decreased by almost a quarter (Shackleton *et al.*, 2013).

Similarly, Puttick *et al.* (2011) and Stickler and Shackleton (2015) found an increase in woody encroachment at the expense of grassland commons in Bathurst in the Eastern Cape between the 1940s and 2004. Conversely, across the Eastern Cape province, Schoeman *et al.* (2010) found that cultivated land, despite momentarily declining to 2.9 % between 1994 and 2000, retained a constant cover of approximately eight percent between 1994 and 2005, while urban and plantation land-uses expanded by 1.1 % and 0.3 % (1994–2005), respectively. However, Schoeman *et al.* (2010) also found that national changes reflected an overall decline in cultivated cover (12.4–11.9 %) and an increase in urban (0.8–2.0 %), plantation (1.2–1.6 %) and mining (0.1–0.2 %) cover between 1994 and 2005.

Collectively, these studies are indicative of contemporary national and international environmental and LULC changes, namely an increase in soil erosion and land degradation (e.g. Manjoro *et al.*, 2012; Nkonya *et al.*, 2013; Rutherford *et al.*, 2013; Dlamini *et al.*, 2014); deagrarianisation (e.g. Díaz *et al.*, 2011; Shackleton *et al.*, 2013; Connor and Mtwana, 2017; Pritchard *et al.*, 2017); industrialisation, infrastructure development and urban sprawl (e.g. Gavier-Pizarro *et al.*, 2010; Zhang *et al.*, 2013; Liu *et al.*, 2014; Teixeira *et al.*, 2014); bush encroachment (e.g. Puttick *et al.*, 2011; Manjoro *et al.*, 2012; Shackleton *et al.*, 2013; Stafford *et al.*, 2017); and the invasion of IAPs (e.g. De Neergaard *et al.*, 2005; Kannan *et al.*, 2013; Hernández *et al.*, 2014; Wilson *et al.*, 2014; Masocha *et al.*, 2017; Montti *et al.*, 2017; Stafford *et al.*, 2017).

3.4.3. Dynamism of invasion and LULC change

Markedly dynamic, multi-directional and spatio-temporally variable LULC transitions were observed across the northern Eastern Cape over the last six decades. The *A. dealbata* class frequently retained a high proportion of its cover over time. Moreover, the proportion of *A. dealbata* cover transitioning to already-extensive LULC classes contributed a relatively small aerial gain to each of the respective recipient classes. Conversely, even a small proportion of cover transitioning from extensive LULC classes to *A. dealbata* could potentially contribute a substantially large area to the invasion. For instance, *A. dealbata* and grasslands occupied approximately one percent and 48 % cover in the 1950s, respectively. However, were a tenth to transition from each class to the other, *A. dealbata* would gain almost five times more cover than grasslands. Despite the loss of *A. dealbata* cover to other LULC classes, including the degradation of wattle patches to bare ground, the clearance of woody species for cultivation or the recovery of formerly invaded areas to grasslands, a net increase in *A. dealbata* cover occurred as *A. dealbata* increasingly spread to previously uninvaded locations.

Lambin and Meyfroidt (2010: 109) assert that LULC transitions “. . . must be viewed as multiple and reversible dynamics” to understand the variable, indeterministic and non-linear nature of

LULC change, acting in concert with broader social and environmental changes. Both biological invasions and broader LULC changes are highly dynamic processes, etched into the social-ecological fabric of the landscape (With, 2002; Harden *et al.*, 2014). Dynamic LULC transitions can be attributed to a multitude of interacting cultural, demographic, economic, environmental, political, social and technological drivers (Lambin and Meyfroidt, 2010; Meyfroidt *et al.*, 2013; Munroe *et al.*, 2014; Tizora *et al.*, 2016).

South Africa has had an especially tumultuous history, intertwining social injustice and political upheaval with economic development, environmental change and land reform. The abolishment of apartheid in 1994 brought about significant changes in land access, use and tenure in South Africa, resulting in more pronounced, frequent and widespread changes in LULC (Giannecchini *et al.*, 2007; Puttick *et al.*, 2011; Stickler and Shackleton, 2015; Tizora *et al.*, 2016). For example, Shackleton *et al.* (2013) noted that, despite a steady increase in deagrarianisation over the last half-century, peak field abandonment along the Wild Coast coincided with the advent of democracy in South Africa. This may be attributed to the coalescence of shifting socio-economic and political priorities, away from local resource- and livestock-based assets towards social grant and income-based investments, and away from state-supported livestock farming and rural development towards urban development, respectively (Shackleton *et al.*, 2013).

3.5. Conclusion

This chapter tracked the historical progression of the *A. dealbata* invasion at sampled sites in the northern Eastern Cape using a time-series of aerial photographs and GIS-based mapping techniques, highlighting the spatio-temporal variability of invasive spread and broader land cover changes at different scales. The spatio-temporal landscape approach adopted here quantified the extent and rate of invasion, complimenting and echoing the sentiments of the local communities residing in these areas that *A. dealbata* has indeed spread to undesirable levels, as expressed in focus group discussions held by Ngorima (2016). Although *A. dealbata* has become increasingly widespread in these areas, invasive spread differs significantly from one landscape or region to another. Broader land-use and cover changes show a similar degree of spatio-temporal variation. Moreover, certain LULC classes and histories may be more susceptible to invasion than others (Vilà and Ibáñez, 2011). For example, in the northern Eastern Cape, bare ground, cultivated land and grasslands were found to be particularly susceptible to the invasion of *A. dealbata*. Indeed, biological invasions are dynamic, context-specific phenomena, shaped by the inherent heterogeneity of landscapes (Theoharides and Dukes, 2007; Vilà and Ibáñez, 2011). A spatio-temporal perspective can therefore provide a better understanding of biological invasions and broader LULC changes in the landscape, informing the effective management of IAPs. The chapter to follow will further explore the

relationship between the abundance of *A. dealbata* and different biophysical and LULC conditions.

CHAPTER FOUR: ABUNDANCE AND CORRELATES OF INVASION

Abstract

An increase in the density and biomass of woody invasive plants contributes to the intensification of ecological impacts and can often be met with dissatisfaction by local communities. Villagers in the northern Eastern Cape have expressed concerns about the high densities of *Acacia dealbata*, linking dense thickets to recent criminal activity, as well as a general sense of fear for the safety of children on the way to school and for women harvesting firewood. Although *A. dealbata* is a valued resource and should not be completely eradicated, villagers would prefer lower densities. To effectively manage this highly invasive species, while not undermining the livelihood needs of the local villagers, it is critical to take inventory of the current abundance of *A. dealbata* in the area. This study sought to determine the growth rate and current abundance of *A. dealbata* in selected locations and landscapes in the northern Eastern Cape. Research was conducted in nine villages in rural Matatiele, Mount Fletcher and Maclear. Standard ecological and vegetation survey techniques were adopted to quantify the density, biomass and growth rate of *A. dealbata*, while principal component analysis (PCA) and multiple regression analysis (MRA) were used to determine the correlates of the *A. dealbata* invasion. Overall, the average density, biomass and productivity of *A. dealbata* were estimated at approximately 7 000 stems.ha⁻¹, 12 t.ha⁻¹ and 4 t.ha⁻¹.yr⁻¹, respectively. However, the results showed that the abundance and productivity of *A. dealbata* were spatially variable between study areas. *Acacia dealbata* stems experienced significant growth over the period of a single year, contributing to substantial biomass production at the landscape level, despite continued harvest. Furthermore, relatively few biophysical variables were significantly influential correlates with the abundance of *A. dealbata*, with the presence of low grass cover being the most significant correlate of high *A. dealbata* densities and biomass. Any management interventions to limit or control *A. dealbata* should therefore consider the local-scale abundance, productivity and biophysical conditions of the area, while taking into consideration the livelihood requirements of the local communities.

4.1. Introduction

This chapter deals with the second objective, namely to determine the growth rate and current abundance of *A. dealbata* in selected locations and landscapes. Complementing the landscape perspective of invasive spread in the previous chapter, this chapter opens with an overview of the local-scale dynamics of biological invasions. This includes a focus on the relationship between the abundance of the IAP, species invasiveness, habitat invasibility, the impact of the invasion and the perceptions surrounding the species. The methods and results

then are described, followed by a discussion of pertinent findings in this chapter, leading to the concluding chapter of this thesis.

4.1.1. Biological invasion at the local scale

Invasion ecology literature supports the notion that “landscape configuration . . . is of primary importance to the presence and establishment of alien species while local scale factors . . . are of key importance for population growth” (Vilà and Ibáñez, 2011: 463). Moreover, while quantifying the aerial extent of IAPs is undoubtedly important for understanding the spatio-temporal dynamics of biological invasions in the landscape, assessing the growth and abundance of the invader at the ground-level offers deeper insights into the local-scale dynamics of invasion (Theoharides and Dukes, 2007; Vilà and Ibáñez, 2011; Cross *et al.*, 2017). The abundance and growth of an invasive plant population, as well as the local-scale biophysical conditions of the area, may determine the overall success of the biological invasion (e.g. Davis *et al.*, 2004; Taylor and Hastings, 2004; Carboni *et al.*, 2016); the magnitude of impact (e.g. Parker *et al.*, 1999; Kumschick *et al.*, 2015; Panetta and Gooden, 2017); the perceptions surrounding the species (e.g. Shackleton *et al.*, 2007; Shackleton *et al.*, 2015a; Ngorima, 2016); and the options available for managing the species (e.g. Van Wilgen *et al.*, 2000; Panetta and Gooden, 2017; Witt *et al.*, 2017). Consequently, traditional ecological inquiry and fieldwork remain a staple of invasion science research (Richardson, 2011).

4.1.1.1. Invasiveness, invasibility and degree of invasion

The success and degree of biological invasion (i.e. the measure of currently invaded habitat) hinge on the invasiveness of the species, the suite of characteristics affording the species a competitive advantage, as well as the invasibility of the habitat, the intrinsic susceptibility of the habitat to invasion given the favourability of the local biophysical conditions (Carboni *et al.*, 2016; Hui *et al.*, 2016). As previously discussed, the invasiveness of an IAP species may depend on its superior biological traits, competitive ability and/or preadaptations to certain biophysical conditions, while the invasibility of the habitat may depend on the structure, composition and stability (or rather, instability) of the local environment and its surroundings (Hufbauer and Torchin, 2008; Hui *et al.*, 2016). Identifying the universal traits and correlates of invasiveness and invasibility has long been an objective of, and challenge to, invasion ecologists (Drake *et al.*, 1989; Alpert *et al.*, 2000; Pyšek and Richardson, 2008; Guo *et al.*, 2015; Mainali *et al.*, 2015).

Invasive plant species are commonly early-successional r-strategists (Ordoñez *et al.*, 2010; Fuentes-Ramírez *et al.*, 2011). Consequently, rapid germination, growth and maturation, as well as high reproductive rates, are traits typically associated with invasiveness amongst IAPs (Chamier *et al.*, 2012; Parker *et al.*, 2013; Souza-Alonso *et al.*, 2017). In addition, the

densification and proliferation of IAPs can be accelerated and amplified through vegetative propagation and coppice regeneration, prevalent strategies amongst invasive genera such as *Acacia* (Pyšek and Richardson, 2008; Lorenzo *et al.*, 2010a; Le Maitre *et al.*, 2011). Moreover, Parker *et al.* (2013) recently confirmed the long-suspected notion that, although there is a high degree of species specificity, IAPs generally grow larger, reproduce more effectively and become more abundant in their introduced range compared to their native ranges, *inter alia*, by escaping natural enemies, introducing novel weapons and outcompeting native species. The survival and growth of an individual organism may also improve at higher population densities due to collective defences, reduced inbreeding and increased reproductive success (Stephens *et al.*, 1999). Sparse non-native populations can, in some cases, succumb to Allee effects, which hinder the establishment of a potential invader (Tobin *et al.*, 2011).

Allee effects manifest from a positive correlation between population density and the fitness of the individual, whereby the population becomes vulnerable to local extinctions at low densities and increasingly resilient at higher densities (Stephens *et al.*, 1999). For example, Davis *et al.* (2004) found that *Spartina alterniflora*, an invasive cordgrass in Willapa Bay (Washington, USA), produced fewer viable seeds per capita at lower densities than when integrated into the larger, denser rhizomatous network. However, Taylor and Hastings (2004) found that rapid vegetative propagation can overcome Allee effects in sparse populations of *Spartina alterniflora*. Consequently, many highly invasive IAPs (such as *Spartina* and *Acacia* spp.) can circumvent deleterious Allee effects at lower densities through rapid vegetative propagation and long-distance pollination and seed dispersal, while exploiting beneficial Allee effects at higher densities by ousting native competitors, and in the case of woody invaders, limiting the access of herbivores and fuelwood harvesters to the interior of dense patches.

Local-scale biophysical characteristics of the environment determine the susceptibility and degree of habitat invasion (Vilà and Ibáñez, 2011; Guo *et al.*, 2015; Carboni *et al.*, 2016; Grace *et al.*, 2017). Although these characteristics are highly contextual and species-specific (Perkins and Nowak, 2013; Pyšek and Chytrý, 2014), invulnerable and invaded habitats are often associated with early ecological succession (Shea and Chesson, 2002); frequent disturbances (Sax and Brown, 2000; Dietz and Edwards, 2006); a fluctuating availability of resources (Davis *et al.*, 2000; Pyšek and Chytrý, 2014); the underutilisation of niches (Elton, 1958); and/or deficiencies in biotic resistance, i.e. low native species cover, diversity and/or richness (Elton, 1958; Levine *et al.*, 2004). Correspondingly, the presence and abundance of the invader can alter components of the invaded habitat to increase invasibility (Chamier *et al.*, 2012; Simberloff *et al.*, 2013). The biophysical composition of a landscape can differ significantly between habitat patches, depending on the degree of invasion, specifically the abundance of the invader (e.g. Sitters *et al.*, 2013; Monteiro *et al.*, 2017).

4.1.1.2. Impacts and perceptions

The impacts of an IAP are largely contingent on the extent and abundance of the species in the introduced habitat (Parker *et al.*, 1999; Ricciardi *et al.*, 2013; Kumschick *et al.*, 2015). However, not all plant introductions result in significant impact (Richardson *et al.*, 2000). Jeschke *et al.* (2014: 1190-1192) assert that the “thresholds of impact are potentially important because they relate to the magnitude and potential reversibility of different changes.” Many socio-economic and ecological systems are sufficiently resilient to the impact of IAPs to a certain abundance threshold, beyond which the impact of the invasion can become increasingly detrimental as the abundance of the species increases (Jeschke *et al.*, 2014; Panetta and Gooden, 2017). For example, Gooden *et al.* (2009) found a non-linear relationship between invasive *Lantana camara* cover and native species richness in southeastern Australia, whereby species richness remained unaffected below a threshold of three-quarters *Lantana* cover, but decreased substantially above this threshold.

While many impacts of an IAP may only occur beyond an abundance threshold (Jeschke *et al.*, 2014; Panetta and Gooden, 2017), a few impacts are observed even at low IAP population densities (Malinichi *et al.*, 2017). Nonetheless, unrestrained increases in the abundance of IAPs could result in more severe and widespread ecological and socio-economic impacts, which may include an accelerated loss of native species biodiversity, richness and cover; more drastic shifts in disturbance regimes; changes in nutrient and hydrological cycles; an increase in economic losses; and a decrease in ecosystem services (e.g. Le Maitre *et al.*, 2000; Reaser *et al.*, 2007; Richardson *et al.*, 2007; Binimelis *et al.*, 2008; De Lange and Van Wilgen, 2010; Pyšek *et al.*, 2012b; Meiners and Pickett, 2013).

Similarly, the local perceptions of an IAP species depend on the extent and abundance of the species, in addition to other familiarity factors, including the residence time of species in its introduced range, the reason(s) for introduction and the proximity of the species to the surrounding communities; biophysical characteristics, including the invasiveness of the species and the invasibility of the habitat; and the social context, including the use and value of the species, the resource requirements of the local communities, resource access and the accompanying local norms, traditions and broader legislative frameworks guiding the harvest and use of the species (Shackleton *et al.*, 2007; Kull *et al.*, 2011; Rai *et al.*, 2012; Shackleton *et al.*, 2015a; Souza-Alonso *et al.*, 2017). An increase in the abundance of an IAP species can therefore be welcomed by some, while being met with discontent by others, depending on the dynamic social-ecological context (Shackleton *et al.*, 2007). Conflicting perceptions surrounding an IAP species pose management challenges, which in turn impede control efforts (Dickie *et al.*, 2014; Hoffman, 2014; Zengeya *et al.*, 2017).

4.1.2. Abundance and correlates of *A. dealbata* in the northern Eastern Cape

An increase in the density and biomass of woody invasive thicket contributes to the intensification of ecological impacts and can often be met with dissatisfaction by local communities (Shackleton *et al.*, 2007). According to Ngorima (2016), villagers in the northern Eastern Cape have already expressed concerns about the high densities of *A. dealbata*, linking dense thickets to recent criminal activity, including cases of livestock theft in Caba and a burglary at a local school in Chevy Chase, as well as a general sense of fear for the safety of children on the way to school and for women harvesting firewood. Consequently, most villagers (>80 %) reportedly stated that although *A. dealbata* is a valued resource and should not be completely eradicated, they would prefer lower densities (Ngorima, 2016). To gain ground-level insights into the current state of the invasion, this study sought to determine the growth rate and current abundance of *A. dealbata* in selected locations and landscapes in the northern Eastern Cape, answering the following questions i) What is the growth and production rate of *A. dealbata*?; ii) What is the current density and biomass of the invasion in different landscapes?; and iii) Is the invasion associated with any specific biophysical conditions?

4.2. Methods

Standard ecological and vegetation survey techniques were employed to quantify the density, biomass and growth rate of *A. dealbata* (Bullock, 2006). Biophysical characteristics were then summarised for different density and biomass classes to provide an invasion profile for *A. dealbata*. Thereafter, these data were analysed to identify the correlates of invasion, i.e. the biophysical and/or land-use conditions associated with the abundance of *A. dealbata*.

4.2.1. Data collection

The count-plot method (Mueller-Dombois and Ellenberg, 1974) was used to determine the density of *A. dealbata*. Seventy-seven 20 m x 10 m plots ($n = 8-10$ for each of the nine villages) were randomly sampled from the 2013 ACA maps (Chapter 3) in ArcGIS (ESRI, 2011). The coordinates of each plot were recorded, located in the field using a GPS and marked. For each plot, the slope (Abney level), altitude (GPS), slope position (six-point scale) and aspect (compass) were recorded (Shackleton *et al.*, 2013). Stem diameters were measured at a height of 35 cm above ground level on the downslope side of the stem. The height of measurement was selected instead of the diameter at breast height (DBH) to be more inclusive of shorter stems and cut stems. Only stems with a diameter of 10 mm or more at the specified height were measured, while stems less than 10 mm in diameter were counted as seedlings. Each stem of multi-stemmed individuals was measured. Both living and dead stems were measured and noted as such. The presence of flowers and/or pods on the stem and any evidence of burning and/or chopping on stems were also recorded.

Percentage cover of rock, bare ground, litter, grass, *A. dealbata* and other woody species were estimated visually. The species and number of individuals per species were recorded for all woody species in each plot. Specimens were collected and identified in the Selmar Schonland Herbarium if unknown at the time. Soil samples were collected at an approximate depth of 10 cm from a 1 m x 1 m quadrat located in the bottom left corner of each plot. Additional soil samples were collected from outside of the plots, approximately 50 m along the contour of the sampled plot (n = 63). In the laboratory, preliminary analyses were conducted on the soil samples to determine the pH and organic carbon content.

A subsample of approximately 50 g from each soil sample was sieved through a two millimetre mesh to remove larger particles (Head, 2006). The procedure described by Okalebo *et al.* (2002) was used to determine the soil pH. For each sample, 20 g of sieved soil was weighed out into a 100 ml beaker, 50 ml of distilled water was added and the mixture was stirred for 10 minutes. After letting stand for 30 minutes, the mixture was vigorously stirred for two minutes. A calibrated electronic pH meter was then used to measure the pH of the suspension.

The loss on ignition method was used to determine the organic carbon content of the soil samples (Head, 2006). Empty crucibles were heated in a muffle furnace at 400 °C for one hour, then allowed to cool to room temperature in a desiccator. The mass of each crucible was measured to the nearest 0.0001 g using an electronic scale and recorded. Approximately ten grams of each sieved sample was carefully spooned into individual crucibles, the combined mass of soil and crucible were recorded, and the mass of the crucible was subtracted to give the total mass of the soil to the nearest 0.0001 g. Thereafter, the filled crucibles were placed in the muffle furnace at 400 °C for four hours, then removed and allowed to cool to room temperature in the desiccator. The ash-filled crucibles were then reweighed and the mass of the crucible was again subtracted to determine the mass of the ashed soil. Carbon content was calculated as the percentage of soil mass lost on ignition. The soil samples were then sent to Elsenburg Laboratories (Western Cape Department of Agriculture) for the following analyses: three-faction texture analysis (sand, silt and clay); ammonium nitrogen (NH₄-N), as a proxy for total nitrogen content; phosphorus and potassium, as well as calcium, magnesium and sodium.

Following the procedure outlined by Picard *et al.* (2012), allometry was used to calculate the biomass of the *A. dealbata* invasion. Thirty trees were sampled across the full range of size classes, the trees were marked, measured at a height of 35 cm above ground level on the downslope side of the stem and felled. The trunks and branches were cut into manageable logs and weighed in the field, with foliage intact, to obtain the total fresh biomass of each tree. Foliage was then removed, collected in separate plastic bags and weighed. The fresh wood mass was calculated as the difference between the total fresh mass and the mass of the

foliage. Cylindrical aliquots were cut for nine of the trees, weighed in the field, oven dried for seven days at 105 °C and reweighed (Picard *et al.*, 2012). The total dry mass of each tree was then calculated as the product of their fresh wood mass and the average dry wood mass to fresh wood mass ratio of the aliquots (Picard *et al.*, 2012).

The growth rate of *A. dealbata* was determined from a sample of stems. Stems were selected along several transects on different slopes, aspects and slope positions. Successive stems were typically 5–10 m apart. For safety and convenience, transects varied in length and trajectory, occasionally changing direction to avoid steep slopes, rivers and/or extremely dense thicket. A range of stem sizes was selected. Each stem was marked with white spray paint, numbered with a permanent marker and the coordinates were logged with a GPS. The diameter was measured at 35 cm above ground-level on the downslope side of the stem and additional notes were taken where necessary. During March 2016, a total of 382 stems were measured in the Matatiele (n = 140), Mount Fletcher (n = 122) and Maclear (n = 120) study areas. Although 331 stems were located again during March 2017, 37 of these stems had been cut below the height of 35 cm. The remaining 294 stems were remeasured as before.

4.2.2. Data analysis

Data were analysed in R version 3.4.1 (R Core Team, 2017). A regression analysis was run to determine the relationship between the stem diameter and (dry wood) biomass of *A. dealbata* (R package: stats; R Core Team, 2017). Both variables were transformed to the natural log scale to account for non-normality of residuals and heterogeneity of variance (Picard *et al.*, 2012). Following Picard *et al.* (2012), the inverse variables transformation was used to return the log-normal allometric equation, taking into account the correction factor for predicted biomass (Parresol, 1999). Subsequently, the allometric equation was applied to the recorded stem diameters from the growth transects and density plots. The stem counts and biomasses were summed for each plot and scaled to determine the density and biomass of *A. dealbata* per hectare, respectively. Cut stems were excluded from the calculation to reflect the current standing biomass.

Acacia dealbata productivity was calculated as the difference in stem biomass between 2016 and 2017 and a Wilcoxon paired-sample test was run to determine the statistical significance of the change (R package: stats; R Core Team, 2017). Additionally, a regression analysis was run on the diameter of stems recorded in 2016 and the change in their respective biomasses between 2016 and 2017. The derived equation was then applied to the stem diameters from the density plots and the outputs were summed for each plot and scaled to determine the annual productivity of *A. dealbata* per hectare. Dead stems were excluded from the calculation. Annual harvest was estimated from the percentage cut stem biomass between

2016 and 2017. A regression analysis was run to determine the relationship between stem diameter and the proportion of biomass accumulation in relation to the biomass of the stem, the latter of which was scaled using an inverse transformation. Regression analysis was also used to determine the relationship between stem density and the annual biomass production per hectare. Thereafter, the differences in the average density, biomass and productivity of *A. dealbata* between study areas and villages were assessed with an ANOVA (R package: car; Fox and Weisberg, 2011) or Kruskal-Wallis test (R package: stats; R Core Team, 2017), confirmed with a Tukey test (R package: stats; R Core Team, 2017) or Dunn's test (R package: dunn.test; Dinno, 2017), and represented graphically (R package: ggplot2; Wickham, 2009).

Biophysical data from the density plots were then summarised according to three assigned categories of *A. dealbata* density (dense, moderate and sparse) and biomass (high, moderate and low) to give a general profile of the invasion. This included the average composition of *A. dealbata* per category, as well as data on the topography, soil properties, ground cover, woody species diversity and the proximity of the plot to rivers and roads. Proximity data were determined from Euclidian distance rasters generated in ArcGIS from vector datasets of Eastern Cape rivers and roads (ESRI, 2011). In addition to the field-collected data and proximity data, historical LULC data were extracted from the GIS analysis for each plot. The differences between categories were assessed with Kruskal-Wallis tests (R package: stats; R Core Team, 2017) and confirmed with Dunn's test (R package: dunn.test; Dinno, 2017).

Principal component analysis (PCA) and multiple regression analysis (MRA) were used to determine the correlates of the *A. dealbata* invasion. The additional 63 sample points from outside the density plots were included in the analyses as control plots, with *A. dealbata* density and biomass set to zero and grass cover estimated at 80 %. To account for circular data, aspect was transformed into 'Northness' and 'Eastness' data, using the cosine and sine transformations, respectively. The PCA was first used to examine and eliminate highly correlated biophysical and LULC variables to pinpoint possible predictors of *A. dealbata* abundance (R package: GGEBiplots; Dumble, 2017). Data were centred and scaled.

The MRA was conducted to determine the relationship between these variables and the density or biomass of *A. dealbata* (R package: stats; R Core Team, 2017). Stepwise model selection based on Akaike's information criteria (AIC; Logan, 2010) was used to further simplify the MRA models (R package: MASS; Venables and Ripley, 2002). Finally, the relative importance of predictors were assessed using the 'calc.relimp', 'boot.relimp' and 'booteval.relimp' tools, which partitioned and normalised the R^2 values of the predictors and quantified their bootstrap confidence intervals and the differences between their relative contributions (R packages: relaimpo and boot; Grömping, 2006; Canty and Ripley, 2017, respectively).

4.3. Results

The results of this chapter are presented in two sections. Opening with allometry, the first section proceeds to determine the relationships between stem diameter and growth (i.e. the change in biomass over one year) as an indicator of the annual productivity of *A. dealbata*; stem diameter and proportional biomass accumulation; and, stem density and the rate of annual biomass production. The average density, biomass and productivity of *A. dealbata* are then presented following the structure of Chapter 3, zoning in from a broad scale, through an interregional comparison of the three study areas, to intraregional comparisons of the respective villages within the Matatiele, Mount Fletcher and Maclear areas. Thereafter, the second section delves into the correlates of invasion, providing a general biophysical profile of landscapes at various levels of invasion and then determining which biophysical and/or LULC conditions are associated with the current invasion of *A. dealbata*.

4.3.1. Current abundance, productivity and harvest of *A. dealbata*

Once transformed to the natural logarithm scale, there was a significant allometric relationship between the stem diameter and biomass of *A. dealbata* ($\beta = 2.28$, $t = 24.14$, $P < 0.001$; Fig. 4.1). Moreover, the stem diameter explained a significant proportion of the variance in biomass ($R^2 = 0.95$, $F = 583$, $P < 0.001$; Fig. 4.1). The derived inverse variable transformation equation ($y = X^{2.28} \times 9.32 \times 10^{-5}$) could therefore be applied to the field-measured stem diameters to estimate the dry wood biomass, whereby a stem with a diameter of one centimetre would equate to approximately 93 g of dry wood, while a stem with a diameter of 10 cm would equate to approximately 18 kg of dry wood.

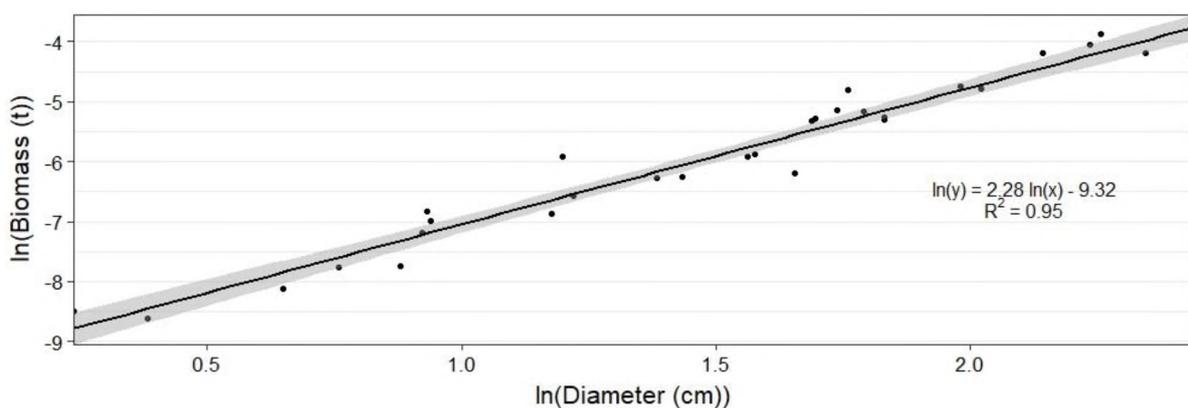


Fig. 4.1: Allometric relationship between the stem diameter (35 cm above ground-level) and the dry wood biomass of *A. dealbata*, with confidence interval (shaded).

A significant difference was found between the stem biomasses in 2016 compared to those in 2017 ($V = 39\,666$, $P < 0.001$), with an average increase of 1.03 ± 1.39 kg per stem. The stem diameter of *A. dealbata* in 2016 was a significant predictor of the change in biomass between 2016 and 2017 ($\beta = 2.63 \times 10^{-4}$, $t = 14.82$, $P < 0.001$; Fig. 4.2). Despite a relatively low

coefficient of determination, stem diameter explained a significant proportion of variance in the change in biomass ($R^2 = 0.43$, $F = 220$, $P < 0.001$; Fig. 4.2). The derived equation could therefore be applied to the stem diameters from the density plots to provide an estimate of the annual productivity of *A. dealbata*, where a stem with a diameter of one centimetre could potentially increase its biomass by 263 g per annum.

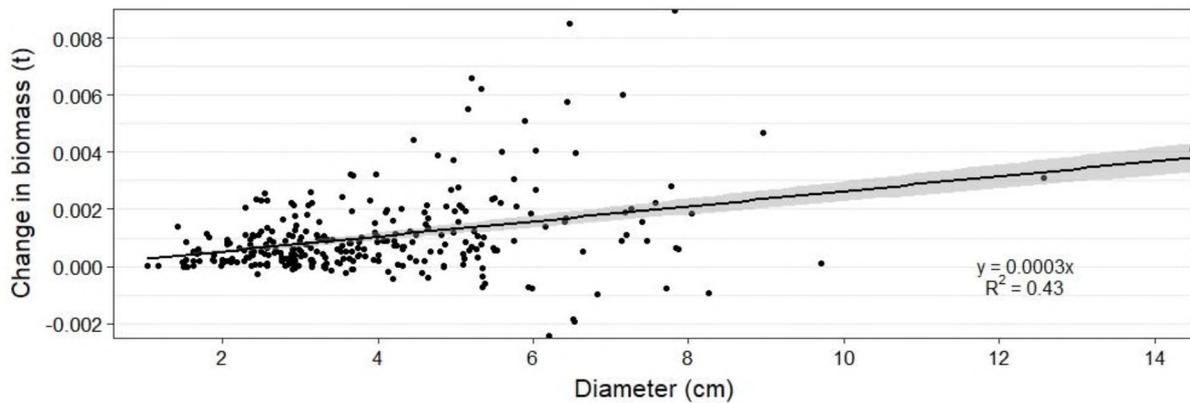


Fig. 4.2: Annual change in *A. dealbata* biomass (2016–2017) per stem diameter, with confidence interval (shaded).

There was a strong linear relationship between the diameter of the stem and the inverse of its proportional biomass accumulation ($\beta = 7.09 \times 10^{-3}$, $t = 876$, $P < 0.001$; Fig. 4.3), with the former explaining a significantly high proportion of the variance in the latter ($R^2 = 0.99$, $F = 7\,6737$, $P < 0.001$; Fig. 4.3). Small stems therefore had a very high relative growth rate compared to large stems, hence a proportionally higher annual productivity, which rapidly declined as the stems increased in size.

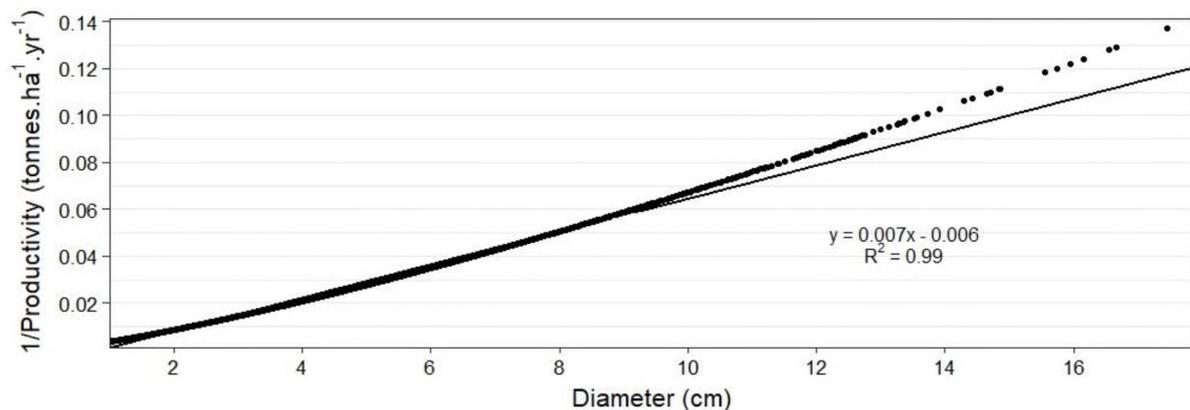


Fig. 4.3: Relationship between stem diameter and proportional biomass accumulation.

A significant polynomial relationship was found between the density and productivity of the plots, with a high proportion of the variance explained by a quadratic function ($R^2 = 0.77$, $F = 124$, $P < 0.001$; Fig. 4.4). Although the productivity of the plot generally increased with the

density of *A. dealbata* stems, the productivity of the plot reached a plateau at a density of approximately 16 000 stems.ha⁻¹ and subsequently decreased thereafter (Fig. 4.4).

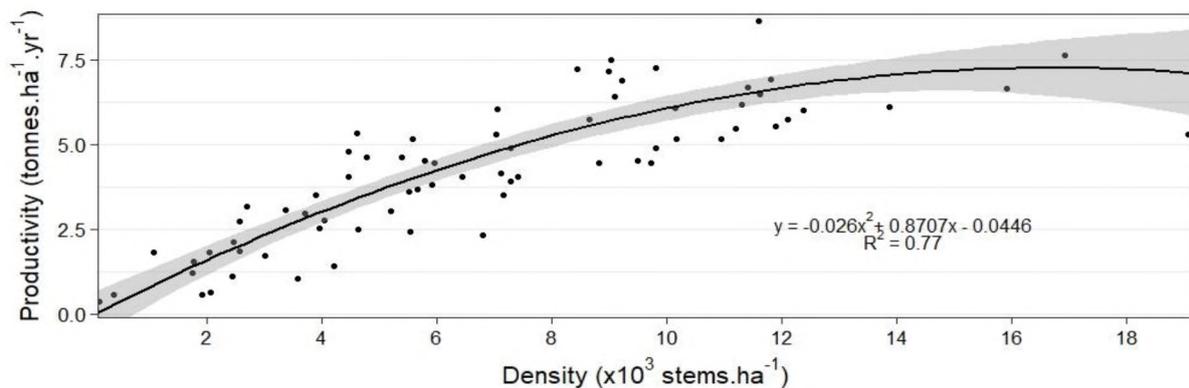


Fig. 4.4: Relationship between the density and productivity of *A. dealbata*, with confidence interval (shaded).

The invasion of *A. dealbata* varied in abundance across plots in terms of stem density, averaging $6\,939 \pm 4\,409$ stems.ha⁻¹ and ranging between 0–19 250 stems.ha⁻¹, as well as standing biomass, averaging 11.99 ± 7.90 t.ha⁻¹ and ranging between 0–33.03 t.ha⁻¹ (Fig. 4.5). Overall, annual productivity of *A. dealbata* was estimated at 4.25 ± 2.35 t.ha⁻¹.yr⁻¹ (41.40 ± 23.27 %; Fig. 4.5), ranging between 0–9.45 t.ha⁻¹.yr⁻¹ across plots, while the annual *A. dealbata* harvest (i.e. the percentage biomass of stems cut between 2016 and 2017) was estimated at 15.43 %. The net annual increase in *A. dealbata* biomass (uncut, dry wood biomass) was therefore estimated at 26 %.

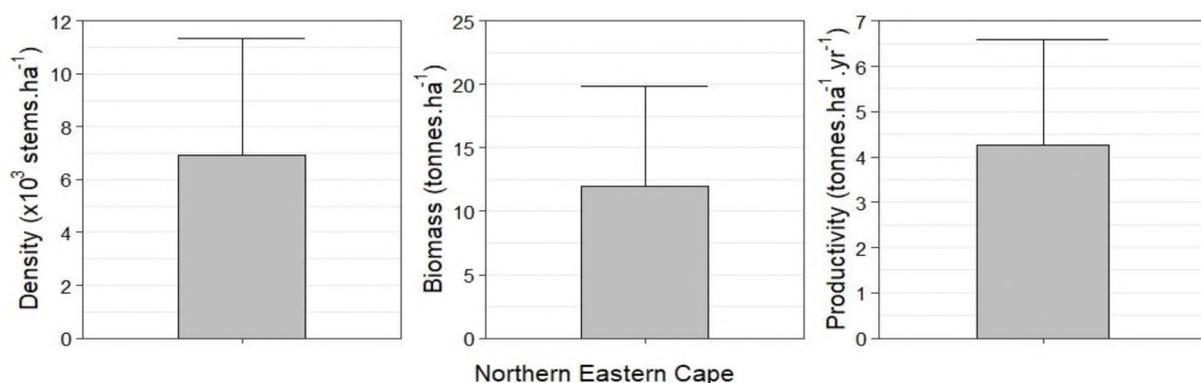


Fig. 4.5: Current *A. dealbata* density (left), biomass (centre) and annual productivity (right) across all sampled sites (mean + absolute SD).

The density ($H = 8.18$, $P < 0.05$), biomass ($H = 12.45$, $P < 0.05$) and annual productivity ($F = 4.95$, $P < 0.05$) differed significantly between study areas (Fig. 4.6). Of the three study areas, Maclear had a higher mean density ($9\,316 \pm 5\,053$ stems.ha⁻¹), biomass (16.20 ± 6.78 t.ha⁻¹) and annual productivity (5.40 ± 2.23 t.ha⁻¹.yr⁻¹) of *A. dealbata* compared to both Matatiele and Mount Fletcher ($P < 0.05$; Fig. 4.6). Although an insignificant difference was observed between

Matatiele and Mount Fletcher, the former had an overall higher biomass and annual productivity ($10.42 \pm 7.93 \text{ t.ha}^{-1}$ and $3.82 \pm 1.86 \text{ t.ha}^{-1}.\text{yr}^{-1}$, respectively) compared to the latter ($9.56 \pm 7.50 \text{ t.ha}^{-1}$ and $3.58 \pm 2.54 \text{ t.ha}^{-1}.\text{yr}^{-1}$, respectively), despite more dense patches generally found in Mount Fletcher ($5\,885 \pm 4\,226 \text{ stems.ha}^{-1}$; Fig. 4.6).

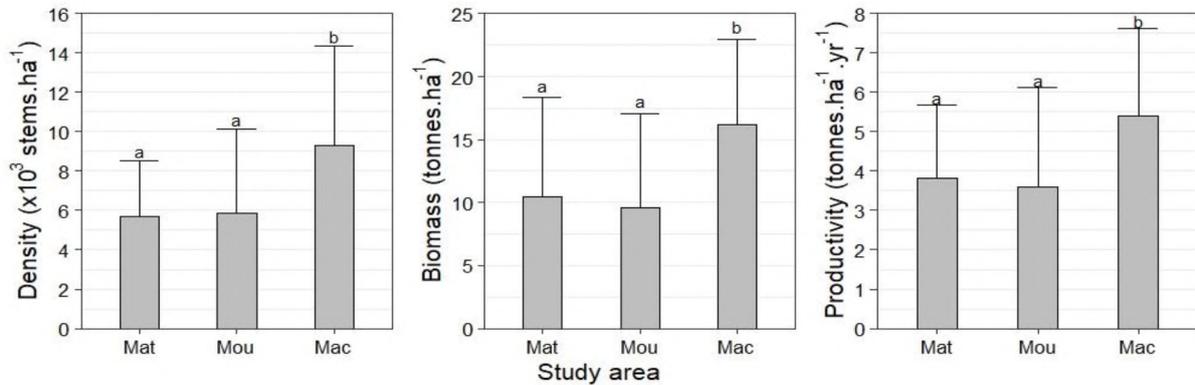


Fig. 4.6: Current *A. dealbata* density (left), biomass (centre) and annual productivity (right) in Matatiele (Mat), Mount Fletcher (Mou) and Maclear (Mac) (mean + absolute SD).

There were no significant differences between villages in the Matatiele area (Fig. 4.7). In general, the villages with the highest stem densities also had the lowest biomasses of *A. dealbata*. For example, the highest density and lowest biomass of *A. dealbata* in the Matatiele region were recorded in Caba, $7\,513 \pm 3\,016 \text{ stems.ha}^{-1}$ and $6.61 \pm 2.42 \text{ t.ha}^{-1}$, respectively (Fig. 4.7). Conversely, the highest biomass and annual productivity were observed in Nkasela, $14.16 \pm 8.02 \text{ t.ha}^{-1}$ and $4.10 \pm 1.69 \text{ t.ha}^{-1}.\text{yr}^{-1}$, respectively (Fig. 4.7).

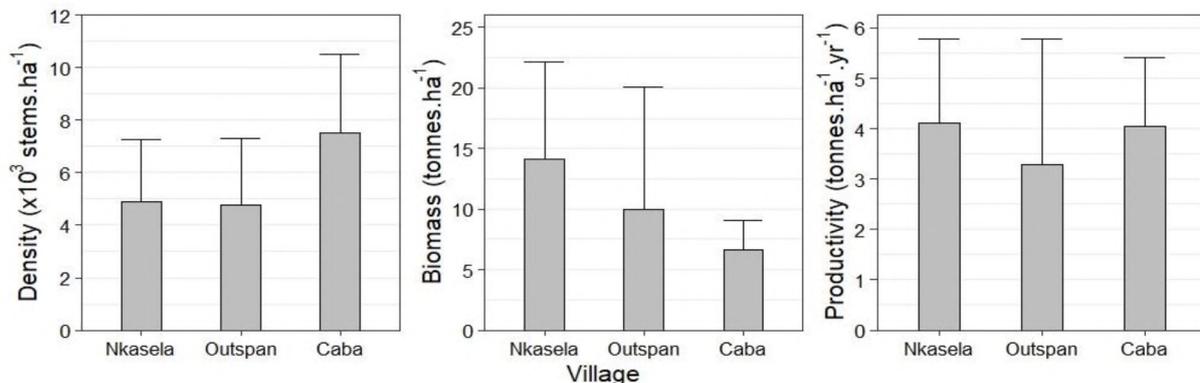


Fig. 4.7: Current *A. dealbata* density (left), biomass (centre) and annual productivity (right) in three villages in Matatiele (mean + absolute SD).

In the Mount Fletcher region, Fletcherville had the highest density of *A. dealbata* ($6\,820 \pm 4\,947 \text{ stems.ha}^{-1}$), followed by HaQhadi ($6\,756 \pm 2\,875 \text{ stems.ha}^{-1}$) and then Printsu ($4\,072 \pm 4\,212 \text{ stems.ha}^{-1}$; Fig. 4.8). However, both the biomass and annual productivity of *A. dealbata* were highest in HaQhadi ($12.97 \pm 8.07 \text{ t.ha}^{-1}$ and $4.11 \pm 1.83 \text{ t.ha}^{-1}.\text{yr}^{-1}$, respectively), followed

by Printsu and then Fletcherville (Fig. 4.8). No significant differences between villages were observed in the Mount Fletcher area (Fig. 4.8).

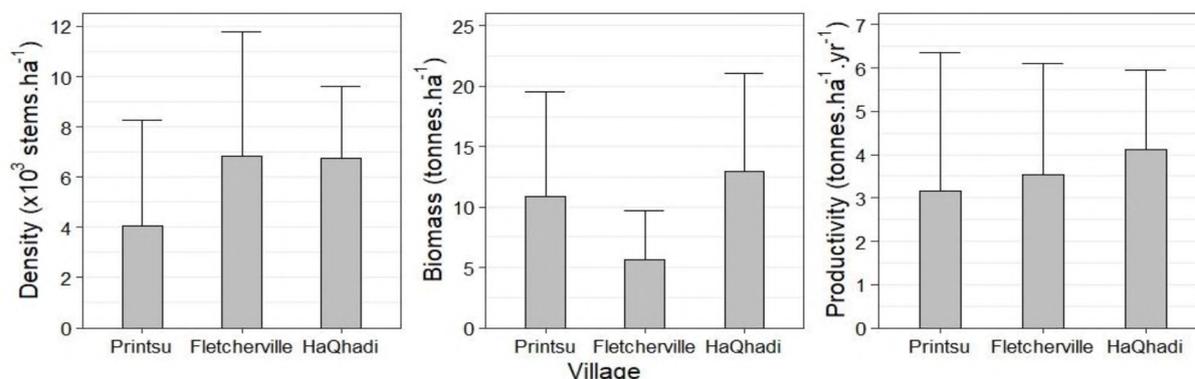


Fig. 4.8: Current *A. dealbata* density (left), biomass (centre) and annual productivity (right) in three villages in Mount Fletcher (mean + absolute SD).

Finally, the highest stem density ($11\ 056 \pm 4\ 589$ stems.ha $^{-1}$) and annual productivity (6.22 ± 2.27 t.ha $^{-1}$.yr $^{-1}$) in the Maclear region were recorded in Katkop, which also had the lowest biomass (14.41 ± 5.46 t.ha $^{-1}$), whereas KuMagwaca had the lowest stem density ($6\ 906 \pm 3\ 654$ stems.ha $^{-1}$) and highest biomass (18.50 ± 4.89 t.ha $^{-1}$; Fig. 4.9). Again, no significant differences between villages were observed in the Maclear area (Fig. 4.9).

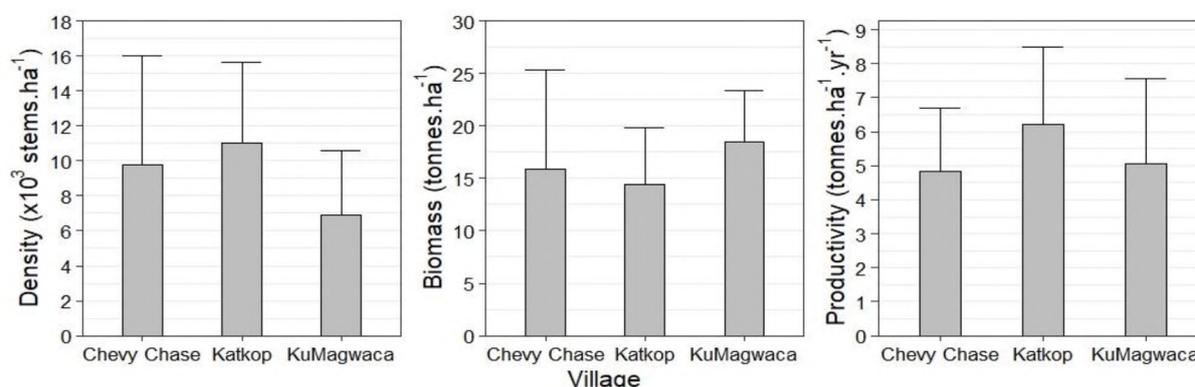


Fig. 4.9: Current *A. dealbata* density (left), biomass (centre) and annual productivity (right) in three villages in Maclear (mean + absolute SD).

4.3.2. Correlates of *A. dealbata* invasion

The biophysical characteristics of *A. dealbata* invaded landscapes are summarised in Tables 4.1 and 4.2. Denser populations of *A. dealbata* ($12\ 950 \pm 2\ 871$ stems.ha $^{-1}$) hosted thinner *A. dealbata* stems (3.59 ± 0.92 cm) and were supported in lower elevation areas ($1\ 511 \pm 72$ m), generally in ammonium nitrogen rich soil (0.31 ± 0.29 %) on the plains of gradual (13 ± 5 °) south-southeast (164 ± 97 °) facing slopes, with high bare ground (59 ± 31 %) and litter (51 ± 27 %) cover, as well as low grassy (32 ± 24 %), herbaceous (0 ± 1 %), rock (10 ± 15 %) and woody species cover (2 ± 5 %) and richness (2 ± 1 species; Table 4.1). There were significant

differences between the density classes in terms of *A. dealbata* biomass, annual productivity, stem density and seedling density; the percentage of cut, flowering and multi-stemmed stems; the slope; and, the percentage of *A. dealbata*, bare ground, herbaceous, litter and woody species cover ($P < 0.05$; Table 4.1).

Densely invaded landscapes had a significantly greater density of seedlings and a significantly higher rate of annual biomass production compared to both moderately and sparsely invaded landscapes ($P < 0.001$), with averages of $6\,275 \pm 5\,227$ seedlings.ha⁻¹ and 6.56 ± 1.31 t.ha⁻¹.yr⁻¹, respectively (Table 4.1). Moreover, a significantly higher percentage of cut and multi-stemmed individuals per hectare were found in densely invaded areas, compared to both moderately and sparsely invaded areas ($P < 0.05$), while a significantly lower percentage of flowering stems were found in densely and moderately invaded areas compared to sparsely invaded areas ($P < 0.05$; Table 4.1). Moderate density landscapes had the highest biomasses (15.22 ± 7.27 t.ha⁻¹), which were significantly higher than sparse density landscapes ($P < 0.001$; Table 4.1). Sparsely invaded landscapes had a significantly lower *A. dealbata* cover (30 ± 19 %) and significantly higher herbaceous (0.8 ± 1.3 %) and other woody species (18 ± 23 %) covers than both moderately and densely invaded landscapes ($P < 0.05$; Table 4.1). Bare ground was significantly higher in densely invaded areas (59 ± 31 %) compared to both moderately (40 ± 29 %) and sparsely (29 ± 26 %) invaded areas ($P < 0.05$; Table 4.1).

High biomass populations of *A. dealbata* were generally supported on gradual ($14 \pm 8^\circ$) south-southeast facing ($164 \pm 73^\circ$) mid-slopes at elevations of $1\,529 \pm 88$ m (Table 4.2). These areas were characterised by high soil ammonium nitrogen content (0.39 ± 0.35 %), as well as high bare ground (59 ± 23 %), herbaceous (2 ± 5 %) and litter (51 ± 27 %) cover, and low grassy (34 ± 28 %) and rock (7 ± 16 %) cover (Table 4.2). There were significant differences between the biomass classes in terms of the average stem diameter, biomass, annual productivity and stem density; the pH, clay content and sodium content of the soil; the percentage of *A. dealbata*, litter and rock cover; and woody diversity ($P < 0.05$; Table 4.2).

Areas supporting a high biomass of *A. dealbata* (24.95 ± 3.48 t.ha⁻¹) had a significantly higher density of stems ($9\,336 \pm 4.314$ stems.ha⁻¹) and rate of annual biomass production (6.78 ± 1.95 t.ha⁻¹.yr⁻¹) compared to areas supporting a low to moderate biomass ($P < 0.05$; Table 4.2). Unlike densely invaded areas, high biomass areas typically had thick stems (5.20 ± 1.05 cm; Table 4.2). The soil pH and clay content were significantly lower in moderate to high biomass areas compared to low biomass areas, while the soil sodium content was significantly higher in moderate biomass areas compared to both low and high biomass areas ($P < 0.05$; Table 4.2). *Acacia dealbata* cover differed significantly between each biomass class ($P < 0.001$), with 37 ± 21 %, 49 ± 16 % and 63 ± 19 % cover found in low, moderate and high biomass areas, respectively (Table 4.2). Litter cover was significantly higher, while rock cover

and species diversity were significantly lower in areas supporting high *A. dealbata* biomasses compared to areas supporting low to moderate biomasses ($P < 0.05$; Table 4.2).

Table. 4.1: Biophysical characteristics (mean \pm SD) of *A. dealbata* density classes: dense ($>10 \times 10^3$ stems.ha⁻¹), moderate (5–10 $\times 10^3$ stems.ha⁻¹) and sparse ($<5 \times 10^3$ stems.ha⁻¹). Statistically significant differences between classes denoted by different superscript letters^{a,b,c}.

Variable	Density class (n = 77)			Statistics	
	Dense (n = 18)	Moderate (n = 30)	Sparse (n = 29)	H	P
Stem diameter (cm)	3.59 \pm 0.92	4.12 \pm 1.11	4.35 \pm 2.61	2.96	0.23
Biomass (t.ha ⁻¹)	13 \pm 6.48 ^a	15.22 \pm 7.27 ^a	8.03 \pm 7.81 ^b	14.70	<0.001
Productivity (t.ha ⁻¹ .yr ⁻¹)	6.56 \pm 1.31 ^a	4.98 \pm 1.64 ^b	2.06 \pm 1.47 ^c	47.05	<0.001
Stem density ($\times 10^3$ ha ⁻¹)	12.95 \pm 2.87 ^a	7.49 \pm 1.59 ^b	2.63 \pm 1.55 ^c	66.50	<0.001
Seedling density ($\times 10^3$ ha ⁻¹)	6.28 \pm 5.23 ^a	3.14 \pm 3.29 ^b	1.65 \pm 1.84 ^c	17.04	<0.001
Alive (%)	67.5 \pm 70.5	16.3 \pm 75.6	67.8 \pm 29.4	0.47	0.79
Burnt (%)	0 \pm 0.1	0.4 \pm 2.6	2.4 \pm 7.2	4.48	0.11
Coppicing (%)	8.5 \pm 7.4	7.2 \pm 7.1	6.4 \pm 9.6	4.46	0.11
Cut (%)	31.2 \pm 21.6 ^a	15.8 \pm 20 ^b	17.9 \pm 17.9 ^b	7.22	0.03
Flowering (%)	0 \pm 0.5 ^a	1.6 \pm 10.1 ^a	9 \pm 21.4 ^b	10.31	0.01
Fruiting (%)	29.4 \pm 18.3	23.9 \pm 29.1	26.1 \pm 30.2	2.72	0.26
Multi-stemmed (%)	75 \pm 61.7 ^a	20.1 \pm 61.3 ^b	54.9 \pm 31.4 ^b	6.07	0.05
Topography					
Altitude (m)	1 511 \pm 72	1 534 \pm 78	1 552 \pm 118	0.85	0.66
Aspect (°)	164 \pm 97	173 \pm 84	200 \pm 51	4.75	0.09
Slope (°)	13 \pm 5 ^a	15 \pm 9 ^a	20 \pm 10 ^b	5.94	0.05
Slope position (6pt)	4 \pm 1	3 \pm 2	3 \pm 2	2.41	0.30
Soil properties					
pH	4.64 \pm 0.45	4.59 \pm 0.53	4.71 \pm 0.76	1.43	0.49
Carbon (%)	0.1 \pm 0.08	0.08 \pm 0.09	0.1 \pm 0.08	2.30	0.32
Clay (%)	11.44 \pm 3.4	9.73 \pm 2.32	11.41 \pm 4.19	3.36	0.19
Silt (%)	9.78 \pm 3.21	8.27 \pm 3.23	9.72 \pm 4.53	2.45	0.29
Sand (%)	78.78 \pm 6.32	82 \pm 5.19	78.86 \pm 8.26	3.20	0.20
NH ₄ -N (%)	0.31 \pm 0.29	0.21 \pm 0.2	0.21 \pm 0.16	1.53	0.47
P (mg.kg ⁻¹)	13.7 \pm 16.1	10.8 \pm 10.4	19.3 \pm 35.1	6.07	0.20
K (mg.kg ⁻¹)	175.7 \pm 118.5	107.4 \pm 54.1	199.2 \pm 376.3	7.07	0.08
Na (mg.kg ⁻¹)	14.7 \pm 6.7	12.8 \pm 6.7	19.8 \pm 16.3	8.07	0.16
Ca (cmol.kg ⁻¹)	3.34 \pm 3.93	2.05 \pm 2.3	3.74 \pm 6.9	2.71	0.26
Mg (cmol.kg ⁻¹)	1.62 \pm 1.62	0.96 \pm 0.72	1.6 \pm 1.61	3.64	0.16
Cover					
<i>A. dealbata</i> (%)	61 \pm 17 ^a	51 \pm 16 ^a	30 \pm 19 ^b	25.24	<0.001
Bare (%)	59 \pm 31 ^a	40 \pm 29 ^b	29 \pm 26 ^b	9.47	0.01
Grass (%)	32 \pm 24	38 \pm 29	49 \pm 32	3.56	0.17
Herb (%)	0 \pm 1 ^a	1 \pm 4 ^a	1 \pm 1 ^b	8.13	0.02
Litter (%)	51 \pm 27 ^a	31 \pm 22 ^b	26 \pm 26 ^b	10.03	0.01
Other woody species (%)	2 \pm 5 ^a	5 \pm 9 ^a	18 \pm 23 ^b	16.52	<0.001
Rock (%)	10 \pm 15	12 \pm 19	18 \pm 21	4.14	0.13
Other woody species					
Shannon-Wiener Index	0.1 \pm 0.23	0.22 \pm 0.35	0.21 \pm 0.3	2.39	0.30
Species richness (count)	2 \pm 1	2 \pm 1	2 \pm 1	0.45	0.80
Proximity					
Distance to closest river (m)	106 \pm 89	111 \pm 124	121 \pm 119	0.15	0.93
Distance to closest road (m)	172 \pm 200	150 \pm 139	146 \pm 143	0.19	0.91

Table. 4.2: Biophysical characteristics (mean \pm SD) of *A. dealbata* biomass classes: high (>20 t.ha⁻¹), moderate (10–20 t.ha⁻¹) and low (<10 t.ha⁻¹). Statistically significant differences between classes denoted by different superscript letters^{a,b,c}.

Variable	Biomass class (n = 77)			Statistics	
	High (n = 14)	Moderate (n = 25)	Low (n = 38)	H	P
Stem diameter (cm)	5.20 \pm 1.05 ^a	4.46 \pm 1.05 ^a	3.42 \pm 2.15 ^b	116.57	<0.001
Biomass (t.ha ⁻¹)	24.95 \pm 3.48 ^a	14.48 \pm 2.71 ^b	5.59 \pm 3.03 ^c	130.75	<0.001
Productivity (t.ha ⁻¹ .yr ⁻¹)	6.78 \pm 1.95 ^a	4.79 \pm 1.59 ^b	2.96 \pm 2.01 ^c	117.10	<0.001
Stem density (x10 ³ ha ⁻¹)	9.34 \pm 4.31 ^a	7.5 \pm 3.68 ^a	5.69 \pm 4.54 ^b	7.83	<0.02
Seedling density (x10 ³ ha ⁻¹)	3.46 \pm 4.54	3.35 \pm 4.57	3.23 \pm 3.04	0.15	0.94
Alive (%)	64.6 \pm 14.1	69.5 \pm 18.4	69.8 \pm 26.6	2.69	0.26
Burnt (%)	0.6 \pm 1.4	0.9 \pm 4.3	1.1 \pm 5.4	2.93	0.23
Coppicing (%)	8.8 \pm 6	6.6 \pm 7.3	7.2 \pm 9.1	2.63	0.27
Cut (%)	27.3 \pm 14.5	24.5 \pm 17.9	19.3 \pm 18	3.74	0.15
Flowering (%)	2.1 \pm 4.7	1.7 \pm 7.2	5.4 \pm 18.4	1.00	0.61
Fruiting (%)	21 \pm 26.3	18.5 \pm 22.6	28.3 \pm 28.4	1.99	0.37
Multi-stemmed (%)	73.6 \pm 13.4	63.7 \pm 24.1	57.1 \pm 28.1	3.33	0.19
Topography					
Altitude (m)	1 523 \pm 88	1 516 \pm 76	1 552 \pm 106	1.25	0.53
Aspect (°)	158 \pm 72	200 \pm 66	177 \pm 85	3.09	0.21
Slope (°)	13 \pm 8	17 \pm 10	18 \pm 9	4.93	0.09
Slope position (6pt)	3 \pm 1	4 \pm 2	4 \pm 2	4.29	0.12
Soil properties					
pH	4.52 \pm 0.55 ^a	4.52 \pm 0.45 ^a	4.78 \pm 0.69 ^b	6.27	0.04
Carbon (%)	0.12 \pm 0.11	0.09 \pm 0.08	0.08 \pm 0.07	0.31	0.86
Clay (%)	10.00 \pm 4.35 ^a	10.20 \pm 3.83 ^a	11.42 \pm 2.68 ^b	6.21	0.04
Silt (%)	9.14 \pm 5.19	8.56 \pm 3.85	9.58 \pm 3.16	2.30	0.32
Sand (%)	80.86 \pm 9.36	81.24 \pm 7.15	79.00 \pm 5.46	3.90	0.14
NH ₄ -N (%)	0.40 \pm 0.36	0.19 \pm 0.15	0.20 \pm 0.15	3.79	0.15
P (mg.kg ⁻¹)	20.4 \pm 20.5	9.7 \pm 5.9	15.9 \pm 31.0	2.83	0.24
K (mg.kg ⁻¹)	152.1 \pm 119.7	109.1 \pm 56.2	192.3 \pm 331	3.47	0.18
Na (mg.kg ⁻¹)	19.3 \pm 12.4 ^a	13 \pm 11.2 ^b	16.6 \pm 11.5 ^a	8.91	0.01
Ca (cmol.kg ⁻¹)	4.65 \pm 4.88	1.95 \pm 1.60	3.06 \pm 6.06	2.82	0.24
Mg (cmol.kg ⁻¹)	1.88 \pm 1.88	1.08 \pm 0.95	1.34 \pm 1.35	2.06	0.36
Cover					
<i>A. dealbata</i> (%)	63 \pm 19 ^a	49 \pm 16 ^b	37 \pm 21 ^c	113.06	<0.001
Bare (%)	51 \pm 32	38 \pm 26	38 \pm 31	2.07	0.36
Grass (%)	35 \pm 28	41 \pm 28	42 \pm 31	0.58	0.75
Herb (%)	2 \pm 5	1 \pm 1	0 \pm 1	0.98	0.61
Litter (%)	53 \pm 28 ^a	32 \pm 23 ^b	28 \pm 25 ^b	7.81	0.02
Other woody species (%)	4 \pm 12	11 \pm 19	10 \pm 17	3.50	0.17
Rock (%)	3 \pm 6 ^a	14 \pm 21 ^b	17 \pm 20 ^b	8.64	0.01
Other woody species					
Shannon-Wiener Index	0.04 \pm 0.14 ^a	0.11 \pm 0.27 ^a	0.29 \pm 0.34 ^b	15.40	<0.001
Species richness (count)	2 \pm 1	2 \pm 1	2 \pm 1	5.08	0.08
Proximity					
Distance to closest river (m)	100 \pm 108	97 \pm 98	129 \pm 125	0.09	0.95
Distance to closest road (m)	170 \pm 114	188 \pm 201	124 \pm 129	3.24	0.20

The PCA biplots for the density and biomass of *A. dealbata* were nearly identical in terms of the configuration of biophysical correlates and the proportion of variance explained by the first two principle components (Fig. 4.10). Density and biomass were strongly correlated with the percentage of bare ground and litter (Fig. 4.10). However, these were excluded from the subsequent MRA because the direction of causation was indeterminant, i.e. a high percentage of bare ground and/or litter could be the cause or result of abundant *A. dealbata*. Soil nutrients revealed a strong correlation with one another, yet were weakly correlated with the density and biomass of *A. dealbata* and were excluded from the MRA (Fig. 4.10), except for ammonium nitrogen ($\text{NH}_4\text{-N}$). Similarly, there was a correlation between the soil pH and texture, where pH and finer soil textures (clay and silt) were positively associated and coarser textures (sand) were negatively associated with the second principal component, although none of these variables were strongly correlated with *A. dealbata* abundance (Fig. 4.10). The aspect variables ('Northness' and 'Eastness') were undoubtedly correlated with one another, but weakly correlated with *A. dealbata* abundance (Fig. 4.10). The geology and proximity to the nearest road showed a weak correlation with the abundance of *A. dealbata* (Fig. 4.10).

The initial MRA therefore included the density and biomass of *A. dealbata* as the response variables, tested against the following remaining variables: topography (altitude, slope and slope position); soil ammonium nitrogen content; cover (rock, grass, herbaceous and non-*Acacia dealbata* woody species cover); non-*Acacia dealbata* woody species diversity; historical LULC; and the proximity to the river. Study area was included as a factorial explanatory variable to take regional differences into account. The stepwise model selection process eliminated additional predictors from both the density and biomass MRA, including, *inter alia*, the historical LULC, slope position, rock cover and the proximity to the nearest river.

The final MRAs revealed significant relationships between the density ($F = 18.82$, $P < 0.001$) and biomass ($F = 15.10$, $P < 0.001$) of *A. dealbata* and their respective predictors, with almost half of the variance explained in each model (50.0 % and 44.4 %, respectively). There were significant differences in the density and biomass of *A. dealbata* between study areas ($P < 0.05$). Stem density increased significantly with an increase in soil ammonium nitrogen content ($t = 1.91$, $P < 0.05$) and decreased with an increase in grass cover ($t = 9.76$, $P < 0.001$), other woody species cover ($t = 3.54$, $P < 0.001$) and diversity ($t = 2.45$, $P < 0.05$). Although density decreased with altitude, this relationship was insignificant ($t = 1.91$, $P = 0.06$). On the other hand, biomass increased with an increase in soil ammonium nitrogen content ($t = 2.35$, $P < 0.05$), while decreasing with an increase in grass cover ($t = 7.11$, $P < 0.001$) and woody species diversity ($t = 3.41$, $P < 0.001$). An insignificant positive relationship was observed between standing biomass and herbaceous cover ($t = 1.92$, $P = 0.06$), while an insignificant negative relationship was observed between standing biomass and slope ($t = 1.92$, $P = 0.06$).

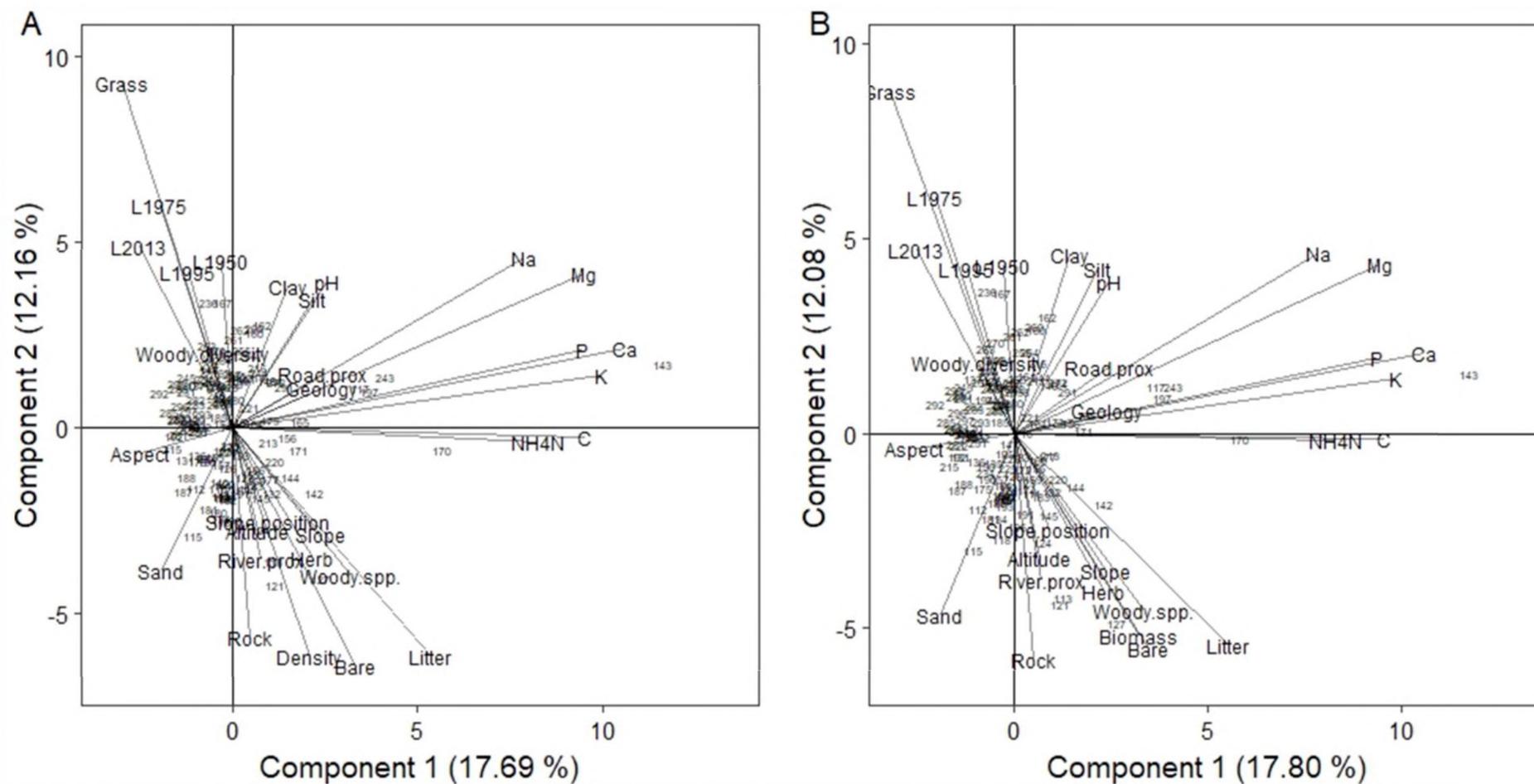


Fig. 4.10: Principal component biplots for *A. dealbata* density (A) and biomass (B).

The relative importance of predictor variables varied for both the density and biomass of *A. dealbata* (Fig. 4.11). Grass cover had the greatest influence on *A. dealbata* abundance, explaining most of the variation in stem density (71.3 %) and biomass (55.8 %) in terms of the proportional contribution to R^2 (Fig. 4.11). This was followed by the diversity of non-*Acacia dealbata* woody species (Shannon-Wiener index), contributing 8.6 % and 15.6 % to the R^2 of the density and biomass models, respectively (Fig. 4.11). A decreasing proportion of the variation was explained by the remaining predictors, including the study area (density: 6.1 %; biomass: 7.5 %); soil ammonium nitrogen content (density: 5.5 %; biomass: 9.6 %); non-*Acacia dealbata* woody cover (density: 5.2 %); herbaceous cover (biomass: 7.8 %); altitude (density: 3.4 %); and slope (biomass: 3.7 %; Fig. 4.11).

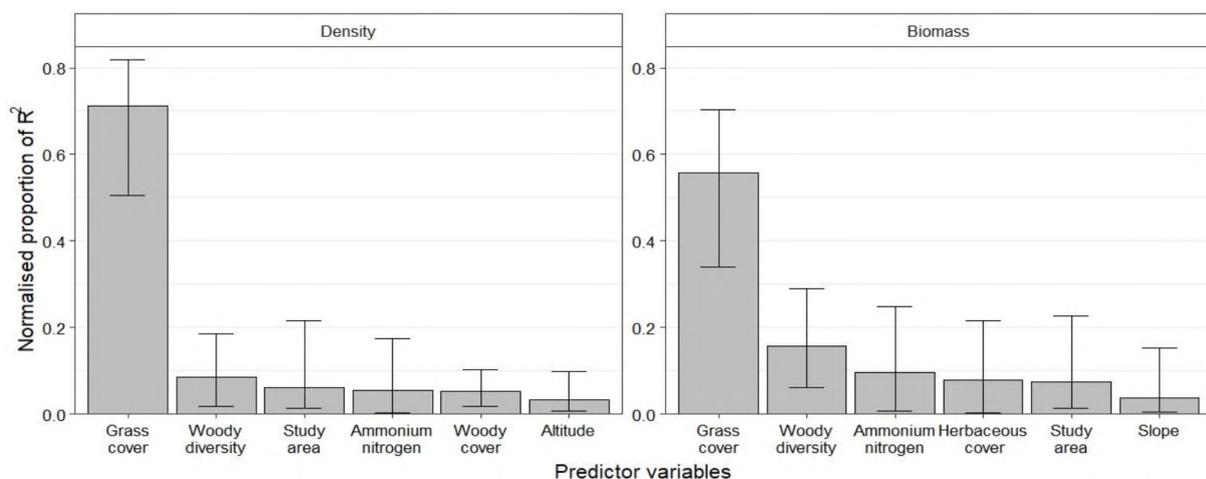


Fig. 4.11: Relative importance of the predictors of *A. dealbata* stem density (left) and biomass (right) with 95 % bootstrap confidence intervals.

4.4. Discussion

These results offer ground-level insights into the current state of the *A. dealbata* invasion in the northern Eastern Cape. Firstly, the abundance and productivity of *A. dealbata* were spatially variable at the regional scale, i.e. between study areas. Secondly, *A. dealbata* stems experienced significant growth over the period of a single year, contributing to a substantial rate of annual biomass production at the landscape level, despite continued harvest. Thirdly, although invaded landscapes varied in terms the abundance of *A. dealbata*, biodiversity, cover, soil properties and topography, only grass cover, woody diversity, study area and ammonium nitrogen were significantly influential correlates of the density and biomass of *A. dealbata*, with the addition of woody cover for the biomass of *A. dealbata*.

4.4.1. Abundance of invasive plants

In the northern Eastern Cape, the current density and biomass of *A. dealbata* across all sites was estimated at just under 7 000 stems.ha⁻¹ and 12 t.ha⁻¹, respectively. Although the density and biomass of *A. dealbata* varied significantly between study areas, no significant differences

were found between villages within study areas. Moreover, despite exhibiting the lowest aerial extent of *A. dealbata* of the three study areas (Chapter 3), the Maclear region had the highest density and biomass of *A. dealbata*, suggesting that the species need not be widespread across a landscape to be abundant in the landscape. The highest recorded stem density (19 250 stems.ha⁻¹) and biomass (33.03 t.ha⁻¹) were observed in plots in Katkop and Chevy Chase, respectively (Fig. 4.9). The density and biomass of *A. dealbata* quantified in this current study was lower than expected, representing conservative estimates, presumably because many of the sample sites were only invaded relatively recently, despite the long history of invasion across the northern Eastern Cape. This is supported by the historical cover classification, which revealed that more than one-quarter of the sites were relatively new invasions, since 21 field plots had no *A. dealbata* cover as recently as 1995, none of which were completely covered by 2013.

Any comparison of IAP density and/or biomass, within or between studies, will undoubtedly have limitations due to the highly variable spatial distribution of IAPs, shaped by the landscape heterogeneity, as well as the context- and species-specific nature of biological invasions. For example, Gwate *et al.* (2016) reported a substantially higher average stem density (27 108 stems.ha⁻¹) and biomass (279 t.ha⁻¹) of the closely-related *A. mearnsii* across three quaternary catchments in the Eastern Cape, one situated approximately 10 km northwest and two 75–100 km southwest of Maclear. Indeed, while their study focussed particularly on markedly dense patches of *A. mearnsii* within these catchments, Gwate *et al.* (2016: 270) noted the “. . . very high variability in density and AGB [above ground biomass] . . . across the sites, suggesting that *A. mearnsii* distribution was highly inconsistent”, ranging between 1 738–13 223 stems.ha⁻¹ and 1.7–866 t.ha⁻¹, respectively.

Far to the southeast, Mugido *et al.* (2014) estimated the biomass of various IAPs in the Coega Industrial Development Zone near Port Elizabeth, which included an average of approximately 60 t.ha⁻¹ of *A. longifolia*, 30 t.ha⁻¹ of *A. mearnsii* and 25 t.ha⁻¹ of *A. saligna* at various stem densities. Along the southern Western Cape, Rogers and Chown (2014) reported various densities of IAPs ranging from an average of about 180 *A. saligna* stems.ha⁻¹ in the Riverlands Nature Reserve to over 12 000 *A. cyclops* and *A. saligna* stems per hectare in the Koeberg Nature Reserve, while Stafford and Blignaut (2017) recently estimated the biomass of *Acacia*, *Eucalyptus* and *Pinus* species on the Agulhas Plain at 36 t.ha⁻¹, 38 t.ha⁻¹ and 51 t.ha⁻¹, respectively. According to Stafford *et al.* (2017), approximately 10 million hectares of South Africa is covered by IAPs, contributing to an estimated 167 million tonnes of woody biomass (16.7 t.ha⁻¹).

4.4.2. Biomass production

On average, *A. dealbata* stems gained approximately one kilogram of dry wood mass between 2016 and 2017, contributing to an annual rate of biomass production of more than four tonnes per hectare (>40 %), while just over 15 % of biomass was harvested over the same period. Consequently, it was estimated that the overall biomass of the invasion has increased by more than a quarter over the past year, despite continued harvest by the local communities. According to Ngorima (2016), approximately 1 800 kg of *A. dealbata* fuelwood was harvested annually per household. The growth and productivity of *A. dealbata* quantified in this current study was lower than expected, representing a conservative annual estimate, presumably due to the widespread and severe drought conditions across the Eastern Cape and many other parts of South Africa between 2015 and 2017 (Muyambo *et al.*, 2017), which likely hampered *A. dealbata* productivity.

Despite this, the annual productivity of *A. dealbata* was proportionally high relative to the current biomass of *A. dealbata*. The relative growth rate of smaller stems was found to be very high compared to larger stems, contributing to a proportionally higher annual productivity, which rapidly decreased as the stem size increased. Since many of the sites were invaded relatively recently, it stands to reason that the average productivity was proportionally high relative to the current average biomass of *A. dealbata*. It was also found that although the annual productivity generally increased with the density of *A. dealbata* stems, there was a threshold beyond which the productivity reached a plateau and subsequently decreased as stem density continued to increase. The most densely invaded sites therefore did not accumulate biomass the most rapidly, despite high individual stem productivity.

Nonetheless, the rate of annual woody biomass production is known to be highly variable for *A. dealbata* in both its native and invasive ranges (Doran and Turnbull, 1997; Kube *et al.*, 1997; Praciak *et al.*, 2013). For example, Kube *et al.* (1997) reported annual production rates ranging between 1–23 m³.ha⁻¹.yr⁻¹ for 8–10 year old *A. dealbata* plantations in Tasmania, equating to approximately 0.6–13 t.ha⁻¹.yr⁻¹, based on an average wood density of 570 kg.m³ for eight-year-old *A. dealbata* trees near Canberra, Australia (from Searle and Owen, 2005). Conversely, Frederick *et al.* (1985) found production rates up to 46 m³.ha⁻¹.yr⁻¹ (26 t.ha⁻¹.yr⁻¹), for eight-year-old *A. dealbata* in New Zealand, whereas Ando and Takeuchi (1973) and Wang and Fang (1991) reported production rates of 15–21 t.ha⁻¹.yr⁻¹ for five-year-old stands and 17–30 t.ha⁻¹.yr⁻¹ for four-year-old stands of invasive *A. dealbata* in China and Japan, respectively.

In addition to the variation due, *inter alia*, to stem age, size, stocking rates, growth patterns and the biophysical and human-induced conditions of the area, annual biomass production

rates also differ according to species. For example, Kimaro *et al.* (2007) compared the mean annual wood increment (MAI) for different species in a five-year rotational woodlot in Morogoro, Tanzania. Kimaro *et al.* (2007) found that *Senegalia polyacantha* (DBH >10 cm) produced about seven tonnes per hectare annually and *Vachellia nilotica* (DBH >7 cm) produced almost five tonnes per hectare annually. On the other hand, *Acacia crassicaarpa* and *Acacia mangium* trees (DBH >10 cm) produced over 10 t.ha⁻¹.yr⁻¹ and almost eight tonnes per hectare per year, respectively (Kimaro *et al.*, 2007). More recently, Bouillet *et al.* (2013) reported the MAI of *A. mangium* stands in Brazil (9.8 t.ha⁻¹.yr⁻¹) and Congo (6.5 t.ha⁻¹.yr⁻¹) at approximately six years of age.

In South Africa, Doran and Turnbull (1997) reported that well-established *A. mearnsii* plantations (>10 year old stands with mean DBH >13 cm) produce 15–25 m³.ha⁻¹.yr⁻¹ or approximately 8–14 t.ha⁻¹.yr⁻¹ (Searle and Owen, 2005) on average over 7–10 years. Gush (2017) recently quantified the annual rate of woody biomass production for a stand of 1 700 stems.ha⁻¹ of *Vachellia kosiensis* (7.2 t.ha⁻¹.yr⁻¹) near Richards Bay in KwaZulu-Natal, as well as for a stand of 1 111 stems.ha⁻¹ of mixed *Eucalyptus grandis* (13.6 t.ha⁻¹.yr⁻¹) and *Casuarina equisetifolia* (10.2 t.ha⁻¹.yr⁻¹). Although these examples primarily focus on managed plantations or woodlots, whereby homogenous stands of broad-stemmed trees are cultivated to achieve maximum timber production, they also illustrate the variability in annual biomass production for *A. dealbata*, amongst other invasive and expansive species.

4.4.3. Biophysical correlates

Acacia dealbata occurred across a range of landscapes in the northern Eastern Cape. However, certain biophysical conditions were found to be more strongly correlated with a higher abundance of the species. Most notably, there was a strong negative correlation between the abundance of *A. dealbata* and grass cover. The density of *A. dealbata* was also negatively correlated with woody species cover and diversity. Moreover, both the density and biomass of *A. dealbata* were positively correlated with the ammonium nitrogen content of the soil. However, the direction of causation for these correlates were indeterminant, since high abundances of *A. dealbata* could be the cause or result of low grass cover, low woody species cover and diversity, and high soil ammonium nitrogen. Nonetheless, several studies corroborate these findings, highlighting the relationship between the abundance of IAPs, soil properties and native plant cover and diversity. For example, *A. dealbata* invaded sites were found to have a significantly lower native species cover, diversity and richness, as well as a significantly higher soil nitrogen content, than transitional and uninvaded sites in northwestern Spain (Lorenzo *et al.*, 2010b; González-Muñoz *et al.*, 2012; Lorenzo *et al.*, 2012) and central Italy (Lazzaro *et al.*, 2014).

Native species cover, diversity and richness are frequently negatively correlated with the abundance of both invasive and expansive woody species (e.g. Gaertner *et al.*, 2009; Hejda *et al.*, 2009; Lorenzo *et al.*, 2012; Sholto-Douglas *et al.*, 2017). Possible explanations for this, illustrating the indeterminate direction of causation, stem from the previously discussed hypotheses of invasion. On the one hand, well-established and diverse native plant communities may provide a higher biotic resistance to invasion (Morris *et al.*, 2015), while disturbance-prone and degraded habitats are generally more susceptible to invasion (Hufbauer and Torchin, 2008). In other words, the level of resistance or disturbance influences the abundance of the IAP, i.e. *A. dealbata* achieved higher abundances in some plots because of their lower grass cover, woody cover and/or woody diversity. Despite this, however, an increasing number of studies suggest that disturbance need not be a prerequisite of *Acacia* invasions (e.g. Fuentes-Ramírez *et al.*, 2011; González-Muñoz *et al.*, 2012; Lorenzo *et al.*, 2012; Rodríguez *et al.*, 2017). On the other hand, invaders may also outcompete native species by exploiting resources more efficiently and/or suppressing the growth of native species by altering local conditions (Bardgett and Wardle, 2010; Chamier *et al.*, 2012; Rodríguez-Echeverría *et al.*, 2013; Simberloff *et al.*, 2013; Sholto-Douglas *et al.*, 2017). In this case, the abundance of the IAP affects the surrounding cover and diversity, i.e. high abundances of *A. dealbata* allowed the species to outcompete and/or suppressed grass cover, woody cover and/or woody diversity.

Acacia spp. are especially effective in both utilising available resources and fostering conditions conducive to their establishment and proliferation (Lorenzo *et al.*, 2017; Souza-Alonso *et al.*, 2017). For example, although nitrogenous soils generally support higher IAP abundances, the leguminous properties of *Acacia* promote the rapid accumulation and efficient fixation of soil nitrogen, even in relatively nitrogen-poor soils (May and Attiwill, 2003; Lorenzo *et al.*, 2010a). Consequently, despite the indeterminate direction of causation, high concentrations of soil nitrogen are frequently correlated with the high abundances of *Acacia*, including *A. dealbata* (Lazzaro *et al.*, 2014; Souza-Alonso *et al.*, 2014b).

Since relatively few biophysical variables correlated with the invasion, *A. dealbata* could presumably invade a wide range of habitats. Generalist invaders become widespread across biophysical gradients due to the broad range of their ecological preferences and tolerances (Carboni *et al.*, 2016; Steyn *et al.*, 2017). Studies of plant invasions across altitudinal gradients are particularly informative in determining whether the IAP species is a generalist or specialist invader (e.g. Kalwij *et al.*, 2015; Steyn *et al.*, 2017), because “elevation is an important indicator of microclimatic variation, which may physiologically constrain alien plant invasion” (Pauchard and Alaback, 2004: 244).

Recently, Steyn *et al.* (2017) found that high-elevation IAP species in the Maloti-Drakensberg Transfrontier Conservation Area (100–150 km northeast of Matatiele) were predominantly generalists, which have adapted along altitudinal gradients of increasingly severe environmental conditions, rather than specialists, which have adapted specifically to the harsh alpine conditions. This supports the *directional ecological filtering hypothesis* (Alexander *et al.*, 2011), which asserts that increasingly severe environmental conditions gradually reduce IAP species richness along abiotic gradients (e.g. as altitude increases) by filtering out species with narrow, highly specialised ecological adaptations, preferences and tolerances (Alexander *et al.*, 2011; Steyn *et al.*, 2017). Moreover, Kalwij *et al.* (2015) recently found that high-altitude IAP species in the Maloti-Drakensberg area are continuing to climb in altitude, suggesting that many of the high-altitude IAS in South Africa are still establishing new invasions.

In this current study, although the density and biomass of *A. dealbata* somewhat decreased with an increase in altitude and slope, respectively, both relationships were found to be insignificant, which points to *A. dealbata* being a generalist invader (Alexander *et al.*, 2011; Steyn *et al.*, 2017). Additionally, *A. dealbata* was found invading an altitudinal range between 1 360 m and 1 750 m at various densities across the sample sites, the upper limit of which reportedly corresponds to the expected upper elevational limit of *A. dealbata* based on local herbarium records, according to Kalwij *et al.* (2015). However, Kalwij *et al.* (2015) observed *A. dealbata* in the Maloti-Drakensberg area at elevations as high as 2 009 m, which suggests that *A. dealbata* may continue to spread and establish new invasions at higher altitudes in the northern Eastern Cape.

4.5. Conclusion

This chapter focused on the current abundance and correlates of the *A. dealbata* invasion at sampled sites in the northern Eastern Cape. The local-scale perspective provided ground-level insights into the dynamics of the invasion, highlighting the spatial variability of *A. dealbata* density, biomass and productivity, as well as the biophysical variability of invaded areas. Cumulatively, the growth of *A. dealbata* stems over a single year contributed to a considerable annual rate of biomass production per hectare, outweighing the estimated annual harvest rate. The abundance of *A. dealbata* is therefore expected to increase, barring additional control interventions. Moreover, although few biophysical variables were correlated with *A. dealbata* densities and biomass, the results were supported by long-standing hypotheses in invasion ecology, namely that high native species cover, diversity and richness offer a biotic resistance towards biological invasions, while perturbed habitats are typically more invasible, as well as the notion that invaders can alter their habitats to foster invasibility. A high abundance of grass cover was found to be particularly important for maintaining a low density and biomass of *A. dealbata* in the area. Indeed, the degree of biological invasion can be highly variable across

the landscape, shaped by the interaction of local- and broader-scale biophysical conditions, namely grass cover, woody diversity and soil ammonium nitrogen at the local scale, and the current and historical distribution of bare grounds, cultivated lands and grasslands at broader scales. In conjunction with a broader landscape perspective, ground-level insights offer a deeper understanding required for managing highly invasive species such as *A. dealbata*. The chapter to follow will highlight and integrate the key findings of this thesis.

CHAPTER FIVE: SYNTHESIS – THE INVASION OF *ACACIA DEALBATA* IN THE NORTHERN EASTERN CAPE

In this thesis, a spatio-temporal, landscape perspective was adopted to better understand the nature and extent of invasion in the northern Eastern Cape, focussing on the historical spread, current abundance and correlates of *A. dealbata* across sampled sites. Following a brief introductory overview of biological invasions, this chapter collates and discusses pertinent findings of the research, delving into the nature of the *A. dealbata* invasion, invasion systems and invaded landscapes. The broader implications for biological invasion research and management are then discussed, including a set of recommendations for the management of the *A. dealbata* invasion moving forward, concluding the thesis.

5.1. Nature and extent of the *A. dealbata* invasion

The dynamic, multidimensional and multi-scalar nature of biological invasions emerged as an overarching theme throughout this study, reiterated in each chapter of the thesis. Initially, the multidimensionality of invasions was alluded to by the range of research approaches, avenues of inquiry and studies conducted over the long history of biological invasion research (Chapter 1, Sections 1.1.1 and 1.1.2). Moreover, it became increasingly apparent that the success and impacts of invasions (Chapter 1, Sections 1.2 and 1.3, respectively) are context- and species-specific, compounding the challenge of IAP management (Chapter 1, Section 1.4). Several concepts and frameworks were then introduced to understand and appreciate the context and complexity of wicked problems, systems and landscapes (Chapter 2, Sections 2.1.1, 2.1.2 and 2.1.3, respectively). The overarching theme, complemented by the dual systems- and landscape-based conceptual and theoretical underpinnings of the thesis, was echoed and empirically exemplified in the third and fourth chapters.

5.1.1. Addressing the research questions

The proposed research questions (Chapter 1, Section 1.6) yielded context-specific, scale-dependent and sometimes ambiguous answers. It would therefore be remiss to address these questions (i–vii) without acknowledging the spatio-temporal variability of their respective answers and referring to the relevant result sections.

For example, although (i) the extent and distribution of the invasion changed over time, with *A. dealbata* spreading at (ii) an overall average annual rate of 0.11–0.21 % since the late 1940s/early 1950s, the extent and rate of spread varied across sites and at different scales (Chapter 3, Section 3.3.1). Similarly, although the general trends in LULC change suggested that (iii) *A. dealbata*, bare ground, plantation, residential, shrubland and wetland cover were increasing, while cultivated land and grassland cover were decreasing over time, there was a significant degree of spatio-temporal variability in LULC changes (Chapter 3, Section 3.3.2).

Furthermore, (iv) *A. dealbata* frequently retained a high proportion of its existing cover across successive timesteps, while most notably invading bare ground, cultivated land and grasslands. However, the proportion of LULC transitioning from one class to another varied at different spatio-temporal scales, as well as over time, between sites and between the different LULC classes (Chapter 3, Section 3.3.3).

On average, (v) *A. dealbata* stems gained approximately one kilogram of dry wood biomass (2016–2017), contributing to an estimated production rate of about four tonnes per hectare per year, while (vi) the density and biomass of *A. dealbata* were measured and calculated at just below 7 000 stems.ha⁻¹ and 12 t.ha⁻¹, respectively. The density, biomass and productivity also varied between sites (Chapter 4, Section 4.3.1). It was also found that (vii) the invasion is indeed associated with specific biophysical conditions, particularly a low percentage of grass cover (Chapter 4, Section 4.3.2). Despite their limitations, the research questions provided a necessary blueprint to assess the *A. dealbata* invasion at multiple spatio-temporal scales and fulfil the objectives of the study.

5.1.2. Key findings

The two research objectives were addressed in the third and fourth chapters, which dealt with the history of invasion and broader LULC changes, and the current abundance and correlates of *A. dealbata*, respectively. In each chapter, three main findings were independently highlighted and examined in their respective discussion sections (Chapter 3, Section 3.4 and Chapter 4, Section 4.4, respectively). The third chapter offered broader scale conclusions regarding the invasion, namely that i) the extent of the invasion has increased, i.e. *A. dealbata* has spread; ii) changes in LULC occurred and were spatio-temporally variable; and, iii) the invasion and broader LULC changes are highly dynamic. In contrast, the fourth chapter offered ground-level insights on the invasion, namely that iv) the abundance and productivity of *A. dealbata* varied between regions; v) the annual rate of stem growth was significant, contributing to significant annual biomass production; and vi) only grass cover, woody diversity, study area and ammonium nitrogen were significantly influential correlates of the density and biomass of *A. dealbata*, with the addition of woody cover for the biomass of *A. dealbata*. Once collated, these findings underscored the following key findings of the thesis in its entirety.

Firstly, there was a high degree of spatial variability in the extent, density and biomass of *A. dealbata*, as well as in the annual rate of spread and biomass production. Since spatial heterogeneity is a defining characteristic of landscapes (Turner and Gardner, 2015), influencing the density, distribution and spread of species (With, 2002), it was not unfounded that the *A. dealbata* invasion displayed high spatial variability. Macroecological studies have

suggested that widespread species typically also have high local abundances (e.g. Gaston and Blackburn, 2000; McKinney and La Sorte, 2007). However, this current study revealed that *A. dealbata* was not particularly abundant across the sample sites, i.e. the average density and biomass were relatively low (Chapter 4, Section 4.4.1), despite a proportionally high annual productivity relative to the current biomass (Chapter 4, Section 4.4.2). Moreover, this study revealed that *A. dealbata* was not always locally abundant in the same areas as where it was more widespread and *vice versa*, at least at the regional and landscape scales. Notably, the invasion was most extensive and least abundant in the Matatiele region, while the opposite was true of the Maclear region. This is likely due to differences in the composition and configuration of invasible patches between the two regions, particularly the differences in the size and connectivity of suitable habitat patches (Vilà and Ibáñez, 2011). Nonetheless, the macroecological relationship between the extent and local abundance of a species would likely be maintained in the case of *A. dealbata*, since the species was found to be widespread across the study areas, with localised pockets of high abundance. Furthermore, *A. dealbata* has long been considered widespread and abundant in South Africa (Nel *et al.*, 2004).

Secondly, the growth, productivity and spread of *A. dealbata* were significantly positive, and thirdly, relatively few biophysical conditions correlated with the invasion, indicative of the broad range of invaded and potentially invasible habitats, suggesting that the extent and abundance of *A. dealbata* will likely continue to increase, barring deliberate intervention. According to Carboni *et al.* (2016: 219), invaders are “considered most successful when they are regionally widespread, locally abundant and have broad ecological preferences”, such as in the case of *A. dealbata* in the northern Eastern Cape. Considering the current rates of growth, productivity and spread, it is expected that *A. dealbata* will not only persist in the northern Eastern Cape, but will inevitably become more widespread and abundant in the absence of effective control. Moreover, with relatively few significant biophysical correlates of invasion *A. dealbata* could presumably invade a wide range of habitats (Chapter 4, Sections 4.3.2 and 4.4.3). The percentage of grass cover was found to be strongly negatively correlated with the abundance of *A. dealbata*, while other woody species diversity and cover were also negatively correlated with the abundance of *A. dealbata*, albeit to a lesser degree than grass cover.

Finally, broader changes in LULC were multidirectional and spatio-temporally variable (Chapter 3, Section 3.3.3). Despite the net increase in the extent and abundance of *A. dealbata*, some, albeit not extensive, of the previously invaded areas have since transitioned to other LULC classes, while previously uninvaded areas have subsequently become invaded. This dynamism is a prominent feature of LULC change and landscape evolution (Chapter 3, Section 3.4.3). Consequently, the density, distribution and extent of the invasion could drastically change in the future, posing further challenges to management. Alarming, should

the current trends in LULC change continue, grasslands would increasingly degrade to bare grounds, which in turn may be more vulnerable to invasion, as suggested by the biotic resistance and disturbance hypotheses (Hufbauer and Torchin, 2008). In conjunction with the current positive annual rates of growth, productivity and spread, as well as the broad ecological preferences of *A. dealbata*, this is likely to facilitate further invasion.

Collectively, these findings underline the complex nature and increasing extent of the *A. dealbata* invasion in the northern Eastern Cape, supporting the overarching theme of the thesis and illustrating the growing wickedness of biological invasions. Moreover, the nature of the *A. dealbata* invasion demonstrates and emphasises some of the core characteristics of complex systems and landscapes.

5.1.3. Invasion systems and invaded landscapes

Systems and landscapes are analogous in several ways (Farina, 2006). Systems are made up of interacting components and subsystems, arranged in a self-organised, hierarchical structure and characterised by emergent properties (Adams *et al.*, 2014). Vertical and horizontal flows stimulate the accumulation or depletion of stocks in response to external, environmental factors, while feedback loops regulate the functioning of the system in service of the overall objective of the system (Adams *et al.*, 2014). Similarly, landscapes are comprised of a hierarchical set of interacting spatial, temporal and thematic elements, with different spatial patterns and processes emerging at broader scales, ranging from a single ecotope at the detailed scale to collections of landscapes at the regional scale (Ingegnoli, 2002, 2011). For both systems and landscapes, local scale alterations can evoke broader scale changes and *vice versa*. Biological invasions exhibit many of the attributes of systems and landscapes (Chapter 2, Sections 2.1.2 and 2.1.3, respectively). These attributes are apparent in invasion systems and invaded landscapes, exemplified in the case of the *A. dealbata* invasion in the northern Eastern Cape.

Biological invasions demonstrate the seven axioms of systems theory (Chapter 2, Section 2.1.2.1; Adams *et al.*, 2014). Invasion systems demonstrate the *centrality* axiom in terms of hierarchy, emergence, control and communication (Adams *et al.*, 2014). This is because species invasiveness and habitat invasibility, as well as the patterns, processes and impacts of invasion, emerge at different biological, ecological, social and spatio-temporal scales (With, 2002; Drake *et al.*, 2007; Shackleton *et al.*, 2007; Theoharides and Dukes, 2007; Vilà and Ibáñez, 2011; Jeschke *et al.*, 2014), while feedback processes and interactions relay *information* within and between hierarchical levels, subsystems and the surroundings (Wu and David, 2002; Farina, 2006; Rammel *et al.*, 2007; Meadows, 2008; Adams *et al.*, 2014).

Moreover, the stock-and-flow *design* of systems (Meadows, 2008; Adams *et al.*, 2014) is evident in the population dynamics of IAPs, whereby the abundance of the invader and the available resources are represented as stocks, which can be altered through the flow of propagules, nutrients, etc. Since the *goal* of many systems is to maintain continued functioning (Adams *et al.*, 2014), it stands to reason that the goal of an invasion system is the continued survival and proliferation of the species. The *viability* and success of an invasion system is therefore contingent on key controlling parameters (Adams *et al.*, 2014), including density-dependent establishment and survival thresholds (Davis *et al.*, 2004), and reproduction and dispersal constraints (Richardson *et al.*, 2000); external *contextual* factors of the surrounding environment (Adams *et al.*, 2014), including the context-specific, biophysical properties of the habitat and the surrounding landscape (Vilà and Ibáñez, 2011); and the *in situ operational* behaviour and performance of the system (Adams *et al.*, 2014).

The extent of *A. dealbata* was tracked over time at different scales of the spatio-temporal hierarchy (Adams *et al.*, 2014). It became evident that the stock of *A. dealbata* is increasing over time because the rates of growth, productivity and spread were all positive. Moreover, the long history of the invasion alludes to the viability of the system (Adams *et al.*, 2014) and it is suspected that the species occupies a sufficient area at high enough abundances that the invasion will persist in the region. However, the *in situ* success and degree of invasion at different localities depends on contextual biophysical factors (Adams *et al.*, 2014).

Biological invasions are complex, dynamic and multidimensional, with an intricate network of interacting components and holons, operating across multiple hierarchies and scales. Invasions can therefore be considered complex systems (specifically CAS) and conceptualised in the framework of panarchical adaptive cycles (Chapter 2, Section 2.1.2.2; Gunderson and Holling, 2002). For example, succession is a prevalent process in ecological systems, whereby habitat community structures transition from a phase of rapid resource exploitation and population growth to a prolonged phase of accumulation, stabilisation and connectivity, followed by an eventual collapse phase, triggered by a disturbance event, and subsequent reorganisation phase, whereby resilience surfaces and builds as an emergent property (Gunderson and Holling, 2002; Allen and Holling, 2010; Allen *et al.*, 2014).

Since many IAP species are pioneering r-strategists (Ordoñez *et al.*, 2010; Fuentes-Ramírez *et al.*, 2011), invaders often infiltrate ecosystems following a recent disturbance, when resource availability is most dynamic and spatially variable (Allen and Holling, 2010; Allen *et al.*, 2014). Invasive species are primed to exploit the discontinuities in ecological patterns and processes, within and between different hierarchical levels of the ecosystem (Allen and Holling, 2010; Allen *et al.*, 2014). Once established in an adaptive cycle, the invasion system can begin to build resilience and increasingly influence the broader panarchical network at

emergent scales (Allen *et al.*, 2014). According to the panarchy framework, alterations in local processes and systems can trigger revolt in broader cycles of change, perturbing social-ecological functions at greater scales, while broader scale processes and systems regulate local cycles (Gunderson and Holling, 2002; Holling, 2004).

Due to the dynamic, multidimensional and multi-scalar nature of the *A. dealbata* invasion, the system can be considered complex and adaptive. *Acacia dealbata* is integrated into the panarchical adaptive cycles (Gunderson and Holling, 2002) of the local ecosystems in the northern Eastern Cape. Long-term, broad-scale trends suggest that the invasion system is currently in the exploitation phase, or at least in an early stage of accumulation (Gunderson and Holling, 2002). Although many of the short-term, local-scale trends may suggest the same, it is important to bear in mind that periodic collapses in the abundance of invasive populations may simply trigger the reorganisation phase of the cycle and build the resistance of the system (Gunderson and Holling, 2002). For example, while disturbance events, including IAP clearance efforts, may temporarily reduce the extent and abundance of an invader, in many cases the disturbance perpetuates the cycle of invasion, as in the case of resprouting species such as *A. dealbata* (Lorenzo *et al.*, 2010a; Le Maitre *et al.*, 2011).

The long-standing association between humans and IAS emphasises the social-ecological dimension of biological invasions, which can be conceptualised using the SES framework (Chapter 2, Section 2.1.2.3; McGinnis and Ostrom, 2014). The *A. dealbata* invasion system can be considered a SES because the species has become so integral to the livelihoods of the local communities (Ngorima, 2016). For example, actors (i.e. local communities) harvest the resource units (i.e. *A. dealbata* biomass) from their surrounding environment to be utilised as a source of livelihood (e.g. for fuelwood), the outcome of which depends on the parameters of the resource system, including the supply and demand of the resource, as well as the regulatory parameters set by governance systems, informed by the social, economic and political setting (McGinnis and Ostrom, 2014).

Since plant biological invasions introduce a foreign phytotopic layer to the landscape, which in turn alters many other thematic layers at multiple spatio-temporal scales, invaded landscapes behave much like panarchical invasion systems. Consequently, biological invasions can also be examined from a landscape ecological perspective and conceptualised in terms of the landscape ecotissue model (Chapter 2, Section 2.1.3; Ingegnoli, 2002). Invasive spread across the landscape would not be possible if not for localised introduction(s), establishment and population growth of the introduced species (Richardson *et al.*, 2000; Theoharides and Dukes, 2007; Vilà and Ibáñez, 2011). Once introduced, the species must overcome local biophysical constraints (Richardson *et al.*, 2000) and integrate into the local

ecotope (Ingegnoli, 2002). Following establishment, the species must overcome dispersal constraints across landscape and broader scale biophysical barriers (Richardson *et al.*, 2000).

The introduction of an alien plant species to an area alters the structure and composition of the ecotope, which may subsequently evoke broader changes in the landscape, perpetuating conditions conducive to its survival and spread (Ingegnoli, 2002; With, 2002; Theoharides and Dukes, 2007; Vilà and Ibáñez, 2011). Landscape invasibility is therefore contingent, *inter alia*, on the composition, configuration and connectivity of the constituent suitable (invasible) habitat patches and their responses to the invasion (Vilà and Ibáñez, 2011). However, since regional and global bioclimatic conditions shape local-scale habitat structures, broader-scale changes (such as global climate change) also influence the process of invasion (Hellmann *et al.*, 2008). The spatial heterogeneity and spatio-temporal dynamism of the collective past, present and future invaded ecotopes, landscape units, landscapes and regions underscore the multi-scalar complexity of the overall invaded ecotissue.

5.2. Implications

The emergence of the transdisciplinary field of invasion science has shifted the invasive species discourse and agenda towards more social-ecological and people-orientated approaches, both in terms of invasion research and management (Richardson, 2011; Packer *et al.*, 2017; Vaz *et al.*, 2017). Biological invasions are increasingly being viewed as complex, multidimensional and multi-scalar SES (Pyšek and Hulme, 2005; McNeely, 2013; Kannan *et al.*, 2014). This is exemplified in the case of the *A. dealbata* invasion in the northern Eastern Cape, which poses a wicked problem for the management of the species (Ngorima, 2016). The contribution of this thesis to invasion research and the implications of the key findings for *A. dealbata* management are discussed in this section.

5.2.1. Research

The boundaries of invasion science are continuously expanding and becoming increasingly porous, allowing for new transdisciplinary combinations of theories, methodologies and practices (Hulme, 2011; Richardson, 2011; Wilson *et al.*, 2016; Packer *et al.*, 2017; Vaz *et al.*, 2017). In this thesis, established frameworks informed and guided the research component, which in turn exemplified many facets of the frameworks. This suitably captured the complexity of biological invasions (Pyšek and Hulme, 2011), reflecting some of the contemporary conceptualisations of biological invasions in terms of wicked problems (e.g. Evans *et al.*, 2008; McNeely, 2013; Gaertner *et al.*, 2016; Woodford *et al.*, 2016), systems (e.g. Sundaram *et al.*, 2012; Kannan *et al.*, 2014; Wilson *et al.*, 2016; Packer *et al.*, 2017) and landscapes (e.g. With, 2002; Pyšek and Hulme, 2005; Theoharides and Dukes, 2007; Vilà and Ibáñez, 2011). The combination of the desktop-based GIS analysis of aerial photographs and field-based

vegetation surveys provided complementary top-down and bottom-up perspectives of the *A. dealbata* invasion. This i) revealed an apparent mismatch between areas of extensive *A. dealbata* cover and those with an abundance of *A. dealbata* in terms of density and biomass, and ii) provided an explanation for the proportionally high annual productivity rate relative to the current biomass of *A. dealbata*, since the historical cover classification revealed that many sites had only become invaded relatively recently, underlining the importance of the dual methodological approaches.

The overarching theme and key findings of this thesis were not especially novel, considering that numerous studies and meta-analyses in invasion science and LULC change research reiterate that biological invasion are spatio-temporally variable and context-specific (e.g. With, 2002; Pyšek and Hulme, 2005; Theoharides and Dukes, 2007; Vilà and Ibáñez, 2011; Latzka *et al.*, 2016); that the extent and abundance of IAP species are increasing and will likely continue to increase in many places (e.g. De Neergaard *et al.*, 2005; Hernández *et al.*, 2014; Wilson *et al.*, 2014; Masocha *et al.*, 2017; Seath, 2017); that particularly invasive species like *A. dealbata* have broad ecological preferences (e.g. Lorenzo *et al.*, 2010a; Morris *et al.*, 2011; Richardson and Rejmánek, 2011; Carboni *et al.*, 2016; Souza-Alonso *et al.*, 2017); and that LULC changes are highly dynamic (e.g. Lambin and Meyfroidt, 2010; Meyfroidt *et al.*, 2013; Harden *et al.*, 2014; Munroe *et al.*, 2014; Tizora *et al.*, 2016). However, it is this i) emphasis on the contextual understanding of biological invasions that underscores the importance of such research and informs the development of tailored management strategies, and ii) the integration across scales which allows interventions to be appropriately targeted. These are necessary to improve the confidence in the knowledge of the species and hence determine the prioritisation of the IAS for control (Robertson *et al.*, 2003).

5.2.2. Management

The extent and abundance of an IAP species in different localities and the biophysical characteristics of the invaded range influence the feasibility and efficacy of management and control efforts (Van Wilgen *et al.*, 2000; Hulme, 2006; Shackleton *et al.*, 2016). For example, Shackleton *et al.* (2016) recently identified the barriers impeding the management of *Prosopis* in South Africa. In addition to the biology and ecology of the invader, the natural barriers to management included the extent, density and remoteness of some invasive populations, as well as the occupational hazard of working at the invaded sites (Shackleton *et al.*, 2016). Consequently, despite successful localised clearances, broad-scale *Prosopis* control remains limited (Van Wilgen *et al.*, 2012b; Wise *et al.*, 2012; Shackleton *et al.*, 2016). This raises concerns for the management and control, particularly the mechanical control, of *A. dealbata*.

Acacia dealbata is a highly invasive, widespread and abundant transformer species (Nel *et al.*, 2004; Lorenzo *et al.*, 2010a). The findings of this study suggest that the extent and abundance of *A. dealbata* will continue to increase, which would undoubtedly amplify the severity of the invasion problem. Since the impacts and perceptions of an invasive species are largely contingent on its coverage and abundance in an area (Parker *et al.*, 1999; Shackleton *et al.*, 2007; Ricciardi *et al.*, 2013; Kumschick *et al.*, 2015), an increase in the extent, density and biomass of *A. dealbata* could result in more severe and widespread ecological and socio-economic impacts, which may include an accelerated loss of native species biodiversity, richness and cover; more drastic shifts in disturbance regimes; changes in nutrient and hydrological cycles; an increase in economic losses; a decrease in ecosystem services; and increasingly negative perceptions of the species (e.g. Parker *et al.*, 1999; Le Maitre *et al.*, 2000; Shackleton *et al.*, 2007; Binimelis *et al.*, 2008; Pyšek *et al.*, 2012b; Panetta and Gooden, 2017). This would undoubtedly place further pressure on management institutions and objectives. Furthermore, conflicting perceptions surrounding *A. dealbata* (Ngorima, 2016) pose management challenges, which in turn impede control efforts (Dickie *et al.*, 2014; Hoffman, 2014; Zengeya *et al.*, 2017).

5.2.3. Recommendations

The severity of the invasion problem will only worsen under the current projection of *A. dealbata* spread and productivity in the northern Eastern Cape. It is therefore imperative that more effective control measures be incorporated into the management of the species. The complete eradication of the species is likely unfeasible, due to the widespread extent and high abundance of the species (Nel *et al.*, 2004), but also unwanted because the local communities still make frequent use of *A. dealbata* (Ngorima, 2016). Consequently, management imperatives should focus on reducing and controlling the species. Justifiably, the mechanical clearance and chemical treatment of invasive *Acacia* spp. should indeed remain a component of the IAP management under the WFW programme, as it is a vital source of employment and poverty alleviation nationwide (Turpie *et al.*, 2008; Van Wilgen *et al.*, 2012b; Van Wilgen and Wannenburg, 2016). However, concerted efforts should be made to rehabilitate and monitor cleared sites to prevent reinvasion (De Neergaard *et al.*, 2005; Witkowski and Garner, 2008; McConnachie *et al.*, 2012).

Although *A. dealbata* has relatively few biophysical correlates and could presumably invade a wide range of habitats, grass and indigenous tree cover were both found to be negatively correlated with the abundance of *A. dealbata*. This points to broader ecosystem management regimes playing a role in the management of *A. dealbata* invasions and the limitations thereof. Management strategies to optimise grass and indigenous tree cover could therefore contribute

to both slowing the invasion of *A. dealbata* improving the success of post-clearance rehabilitation measures. Such strategies could include grazing and fire regime management.

Additionally, the deployment of biological control should undoubtedly be considered for the northern Eastern Cape, since it is arguably the most efficient, effective and sustainable means of control (Van Wilgen *et al.*, 2012b). Perhaps the question is not if biological control should be used, but rather which agents are most suitable to achieve the desired management objectives. *Melanterius maculatus* has been deployed on *A. dealbata* across sites in South Africa since the late 1990s/early 2000s (Impson *et al.*, 2011). Notably, approximately 80 % of seed damage occurred between 2001 and 2003 across sites in Kylemore in the Western Cape, while the agent has been confirmed to have established on *A. dealbata* at two sites in Mpumalanga and one in KwaZulu-Natal (Impson *et al.*, 2011). The deployment of *M. maculatus* could be a feasible option for limiting the spread of *A. dealbata* in the northern Eastern Cape, provided that the agent can successfully establish on the various populations of the invader. This option would leave the resource base of the local communities relatively secure over the short- to medium-term if effective, since *M. maculatus* only targets the seeds of *A. dealbata* (Impson *et al.*, 2011). Consequently, significant reductions in the extent and abundance of *A. dealbata* are likely only to incur over the long-term and/or in cases of overharvesting and mechanical clearance.

However, considering the extent and abundance of *A. dealbata* and substantial social-economic and ecological threats the invasion poses, it may be necessary to consider more drastic forms of biological control. According to Impson *et al.* (2011), bud-galling wasps (Pteromalidae) and the gall-forming rust fungus (*Uromycladium acaciae*) are potential candidates for controlling *A. dealbata* in South Africa. The latter is a congener of *U. tepperianum*, which has shown some success in controlling *A. saligna* through a “dramatic decline in population density and longevity of mature trees, as well as a reduction in canopy cover and seed production” (Impson *et al.*, 2011: 203). However, even such drastic measures may take some many years to make a significant impact on the extent and abundance of *A. dealbata*, considering that *A. saligna* populations were only reduced to significantly low abundances a decade after *U. tepperianum* was introduced (Wood and Morris, 2007). Nonetheless, the deployment of any biological control agent would require further research, including host specificity, impact efficacy and climate compatibility tests (Adair, 2008), as well as socio-economic assessments to determine the potential impacts of *A. dealbata* control on the livelihoods of the local communities (Ngorima, 2016).

5.3. Conclusion

Biological invasions are an upward cascade of wickedness, amassing emergent complexity at broader spatio-temporal scales (With, 2002; Drake *et al.*, 2007; Theoharides and Dukes, 2007). A spatio-temporal, landscape perspective offers a means of understanding the nature and extent of biological invasions in attempt to better manage invasive plants. The invasion of *A. dealbata* in the northern Eastern Cape is dynamic, multidimensional and multi-scalar. Moreover, the species is one of the most invasive and ecologically destructive alien species in South Africa (Richardson and Rejmánek, 2011). However, it is also an important local natural resource in the livelihoods of local communities in the northern Eastern Cape (Ngorima, 2016). This poses a wicked, social-ecological problem for IAP management. Consequently, any management interventions to limit or control *A. dealbata* need to consider the spatio-temporal dynamics of invaded landscapes, as well as the local-scale abundance, productivity and biophysical conditions of the area, while taking into consideration the livelihood requirements of the local communities.

REFERENCES

- Acocks, J.P.H. (1953) Veld types of South Africa. *Memoir of the Botanical Survey of South Africa*, **28**, 1-192.
- Adair, R.J. (2008) Galling guilds associated with *Acacia dealbata* and factors guiding selection of potential biological control agents. *Proceedings of the XII International Symposium on Biological Control of Weeds*, pp. 22-27. CAB International, La Grande Motte, France.
- Adams, K.M., Hester, P.T., Bradley, J.M., Meyers, T.J. and Keating, C.B. (2014) Systems theory as the foundation for understanding systems. *Systems Engineering*, **17**(1), 112-123.
- Aguilera, N., Becerra, J., Villaseñor-Parada, C., Lorenzo, P., González, L. and Hernández, V. (2015) Effects and identification of chemical compounds released from the invasive *Acacia dealbata* Link. *Chemistry and Ecology*, **31**(6), 479-493.
- Alexander, J.M., Kueffer, C., Daehler, C.C., Edwards, P.J., A, P., Seipel, T., Arévalo, J., Cavieres, L., Dietz, H., Jakobs, G., McDougall, K., Naylor, B., Otto, R., Parks, C.G., Rew, L.J. and Walsh, N. (2011) Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences of the United States of America*, **108**(2), 656-661.
- Allan, H.H. (1936) Indigene versus alien in the New Zealand plant world. *Ecology*, **17**, 187-193.
- Allen, C.R., Angeler, D.G., Garmestani, A.S., Gunderson, L.H. and Holling, C.S. (2014) Panarchy: theory and application. *Ecosystems*, **18**(4), 578-589.
- Allen, C.R. and Holling, C.S. (2010) Novelty, adaptive capacity, and resilience. *Ecology and Society*, **15**(3), 1-15.
- Alpert, P., Bone, E. and Holzapfel, C. (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native species. *Perspectives in Plant Ecology, Evolution and Systematics*, **3**(1), 52-66.
- Anderies, J.M., Janssen, M.A. and Ostrom, E. (2004) A framework to analyze the robustness of social-ecological systems from an institutional perspective. *Ecology and Society*, **9**(1), 18.
- Ando, T. and Takeuchi, I. (1973) Growth and production structure of *Acacia mollissima* Willd. and *Acacia dealbata* Link in Saujo Experimental Stand. *Bulletin of the Government Forest Experiment Station (Meguro)*, **252**, 149-159.
- Baker, H.G. (1965) Characteristics and modes of origin of weeds. *The Genetics of Colonizing Species* (eds Baker, H.G. and Stebbins, G.L.), pp. 147-172. Academic Press, New York, USA.
- Baker, H.G. and Stebbins, G.L. (1965) *The Genetics of Colonizing Species*. Academic Press, New York, USA.
- Bardgett, R.D. and Wardle, D.A. (2010) *Aboveground–Belowground Linkages: Biotic Interactions, Ecosystem Properties and Global Change*. Oxford University Press, Oxford, UK.
- Barney, J.N. (2016) Invasive plant management must be driven by a holistic understanding of invader impacts. *Applied Vegetation Science*, **19**(2), 183-184.
- Barton, K. (2016) MuMIn: multi-model inference. R package version 1.15.6.
- Bellard, C., Thuiller, W., Leroy, B., Genovesi, P., Bakkenes, M. and Courchamp, F. (2013) Will climate change promote future invasions? *Global Change Biology*, **19**(2), 3740-3748.
- Bernhardt, P. (1989) Floral ecology of the Australian *Acacia*. *Advances in Legume Biology: Monographs in Systematic Botany from the Missouri Botanical Gardens* 29 (eds Stirton, C.H. and Zarucchi, J.L.), pp. 263-281. Missouri Botanical Gardens, St Louis, USA.
- Binggelli, P. (2001) The human dimensions of invasive woody plants. *The Great Reshuffling: Human Dimensions of Invasive Alien Species* (ed McNeely, J.A.), pp. 145-159. IUCN, Gland, Switzerland and Cambridge, UK.

- Binimelis, R., Born, W., Monterroso, I. and Rodríguez-Labajos, B. (2008) Socio-economic impact and assessment of biological invasions. *Biological Invasions* (ed Nentwig, W.), pp. 331-347. Springer, Berlin, Germany.
- Black, R.A., Richards, J.H. and Manwaring, J.H. (1994) Nutrient uptake from enriched soil microsites by three Great Basin perennials. *Ecology*, **75**(1), 110-122.
- Blair, A.C., Hanson, B.D., Brunk, G.R., Marrs, R.A., Westra, R., Niessen, S.J. and Hufbauer, R.A. (2005) New techniques and findings in the study of a candidate allelochemical implicated in invasion success. *Ecology Letters*, **8**(10), 1039-1047.
- Blossey, B. and Nötzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology*, **83**(5), 887-889.
- Bouillet, J.P., Laclau, J.P., De Moraes Gonçalves, J.L., Voigtlaender, M., Gava, J.L., Leite, F.P., Hakamada, R., Mareschal, L., Mabiala, A., Tardy, F. and Levillain, J. (2013) *Eucalyptus* and *Acacia* tree growth over entire rotation in single- and mixed-species plantations across five sites in Brazil and Congo. *Forest Ecology and Management*, **301**, 89-101.
- Bradley, B.A., Blumenthal, D.M., Wilcove, D.S. and Ziska, L.H. (2010) Predicting plant invasions in an era of global change. *Trends in Ecology and Evolution*, **25**(5), 310-318.
- Broadhurst, L.M. and Young, A.G. (2006) Reproductive constraints for the long-term persistence of fragmented *Acacia dealbata* (Mimosaceae) populations in southeast Australia. *Biological Conservation*, **133**, 512-526.
- Brooks, M.L., D'Antonio, C.M.D., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomasso, J.M., Hobbs, R.J., Pellant, M. and Pyke, D.A. (2004) Effects of invasive alien plants on fire regimes. *BioScience*, **54**(7), 677-688.
- Brown, G.K., Murphy, D.J. and Ladiges, P.Y. (2011) Relationships of the Australo-Malesian genus *Paraserianthes* (Mimosoideae: Leguminosae) identifies the sister group of *Acacia* sensu stricto and two biogeographical tracks. *Cladistics*, **27**, 380-390.
- Bullock, J.M. (2006) Plants. *Ecological Census Techniques: a Handbook* (ed Sutherland, W.J.), pp. 186-213. Cambridge University Press, Cambridge, UK.
- Burnham, K.P. and Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media.
- Burnham, K.P. and Anderson, D.R. (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research*, **33**(2), 261-304.
- Cadotte, M.W. (2006) Darwin to Elton: early ecology and the problem of invasive species. *Conceptual Ecology and Invasion Biology: Reciprocal Approaches to Nature* (eds Cadotte, M.W., McMahon, S.M. and Fukami, T.), pp. 15-34. Springer, Dordrecht, Netherlands.
- Caldwell, M.M., Richards, J.H., Johnson, D.A. and Dzurec, R.S. (1981) Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia*, **50**, 14-24.
- Callaway, J.C. and Josselyn, M.N. (1992) The introduction and spread of smooth cordgrass (*Spartina alternifolia*) in south San Francisco Bay. *Estuaries*, **15**(2), 218-226.
- Callaway, R.M. and Ridenour, W.M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment*, **2**(8), 436-443.
- Canty, A. and Ripley, B.D. (2017) boot: Bootstrap R (S-Plus) functions. R package version 1.3-19.
- Carboni, M., Münkemüller, T., Lavergne, S., Choler, P., Borgy, B., Violle, C., Essl, F., Roquet, C., Muñoz, F., DivGrass Consortium and Thuiller, W. (2016) What it takes to invade grassland ecosystems: traits, introduction history and filtering processes. *Ecology Letters*, **19**, 219-229.
- Carruthers, J., Robin, L., Hattingh, J.P., Kull, C.A., Rangan, H. and Van Wilgen, B.W. (2011) A native at home and abroad: the history, politics, ethics and aesthetics of acacias. *Diversity and Distributions*, **17**(5), 810-821.

- Castro-Díez, P., Godoy, O., Saldaña, A. and Richardson, D.M. (2011) Predicting invasiveness of Australian acacias on the basis of their native climatic affinities, life history traits and human use. *Diversity and Distributions*, **17**(5), 934-945.
- Cavin, J.S. and Kull, C.A. (2017) Invasion ecology goes to town: from disdain to sympathy. *Biological Invasions*, **19**(12), 3471-3487.
- Chamier, J., Schachtschneider, K., Le Maitre, D.C., Ashton, P.J. and Van Wilgen, B.W. (2012) Impacts of invasive alien plants on water quality, with particular emphasis on South Africa. *Water SA*, **38**(2), 345-356.
- Chapin, F.S., Trainor, S.F., Huntington, O., Lovcraft, A.L., Zavaleta, E., Natcher, D.C., McGuire, A.D., Nelson, J.L., Ray, L., Calef, M. and Fresco, N. (2008) Increasing wildfire in Alaska's boreal forest: pathways to potential solutions of a wicked problem. *BioScience*, **58**(6), 531-540.
- Charles, H. and Dukes, J.S. (2008) Impacts of invasive species on ecosystem services. *Biological Invasions* (ed Nentwig, W.), pp. 79-96. Springer, Berlin, Germany.
- Chytrý, M., Jarošík, V., Pyšek, P., Hájek, O., Knollová, I., Tichý, L. and Danihelka, J. (2008) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology*, **89**(6), 1541-1553.
- Chytrý, M., Wild, J., Vojtech, J., Dendoncker, N., Reginster, I., Pino, J., Vilà, M., Maskell, L., Kuhn, I., Spangenberg, J. and Settele, J. (2012) Projecting trends in plant invasions in Europe under different scenarios of future land-use change: policy orientations will not reduce invasions. *Global Ecology and Biogeography*, **21**(1), 75-87.
- Colautti, R.I. and MacIsaac, H.J. (2004) Neutral terminology to define 'invasive' species. *Diversity and Distributions*, **10**, 135-141.
- Common Ground (2003) *Working for Water External Evaluation: Synthesis Report*. Cape Town, South Africa.
- Connor, T. and Mtwana, N. (2017) Vestige garden production and deagrarianization in three villages in the Eastern Cape, South Africa. *South African Geographical Journal*, <https://doi.org/10.1080/03736245.2017.1301268>, 1-22.
- Correia, M., Montesinos, D., French, K. and Rodríguez-Echeverría, S. (2016) Evidence for enemy release and increased seed production and size for two invasive Australian acacias. *Journal of Ecology*, **104**, 1391-1399.
- Costanza, D., D'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. and Van den Belt, M. (1997) The value of the world's ecosystem service and natural capital. *Nature*, **387**(6630), 253-260.
- Crawley, M.J., Harvey, P.H. and Purvis, A. (1996) Comparative ecology of the native and alien Floras of the British Isles. *Philosophical Transactions: Biological Sciences*, **351**(1345), 1251-1259.
- Cross, T., Finn, J.T. and Bradley, B.A. (2017) Frequency of invasive plant occurrence is not a suitable proxy for abundance in the northeast United States. *Ecosphere*, **8**(5), 1-12.
- Cundill, G., Roux, D.J. and Parker, J.N. (2015) Nurturing communities of practice for transdisciplinary research. *Ecology and Society*, **20**(2).
- Daehler, C.C. (2001) Darwin's naturalization hypothesis revisited *The American Naturalist*, **158**(3), 324-330.
- Danthu, P., Ndongo, M., Diaou, M., Thiam, O., Sarr, A., Dedhiou, B. and Vall, A.O.M. (2003) Impact of bush fire on germination of some West African acacias. *Forest Ecology and Management*, **173**(1), 1-10.
- Darlington, W. (1849) *Memorials of John Bartram and Humphrey Marshall*. Lindsay & Blakiston, Philadelphia, USA.
- Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. J. Murray, London, UK.
- Davis, H.G., Taylor, C.A., Cville, J.C. and Strong, D.R. (2004) An Allee effect at the front of a plant invasion: *Spartina* in a Pacific estuary. *Journal of Ecology*, **92**, 321-327.
- Davis, M.A. (2006) Invasion biology 1958-2005: the pursuit of science and conservation. *Conceptual Ecology and Invasion Biology: Reciprocal Approaches to Nature* (eds

- Cadotte, M.W., McMahon, S.M. and Fukami, T.), pp. 35-64. Springer, Dordrecht, Netherlands.
- Davis, M.A., Grime, J.P. and Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528-534.
- Davis, M.A., Thompson, K. and Grime, J.P. (2001) Charles S. Elton and the dissociation of invasion ecology from the rest of ecology. *Diversity and Distributions*, **7**(1/2), 97-102.
- De Candolle, A. (1855) *Géographie Botanique Raisonné*. V. Masson, Paris, France.
- De Lange, W.J. and Van Wilgen, B.W. (2010) An economic assessment of the contribution of weed biological control to the management of invasive alien plants and to the protection of ecosystem services in South Africa. *Biological Invasions*, **12**(12), 4113-4124.
- De Neergaard, A., Saarnak, C., Hill, T., Khanyile, M., Berzosa, A.M. and Birch-Thomsen, T. (2005) Australian wattle species in the Drakensberg region of South Africa - an invasive alien or a natural resource? *Agricultural Systems*, **85**, 216-233.
- De Wit, M.P., Crookes, D.J. and Van Wilgen, B.W. (2001) Conflicts of interest in environmental management: estimating the costs and benefits of a tree invasion. *Biological Invasions*, **3**(2), 167-178.
- Dennill, G.B. and Donnelly, D. (1991) Biological control of *Acacia longifolia* and related weed species (Fabaceae) in South Africa. *Agricultural, Ecosystems and Environment*, **37**, 115-135.
- Díaz, G.I., Nahuelhual, L., Echeverría, C. and Marín, S. (2011) Drivers of land abandonment in Southern Chile and implications for landscape planning. *Landscape and Urban Planning*, **99**(3-4), 207-217.
- Dickie, I.A., Bennett, B.M., Burrows, L.E., Nuñez, M.A., Peltzer, D.A., Porté, A., Richardson, D.M., Rejmánek, M., Rundel, P.W. and Van Wilgen, B.W. (2014) Conflicting values: ecosystem services and invasive tree management. *Biological Invasions*, **16**(3), 705-719
- Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A. and Ewers, R.M. (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology and Evolution*, **22**(9), 489-496.
- Didham, R.K., Tylianakis, J.M., Hutchison, M.A., Ewers, R.M. and Gemmell, N.J. (2005) Are invasive species the drivers of ecological change? *Trends in Ecology and Evolution*, **20**(9), 470-474.
- Dietz, H. and Edwards, P.J. (2006) Recognition that causal processes change during plant invasion helps explain conflicts in evidence. *Ecology*, **87**(6), 1359-1367.
- Dinno, A. (2017) dunn.test: Dunn's test of multiple comparisons using rank sums. R package version 1.3.5. <https://CRAN.R-project.org/package=dunn.test>.
- Dlamini, P., Chivenge, P., Manson, A. and Chaplot, V. (2014) Land degradation impact on soil organic carbon and nitrogen stocks of sub-tropical humid grasslands in South Africa. *Geoderma*, **235-236**, 372-381.
- Doran, J.C. and Turnbull, J.W. (1997) *Australian Trees and Shrubs: Species for Land Rehabilitation and Farm Planting in the Tropics*. Australian Centre for International Agricultural Research (ACIAR), Canberra, Australia.
- Drake, J.A., Fuller, M.M., Zimmerman, C.R. and Gamarra, J.G.P. (2007) Emergence in ecological systems. *From Energetics to Ecosystems: the Dynamics and Structure of Ecological Systems* (eds Rooney, N., McCann, K.S. and Noakes, D.L.G.), pp. 157-187. Springer, Dordrecht, Netherlands.
- Drake, J.A., Mooney, H.A., Di Castri, F., Groves, R.H., Kruger, E.J., Rejmánek, M. and Williamson, M.H. (1989) *Biological Invasions: a Global Perspective*. Wiley, Chichester, UK.
- Dumble, S. (2017) GGEBiplots: GGE Biplots with 'ggplot2'. R package version 0.1.1. <https://CRAN.R-project.org/package=GGEBiplots>.
- Egler, E.E. (1942) Indigene versus alien in the development of arid Hawaiian vegetation. *Ecology*, **23**, 14-23.

- El-Barougy, R.F., Cadotte, M.W., Khedr, A.H.A., Nada, R.M. and Maclvor, J.S. (2017) Heterogeneity in patterns of survival of the invasive species *Ipomoea carnea* in urban habitats along the Egyptian Nile Delta. *NeoBiota*, **33**, 1-17.
- Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen & Co. Ltd., London, UK.
- Enright, W.D. (2000) The effect of terrestrial invasive alien plants on water scarcity in South Africa. *Physics and Chemistry of the Earth, Part B: Hydrology, Oceans and Atmosphere*, **25**(3), 237-242.
- ESRI (2011) ArcGIS Desktop: Release 10. Environmental Systems Research Institute (ESRI), Redlands, USA.
- Evans, J.M., Wilkie, A.C. and Burkhardt, J. (2008) Adaptive management of non-native species: moving beyond the "either-or" through experimental pluralism. *Journal of Agricultural and Environmental Ethics*, **21**(6), 521-539.
- Farina, A. (2006) *Principles and Methods in Landscape Ecology: Towards a Science of the Landscape*. Springer, Dordrecht, Netherlands.
- Fei, S., Phillips, J. and Shouse, M. (2014) Biogeomorphic impacts of invasive species. *Annual Review of Ecology, Evolution, and Systematics*, **45**, 69-87.
- Ferreira, S., Gil, N., Queiroz, J.A., Duarte, A.P. and Domingues, F.C. (2011) An evaluation of the potential of *Acacia dealbata* as raw material for bioethanol production. *Bioresource Technology*, **102**(7), 4766-4773.
- Flood, R.L. (2010) The relationship of 'systems thinking' to action research. *Systemic Practice and Action Research*, **23**(4), 269-284.
- Folke, C. (2006) Resilience: the emergence of a perspective for social–ecological systems analyses. *Global Environmental Change*, **16**, 253-267.
- Forman, R.T.T. (1995) *Land Mosaics: the Ecology of Landscapes and Regions*. Cambridge University Press, Cambridge, UK.
- Fox, J. and Weisberg, S. (2011) An {R} Companion to Applied Regression. Sage, Thousand Oaks, USA
- Foxcroft, L.C. (2004) An adaptive management framework for linking science and management of invasive alien plants. *Weed Technology*, **18**, 1275-1277.
- Foxcroft, L.C., Pyšek, P., Richardson, D.M., Pergl, J. and Hulme, P.E. (2013) The bottom line: impacts of alien plant invasions in protected areas. *Plant Invasions in Protected Areas: Patterns, Problems and Challenges* (eds Foxcroft, L.C., Pyšek, P., Richardson, D.M. and Genovesi, P.), pp. 19-41. Springer Science & Business Media, Dordrecht, Netherlands.
- Foxcroft, L.C., Rouget, M., Richardson, D.M. and MacFadyen, S. (2004) Reconstructing 50 years of *Opuntia stricta* invasion in the Kruger National Park, South Africa: environmental determinants and propagule pressure. *Diversity and Distributions*, **10**(5-6), 427-437.
- Frappier, B., Lee, T.D., Olson, K.F. and Eckert, R.T. (2003) Small-scale invasion pattern, spread rate, and lag-phase behavior of *Rhamnus frangula* L. *Forest Ecology and Management*, **186**, 1-6.
- Frederick, D.J., Madgwick, H.A., Jurgensen, M.F. and Oliver, G.R. (1985) Dry matter, energy, and nutrient contents of 8-year-old stands of *Eucalyptus regnans*, *Acacia dealbata*, and *Pinus radiata* in New Zealand. *New Zealand Journal of Forestry Science*, **15**(2), 142-157.
- Fuentes-Ramírez, A., Pauchard, A., Cavieres, L. and Garcia, R.A. (2011) Survival and growth of *Acacia dealbata* vs. native trees across an invasion front in south-central Chile. *Forest Ecology and Management*, **261**(6), 1003-1009.
- Gaertner, M., Biggs, R., Te Beest, M., Hui, C., Molofsky, J. and Richardson, D.M. (2014) Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships. *Diversity and Distributions*, **20**(7), 733-744.
- Gaertner, M., Holmes, P.M. and Richardson, D.M. (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Progress in Physical Geography*, **33**, 319-338.

- Gaertner, M., Larson, B.M.H., Irlich, U.M., Holmes, P.M., Stafford, L., Van Wilgen, B.W. and Richardson, D.M. (2016) Managing invasive species in cities: a framework from Cape Town, South Africa. *Landscape and Urban Planning*, **151**, 1-9.
- Gaston, K.J. and Blackburn, T.M. (2000) *Macroecology*. Blackwell Science, Malden, USA.
- Gavier-Pizarro, G.I., Radeloff, V.C., Stewart, S.I., Huebner, C.D. and Keuler, N.S. (2010) Housing is positively associated with invasive exotic plant species richness in New England, USA. *Ecological Applications*, **20**(7), 1913-1925.
- Giannecchini, M., Twine, W. and Vogel, C. (2007) Land-cover change and human-environment interactions in a rural cultural landscape in South Africa. *The Geographical Journal*, **173**(1), 26-42.
- Gibbons, S.M., Lekberg, Y., Mummey, D.L., Sangwan, N., Ranmsey, P.W. and Gilbert, J.A. (2017) Invasive plants rapidly reshape soil properties in a grassland ecosystem. *mSystems*, **2**(2), 1-13.
- Giometto, A., Altermatt, F. and Rinaldo, A. (2017) Demographic stochasticity and resource autocorrelation control biological invasions in heterogeneous landscapes. *Oikos*, **126**, 1554-1563.
- Glaser, M., Krause, G., Ratter, B. and Welp, M. (2008) Human/nature interaction in the anthropocene potential of social-ecological systems analysis. *Gaia*, **17**, 77-80.
- González-Muñoz, N., Costa-Tenorio, M. and Espigares, T. (2012) Invasion of alien *Acacia dealbata* on Spanish *Quercus robur* forests: impact on soils and vegetation. *Forest Ecology and Management*, **269**, 214-221.
- Gooden, B., French, K., Turner, P.J. and Downey, P.O. (2009) Impact threshold for an alien plant invader, *Lantana camara* L., on native plant communities. *Biological Conservation*, **142**(11), 2631-2641.
- Gorchov, D.L., Henry, M.C. and Frank, P.A. (2014) Invasion of an exotic shrub into forested stands in an agricultural matrix. *Invasive Plant Science and Management*, **7**(2), 336-344.
- Gordon, D.R. (1998) Effect of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. *Ecological Applications*, **8**(4), 975-989.
- Grace, J.B., Harrison, S. and Cornell, H. (2017) Is biotic resistance enhanced by natural variation in diversity? *Oikos*, **126**, 1484-1492.
- Griffin, A.R., Midgley, S.J., Bush, D., Cunningham, P.J. and Rinaudo, A.T. (2011) Global uses of Australian acacias – recent trends and future prospects. *Diversity and Distributions*, **17**(5), 837-847.
- Grömping, U. (2006) Relative importance for linear regression in R: the package relaimpo. *Journal of Statistical Software*, **17**(1), 1-27.
- Gunderson, L.H. and Holling, C.S. (2002) *Panarchy: Understanding Transformations in Human and Natural Systems*. Island Press, Washington DC, USA.
- Guo, Q., Fei, S., Dukes, J.S., Oswalt, C.M., Iannone, B.V. and Potter, K.M. (2015) A unified approach for quantifying invasibility and degree of invasion *Ecology*, **96**(10), 2613-2621.
- Gush, M.B. (2017) The potential of *Vachellia kosiensis* (*Acacia kosiensis*) as a dryland forestry species in terms of its water use, growth rates and resultant water-use efficiency. *Southern Forests: a Journal of Forest Science*, **79**(3), 227-234.
- Gwate, O., Mantel, S.K., Finca, A., Gibson, L.A., Munch, Z. and Palmer, A.R. (2016) Exploring the invasion of rangelands by *Acacia mearnsii* (black wattle): biophysical characteristics and management implications. *African Journal of Range and Forage Science*, **33**(4), 265-273.
- Hamann, M. and Tuinder, V. (2012) *Introducing the Eastern Cape: a Quick Guide to its History, Diversity and Future Challenges*. Stockholm University, Stockholm, Sweden.
- Hamilton, M.A., Murray, B.R., Cadotte, M.W., Baker, A.C., Harris, C.J. and Licari, D. (2005) Life-history of plant invasiveness at regional and continental scales. *Ecology Letters*, **8**(10), 1066-1074.
- Harden, C.P., Chin, A., English, M.R., Fu, R., Galvin, K.A., Gerlak, A.K., McDowell, P.F., McNamara, D.E., Peterson, J.M., Poff, N.L., Rosa, E.A., Solecki, W.D. and Wohl, E.E.

- (2014) Understanding human-landscape interactions in the "Anthropocene". *Environmental Management*, **53**, 4-13.
- Hattingh, J.P. (2011) Conceptual clarity, scientific rigour and 'the stories we are': engaging with two challenges to the objectivity of biological invasions. *Fifty Years of Invasion Ecology: the Legacy of Charles Elton* (ed Richardson, D.M.), pp. 359-375. Blackwell Publishing Ltd, Chichester, UK.
- Head, K.H. (2006) *Manual of Soil Laboratory Testing. Volume 1: Soil Classification and Compaction Tests*. Whittles Publishing, Dunbeath, UK.
- Heger, T. and Jeschke, J.M. (2014) The enemy release hypothesis as a hierarchy of hypotheses *Oikos*, **123**, 741-750.
- Heger, T., Pahl, A.T., Botta-Dukát, Z., Gherardi, F., Hoppe, C., Hoste, I., Jax, K., Lindström, L., Boets, P., Haider, S., Kollmann, J., Wittmann, M.J. and Jeschke, J.M. (2013) Conceptual frameworks and methods for advancing invasion ecology. *Ambio*, **42**(5), 527-540.
- Heger, T. and Trepl, L. (2003) Predicting biological invasions. *Biological Invasions*, **5**, 313-321.
- Hejda, M., Pyšek, P. and Vojtech, J. (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, **97**(3), 393-403.
- Hellmann, J.J., Byers, J.E., Bierwagen, B.G. and Dukes, J.S. (2008) Five potential consequences of climate change for invasive species. *Conservation Biology*, **22**(3), 534-543.
- Henderson, L. (1998) Southern African plant invaders atlas (SAPIA). *Applied Plant Science*, **12**, 31-32.
- Henderson, L. (2007) Invasive, naturalized and casual alien plants in southern Africa: a summary based on the Southern African Plant Invaders Atlas (SAPIA). *Bothalia*, **37**, 215-248.
- Henriques-Silva, R., Boivin, F., Calcagno, V., C, U.M. and Peres-Neto, P.R. (2015) On the evolution of dispersal via heterogeneity in spatial connectivity. *Proceedings of the Royal Society of London B: Biological Sciences*, **282**(1803), 1-10.
- Hernández, L., Martínez-Fernández, J., Cañellas, I. and De la Cueva, A.V. (2014) Assessing spatio-temporal rates, patterns and determinants of biological invasions in forest ecosystems: the case of *Acacia* species in NW Spain. *Forest Ecology and Management*, **329**, 206-2113.
- Hobbs, R.J. (2000) Land-use changes and invasion. *Invasive Species in a Changing World* (eds Mooney, H.A. and Hobbs, R.J.), pp. 55-64. Island Press, Washington, DC, USA.
- Hobbs, R.J. (2004) The Working for Water programme in South Africa: the science behind the success. *Diversity and Distributions*, **10**, 501-503.
- Hobbs, R.J. and Richardson, D.M. (2011) Invasion ecology and restoration ecology: parallel evolution in two fields of endeavour. *Fifty Years of Invasion Ecology: the Legacy of Charles Elton* (ed Richardson, D.M.), pp. 61-69. Blackwell Publishing Ltd, Chichester, UK.
- Hoffman, M.T. (2014) Changing patterns of rural land use and land cover in South Africa and their implications for land reform. *Journal of Southern African Studies*, **40**(4), 707-725.
- Hoffmann, J.H., Moran, V.C. and Van Wilgen, B.W. (2011) Prospects for biological control of invasive *Pinus* species (Pinaceae) in South Africa. *African Entomology*, **19**, 393-401.
- Holling, C.S. (2004) From complex regions to complex worlds *Ecology and Society*, **9**(1), 11-20.
- Holub, J. and Jirásek, V. (1967) Zur vereinheitlichung der terminologie in der phytogeographie. *Folia Geobotanica et Phytotaxonomica*, **2**(1), 69-113.
- Horvitz, N., Wang, R., Wan, F. and Nathan, R. (2017) Pervasive human-mediated large-scale invasion: analysis of spread patterns and their underlying mechanisms in 17 of China's worst invasive plants. *Journal of Ecology*, **105**, 85-94.
- Hothorn, T., Bretz, F. and Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**(3), 346-363.

- Hufbauer, R.A. and Torchin, M.E. (2008) Integrating ecological and evolutionary theory of biological invasions. *Biological Invasions* (ed Nentwig, W.), pp. 79-96. Springer, Berlin, Germany.
- Hui, C., Richardson, D.M., P, L., Minoarivelo, H.O., Garnas, J. and Roy, H. (2016) Defining invasiveness and invasibility in ecological networks. *Biological Invasions*, **18**, 971-983.
- Hulme, P.E. (2006) Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology*, **43**, 835-847.
- Hulme, P.E. (2011) Biosecurity: the changing face of invasion biology. *Fifty Years of Invasion Biology: the Legacy of Charles Elton* (ed Richardson, D.M.), pp. 301-314. Blackwell Publishing Ltd, Chichester, UK.
- Hunt, M.A., Unwin, G.L. and Beadle, C.L. (1999) Effects of naturally regenerated *Acacia dealbata* on the productivity of a *Eucalyptus nitens* plantation in Tasmania, Australia. *Forest Ecology and Management*, **117**, 75-85.
- Impson, F.A.C., Kleinjan, C.A., Hoffmann, J.H., Post, J.A. and Wood, A.R. (2011) Biological Control of Australian *Acacia* Species and *Paraserianthes lophantha* (Willd.) Nielsen (Mimosaceae) in South Africa. *African Entomology*, **19**, 186-207.
- Ingegnoli, V. (2002) *Landscape Ecology: a Widening Foundation*. Springer, Berlin and Heidelberg, Germany and New York, USA.
- Ingegnoli, V. (2011) Non-equilibrium thermodynamics, landscape ecology and vegetation science *Thermodynamics – Systems in Equilibrium and Non-Equilibrium* (ed Moreno-Piraján, J.C.), pp. 139–172. InTech, Rijeka, Croatia.
- Jackson, T. (2015) Addressing the economic costs of invasive alien species: some methodological and empirical issues. *International Journal of Sustainable Society*, **7**(3), 221-240.
- Jeschke, J.M., Aparicio, L.G., Haider, S., Heger, T., Lortie, C.J., Pyšek, P. and Strayer, D.L. (2012) Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota*, **14**, 1-20.
- Jeschke, J.M., Bacher, S., Blackburn, T.M., Dick, J.T., Essl, F., Evans, T., Gaertner, M., Hulme, P.E., Kühn, I., Mrugała, A., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D.M., Sendek, A., Vilà, M., Wiek, A. and Kumschick, S. (2014) Defining the impact of non-native species. *Conservation Biology*, **28**(5), 1188-1194.
- Kalwij, J.M., Robertson, M.P. and Van Rensburg, B.J. (2015) Annual monitoring reveals rapid upward movement of exotic plants in a montane ecosystem. *Biological Invasions*, **17**(12), 3517-3529.
- Kannan, R., Shackleton, C.M. and Shaanker, R.U. (2013) Reconstructing the history of introduction and spread of the invasive species, *Lantana*, at three spatial scales in India. *Biological Invasions*, **15**, 1287-1302.
- Kannan, R., Shackleton, C.M. and Shaanker, R.U. (2014) Invasive alien species as drivers in socio-ecological systems: local adaptations towards use of *Lantana* in Southern India. *Environment, Development and Sustainability*, **16**, 649-669.
- Keane, R.M. and Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **17**(4), 164-170.
- Keeley, J.E., Franklin, J. and D'Antonio, C.M.D. (2011) Fire and invasive plants on California landscapes. *The landscape ecology of fire* (eds McKenzie, D., Miller, C. and Falk, D.A.), pp. 193-221. Springer Science & Business Media, Dordrecht, Netherlands.
- Kelly, R., Lundy, M.G., Mineur, F., Harrod, C., Maggs, C.A., Humphries, N.E., Sims, D.W. and Reid, N. (2014) Historical data reveal power-law dispersal patterns of invasive aquatic species. *Ecography*, **37**(6), 581-590.
- Kenrick, J. (2003) Review of pollen–pistil interactions and their relevance to the reproductive biology of *Acacia*. *Australian Systematic Botany*, **16**(1), 119-130.
- Kimaro, A.A., Timmer, V.R., Mugasha, A.G., Chamshama, S.A. and Kimaro, D.A. (2007) Nutrient use efficiency and biomass production of tree species for rotational woodlot systems in semi-arid Morogoro, Tanzania. *Agroforestry Systems*, **71**(3), 175-184.

- Kowarik, I. (2003) Human agency in biological invasions: secondary releases foster naturalisation and population expansion of alien plant species. *Biological Invasions*, **5**, 293-312.
- Kowarik, I. and Von der Lippe, M. (2008) Pathways in plant invasions. *Biological Invasions* (ed Nentwig, W.), pp. 29-47. Springer, Berlin, Germany.
- Kube, P.D., Brooks, S.J., Brown, D.R. and Peterson, M. (1997) The use of *Acacia dealbata* as a plantation species in Tasmania: a summary of recent research. *Tasforests*, **9**, 71-76.
- Kueffer, C. and Hirsch Hadorn, G. (2008) How to achieve effectiveness in problem-oriented landscape research: the example of research on biotic invasions. *Living Review in Landscape Research*, **2**(2), 1-49.
- Kull, C.A., Shackleton, C.M., Cunningham, P.J., Ducatillon, C., Dufour-Dror, J.M., Esler, K.J., Friday, J.B., Gouveia, A.C., Griffin, A.R., Marchante, E., Midgley, S.J., Pauchard, A., Rangan, H., Richardson, D.M., Rinaudo, T., Tassin, J., Urgenson, L.S., Von Maltitz, G.P., Zenni, R.D. and Zylstra, M.J. (2011) Adoption, use and perception of Australian acacias around the world. *Diversity and Distributions*, **17**(5), 822-836
- Kumschick, S., Bacher, S., Dawson, W., Heikkilä, J., Sendek, A., Pluess, T., Robinson, T. and Kühn, I. (2012) A conceptual framework for prioritization of invasive alien species for management according to their impact. *NeoBiota*, **15**, 69-100.
- Kumschick, S., Gaertner, M., Vilà, M., Essl, F., Jeschke, J.M., Pyšek, P., Ricciardi, A., Bacher, S., Blackburn, T.M., Dick, J.T., Evans, T., Hulme, P.E., Kühn, I., Mrugała, A., Pergl, J., Rabitsch, W., Richardson, D.M., Sendek, A. and Winter, M. (2015) Ecological impacts of alien species: quantification, scope, caveats, and recommendations. *BioScience*, **65**(1), 55-63.
- Lambin, E.F. and Meyfroidt, P. (2010) Land use transitions: socio-ecological feedback versus socio-economic change. *Land Use Policy*, **27**(2), 108-118.
- Lang, D.J., Wiek, A., Bergmann, M., Stauffacher, M., Martens, P., Moll, P., Swilling, M. and Thomas, C.J. (2012) Transdisciplinary research in sustainability science: practice, principles, and challenges. *Sustainability Science*, **7**(1), 25-43.
- Larson, B.M.H. (2005) The war of the roses: demilitarizing invasion biology. *Frontiers in Ecology and the Environment*, **3**(9), 495-500.
- Latzka, A.W., Hansen, G.J.A., Kornis, M. and Vander Zanden, M.J. (2016) Spatial heterogeneity in invasive species impacts at the landscape scale. *Ecosphere*, **7**(3), 1-15.
- Lazzaro, L., Giuliani, C., Fabiani, A., Agnelli, A.E., Pastorelli, R., Lagomarsino, A., Benesperi, R., Calamassi, R. and Foggi, B. (2014) Soil and plant changing after invasion: the case of *Acacia dealbata* in a Mediterranean ecosystem. *Science of the Total Environment*, **497**, 491-498.
- Le Maitre, D.C., Forsyth, G.G., Dzikiti, S. and Gush, M.B. (2013) *Estimates of the impacts of invasive alien plants on water flows in South Africa. Report No. CSIR/NRE/ECO/ER/2013/0067/B*. Natural Resources and the Environment, CSIR, Stellenbosch, South Africa.
- Le Maitre, D.C., Gaertner, M., Marchante, E., Ens, E.J., Holmes, P.M., Pauchard, A., O'Farrell, P.J., Rogers, A.M., Blanchard, R., Blignaut, J.N. and Richardson, D.M. (2011) Impacts of invasive Australian acacias: implications for management and restoration. *Diversity and Distributions*, **17**, 1015-1029.
- Le Maitre, D.C., Kotzee, I.M. and O'Farrell, P.J. (2014) Impacts of land-cover change on the water flow regulation ecosystem service: invasive alien plants, fire and their policy implications. *Land Use Policy*, **36**, 171-181.
- Le Maitre, D.C., Versfeld, D.B. and Chapman, R.A. (2000) The impact of invading alien plants on surface water resources in South Africa: a preliminary assessment. *Water SA*, **26**, 397-408.
- Le Roux, J.J., Brown, G.K., Byrne, M., Ndlovu, J., Richardson, D.M., Thompson, G.D. and Wilson, J.R.U. (2011) Phylogeographic consequences of different introduction

- histories of invasive Australian *Acacia* species and *Paraserianthes lophantha* (Fabaceae) in South Africa. *Diversity and Distributions*, **17**(5), 861-871.
- Lenth, R.V. (2016) Least-squares means: the R package lsmeans. *Journal of Statistical Software*, **69**(1), 1-33.
- Levine, J.M., Adler, P.B. and Yelenik, S.G. (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, **7**, 975-989.
- Liao, C., Peng, R., Zhou, X., Wu, X., Fang, C., Chen, J. and Li, B. (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytologist*, **177**(3), 706-714.
- Liendo, D., Biurrun, I., Campos, J.A., Herrera, M., Loida, J. and García-Mijangos, I. (2015) Invasion patterns in riparian habitats: the role of anthropogenic pressure in temperate streams. *Plant Biosystems*, **14**(2), 289-297.
- Lindroth, C.H. (1957) *The Faunal Connections between Europe and North America*. Wiley, New York, USA.
- Link, H.F. (1822) *Enumeratio Plantarum Horti Regii Botanici Berolinensis altera*. G Reimer, Berlin, Germany.
- Liu, Y., Huang, X., Yang, H. and Zhong, T. (2014) Environmental effects of land-use/cover change caused by urbanization and policies in Southwest China Karst area: a case study of Guiyang. *Habitat International*, **44**, 339-348.
- Lodge, D.M. (1993) Biological invasions: lessons for ecology. *Trends in Ecology and Evolution*, **8**(4), 133-137.
- Logan, M. (2010) Generalized linear models. *Biostatistical Design and Analysis Using R: A Practical Guide* (ed Logan, M.), pp. 483 – 530. Wiley Blackwell, Hoboken, USA.
- Lorenzo, P., González, L. and Reigosa, M.J. (2010a) The genus *Acacia* as invader: the characteristic case of *Acacia dealbata* Link in Europe. *Annals of Forest Science*, **67**(1), 101-112.
- Lorenzo, P., Pazos-Malvido, E., Rubido-Bará, M., Reigosa, M.J. and González, L. (2012) Invasion by the leguminous tree *Acacia dealbata* (Mimosaceae) reduces the native understorey plant species in different communities. *Australian Journal of Botany*, **60**(8), 669-675.
- Lorenzo, P., Pereira, C.S. and Rodríguez-Echeverría, S. (2013) Differential impact on soil microbes of allelopathic compounds released by the invasive *Acacia dealbata* Link. *Soil Biology and Biochemistry*, **57**, 156-163.
- Lorenzo, P., Rodríguez, J., González, L. and Rodríguez-Echeverría, S. (2017) Changes in microhabitat, but not allelopathy, affect plant establishment after *Acacia dealbata* invasion. *Journal of Plant Ecology*, **10**(4), 610-617.
- Lorenzo, P. and Rodríguez-Echeverría, S. (2012) Influence of soil microorganisms, allelopathy and soil origin on the establishment of the invasive *Acacia dealbata*. *Plant Ecology and Diversity*, **5**(1), 67-73.
- Lorenzo, P., Rodríguez-Echeverría, S., González, L. and Freitas, H. (2010b) Effect of invasive *Acacia dealbata* Link on soil microorganisms as determined by PCR-DGGE. *Applied Soil Ecology*, **44**, 245-251.
- MacDonald, I.A.W. and Jarman, M.L. (1984) *Invasive alien organisms in the terrestrial ecosystems of the fynbos biome, South Africa*. Council for Scientific and Industrial Research (CSIR), Pretoria, South Africa.
- Mack, R.N. (2000) Cultivation fosters plant naturalization by reducing environmental stochasticity. *Biological Invasions*, **2**, 111-122.
- Mack, R.N. (2003) Plant naturalizations and invasions in the Eastern United States: 1634-1860. *Annals of the Missouri Botanical Gardens*, **90**(1), 77-90.
- Mack, R.N. and D'Antonio, C.M.D. (1998) Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution*, **13**, 195-198.
- Mainali, K.P., Warren, D.L., Dhileepan, K., McConnachie, A.S., L, Hassan, G., Karki, D., Shrestha, B.B. and Parmesan, C. (2015) Projecting future expansion of invasive species: comparing and improving methodologies for species distribution modeling. *Global Change Biology*, **21**(12), 4464-4480.

- Makiwane, M.B. and Chimere-Dan, D.O. (2010) *The People Matter: Poverty, Population Dynamics and Policy*. Research and Population Unit – Eastern Cape Department of Social Development, Bisho, South Africa.
- Malan, H.L. and Day, J.A. (2002) Linking flow, water quality and potential effects on aquatic biota within the reserve determination process. *Water SA*, **29**(3), 297-304.
- Malavasi, M., Carboni, M., Cutini, M., Carranza, M.L. and Acosta, A.T.R. (2014) Landscape fragmentation, land-use legacy and propagule pressure promote plant invasion on coastal dunes: a patch-based approach. *Landscape Ecology*, **29**, 1541-1550.
- Malinichi, E., Lynn-Bell, N. and Kourtev, P.S. (2017) The effect of the invasive *Elaeagnus umbellata* on soil microbial communities depends on proximity of soils to plants. *Ecosphere*, **8**(5), 1-14.
- Malizia, A., Osinaga-Acosta, O., Powell, P.A. and Aragón, R. (2017) Invasion of *Ligustrum lucidum* (Oleaceae) in subtropical secondary forests of NW Argentina: declining growth rates of abundant native tree species. *Journal of Vegetation Science*, <https://doi.org/10.1111/jvs.12572>, 1-10.
- Mandle, L., Bufford, J.L., Schmidt, I.B. and Daehler, C.C. (2011) Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. *Biological Invasions*, **13**, 1815-1827.
- Manjoro, M., Kakembo, V. and Rowntree, K.M. (2012) Trends in soil erosion and woody shrub encroachment in Ngqushwa District, Eastern Cape Province, South Africa. *Environmental Management*, **49**(3), 570-579.
- Marcus, L. and Colding, J. (2011) Towards a spatial morphology of urban social-ecological systems *Conference Proceedings for the 18th International Conference on Urban Form (ISUF2011)*, 1-20.
- Marshall, G.R. (2013) Transaction costs, collective action and adaptation in managing complex social-ecological systems. *Ecological Economics*, 1-10.
- Martins, F., Alegria, C. and Artur, G. (2016) Mapping invasive alien *Acacia dealbata* Link using ASTER multispectral imagery: a case study in central-eastern of Portugal. *Forest Systems*, **25**(3), 1-15.
- Masocha, M., Dube, T., Skidmore, A., Holmgren, M. and Prins, H. (2017) Assessing effect of rainfall on rate of alien shrub expansion in a southern African savanna. *African Journal of Range and Forage Science*, **34**(1), 39-44.
- Mattingly, W.B. and Orrock, J.L. (2013) Historic land use influences contemporary establishment of invasive plant species. *Oecologia*, **172**, 1147-1157.
- May, B.M. and Attiwill, P.M. (2003) Nitrogen-fixation by *Acacia dealbata* and changes in soil properties 5 years after mechanical disturbance or slash-burning following timber harvest. *Forest Ecology and Management*, **181**, 339-355.
- McConnachie, M., Cowling, R.M., Van Wilgen, B.W. and McConnachie, D.A. (2012) Evaluating the cost-effectiveness of invasive alien plant clearing: a case study from South Africa. *Biological Conservation*, **155**, 128-135.
- McGarry, D., Shackleton, C.M., Fourie, S., Gambiza, J., Shackleton, S.E. and Fabricius, C. (2005) *Rapid Assessment of the Effects of Invasive Species on Human Livelihoods, Especially of the Rural Poor*. Department of Environmental Science, Rhodes University, Grahamstown, South Africa.
- McGinnis, M.D. and Ostrom, E. (2014) Social-ecological systems framework: initial changes and continuing challenges. *Ecology and Society*, **19**(2).
- McKinney, M.L. and La Sorte, F.A. (2007) Invasiveness and homogenization: synergism of wide dispersal and high local abundance. *Global Ecology and Biogeography*, **16**(3), 394-400.
- McNeely, J.A. (2001) An introduction to human dimensions of invasive alien species. *The Great Reshuffling: Human Dimensions of Invasive Alien Species* (ed McNeely, J.A.), pp. 5-20. IUCN, Gland, Switzerland and Cambridge, UK.
- McNeely, J.A. (2013) Global efforts to address the wicked problem of invasive alien species. *Plant Invasions in Protected Areas: Patterns, Problems and Challenges* (eds Foxcroft,

- L.C., Pyšek, P., Richardson, D.M. and Genovesi, P.), pp. 61-71. Springer Science & Business Media, Dordrecht, Netherlands.
- Meadows, D.H. (2008) *Thinking in Systems: a Primer*. Earthscan, London, UK and Sterling, USA.
- Meiners, S.J. and Pickett, S.T.A. (2013) Plant invasions in protected landscapes: exception or expectation? *Plant Invasions in Protected Areas: Patterns, Problems and Challenges* (eds Foxcroft, L.C., Pyšek, P., Richardson, D.M. and Genovesi, P.), pp. 42-60. Springer Science & Business Media, Dordrecht, the Netherlands.
- Meusel, H., Jäger, E., Weinert, E. and Rauschert, S.T. (1978) *Vergleichende Chorologie der Zentraleuropäischen Flora*. Gustav Fischer Jena, Germany.
- Meyer, U., Meinesz, A. and De Vaugelas, J. (1998) Invasion of the accidentally introduced tropical alga *Caulerpa taxifolia* in the Mediterranean Sea. *Plant Invasions: Ecological Mechanisms and Human Responses* (eds Starfinger, U., Edwards, K., Kowarik, I. and Williamson, M.H.), pp. 225-234. Backhuys Publishers, Leiden, Netherlands.
- Meyfroidt, P., Lambin, E.F., Erb, K.H. and Hertel, T.W. (2013) Globalization of land use: distant drivers of land change and geographic displacement of land use. *Current Opinion in Environmental Sustainability*, **5**(5), 438-444.
- Millennium Ecosystem Assessment [MEA] (2003) *Ecosystems and Human Well-being: a Framework for Assessment*. Island Press, Washington, DC, USA.
- Millennium Ecosystem Assessment [MEA] (2005) *Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute, Washington, DC, USA.
- Miller, J.T., Murphy, D.J., Brown, G.K., Richardson, D.M. and González-Orozco, C.E. (2011) The evolution and phylogenetic placement of invasive Australian *Acacia* species. *Diversity and Distributions*, **17**(5), 848-860.
- Miller, P. (1754) *The Gardeners' Dictionary*. Self published, London, UK.
- Minor, E.S., Tessel, S.M., Engelhardt, K.A. and Lookingbill, T.R. (2009) The role of landscape connectivity in assembling exotic plant communities: a network analysis. *Ecology*, **90**(7), 1802-1809.
- Mograbi, P.J., Asner, G.P., Witkowski, E.T., Erasmus, B.F., Wessels, K.J., Mathieu, R. and Vaughn, N.R. (2017) Humans and elephants as treefall drivers in African savannas. *Ecography*, **40**, 1-11.
- Monteiro, A.T., Gonçalves, J., Fernandes, R.F., Alves, S., Marcos, B., Lucas, R., Teodoro, A.C. and Honrado, J.P. (2017) Estimating invasion success by non-native trees in a national park combining WorldView-2 very high resolution satellite data and species distribution models. *Diversity*, **9**(6), 1-18.
- Montti, L., Carrillo, V.P., Gutiérrez-Angonese, J., Gasparri, N.I., Aragón, R. and Grau, H.R. (2017) The role of bioclimatic features, landscape configuration and historical land use in the invasion of an Asian tree in subtropical Argentina. *Landscape Ecology*, <https://doi.org/10.1007/s10980-017-0563-2>, 1-9.
- Mooney, H.A. (2005) Invasive alien species: the nature of the problem. *Invasive Alien Species: a New Synthesis* (eds Mooney, H.A., Mack, R.N., McNeely, J.A., Neville, L.E., Schei, P.J. and Waage, J.K.), pp. 1-15. Island Press, Washington, DC, USA.
- Mooney, H.A. and Hobbs, R.J. (2000) *Invasive Species in a Changing World*. Island Press, Washington, DC, USA.
- Moran, V.C., Hoffmann, J.H. and Zimmermann, H.G. (2013) 100 years of biological control of invasive alien plants in South Africa: history, practice and achievements. *South African Journal of Science*, **109**(9/10), 1-6.
- Morris, T.L., Barger, N.N. and Cramer, M.D. (2015) Competitive resistance of a native shrubland to invasion by the alien invasive tree species, *Acacia cyclops*. *Biological Invasions*, **17**, 3563–3577.
- Morris, T.L., Esler, K.J., Barger, N.N., Jacobs, S.M. and Cramer, M.D. (2011) Ecophysiological traits associated with the competitive ability of invasive Australian acacias. *Diversity and Distributions*, **17**(5), 898-910.
- Mucina, L. and Rutherford, M.C. (2006) *The Vegetation of South Africa, Lesoto and Swaziland*. South African National Biodiversity Institute (SANBI), Pretoria, South Africa.

- Mueller-Dombois, D. and Ellenberg, V. (1974) The count-plot method and plotless sampling techniques. *Aims and Methods of Vegetation Ecology* (eds Mueller-Dombois, D. and Ellenberg, V.), pp. 96-108. Wiley, New York, USA.
- Mugido, W., Blignaut, J., Joubert, M., De Wet, J., Knipe, A., Joubert, S., Cobbing, B., Jansen, J., Le Maitre, D.C. and Van der Vyfer, M. (2014) Determining the feasibility of harvesting invasive alien plant species for energy. *South African Journal of Science*, **110**(11-12), 1-6.
- Muller, G.C., Junnila, A., Traore, M.M., Traore, S.F., Doumbia, S., Sissoko, F., Dembele, S.M., Schlein, Y., Arheart, K.L., Revay, E.E. and Kravchenko, V.D. (2017) The invasive shrub *Prosopis juliflora* enhances the malaria parasite transmission capacity of *Anopheles* mosquitoes: a habitat manipulation experiment. *Malaria Journal*, **16**(1), 1-9.
- Munroe, D.K., McSweeney, K., Olson, J.L. and Mansfield, B. (2014) Using economic geography to reinvigorate land-change science. *Geoforum*, **52**, 12-21.
- Murphy, D.J., Brown, G.K., Miller, J.T. and Ladiges, P.Y. (2010) Molecular phylogeny of *Acacia* s.s. (Mimosoideae: Leguminosae): evidence for major clades and informal classification. *Taxon*, **59**, 7-19.
- Murphy, H.T., Van der Wal, J., Lovett-Doust, L. and Lovett-Doust, J. (2006) Invasiveness in exotic plants: immigration and naturalization in an ecological continuum. *Conceptual Ecology and Invasion Biology: Reciprocal Approaches to Nature* (eds Cadotte, M.W., McMahon, S.M. and Fukami, T.), pp. 65-105. Springer, Dordrecht, the Netherlands.
- Muyambo, F., Jordaan, A.J. and Bahta, Y.T. (2017) Assessing social vulnerability to drought in South Africa: policy implication for drought risk reduction. *Jàmhá: Journal of Disaster Risk Studies*, **9**(1), 1-7.
- Myers, J.H. and Berube, D.E. (1983) Diffuse knapweed invasion into rangeland in the dry interior of British Columbia. *Canadian Journal of Plant Science*, **63**(4), 981-987.
- Nackley, L.L., West, A.G., Skowno, A.L. and Bond, W.J. (2017) The nebulous ecology of native invasions. *Trends in Ecology and Evolution*, **32**(11), 814-824.
- Nel, J.L., Richardson, D.M., Rouget, M., Mgidi, N., Le Maitre, D.C., Van Wilgen, B.W., Schonegevel, L., Henderson, L. and Naser, S. (2004) A proposed classification of invasive plant species in South Africa: towards prioritizing species and areas for management action. *South African Journal of Science*, **100**, 53-64.
- Ngorima, A. (2016) *Perceptions and livelihood uses of invasive alien species (Acacia dealbata) in the Eastern Cape*. Unpublished Masters thesis, Rhodes University, Grahamstown, South Africa.
- Niphadkar, M. and Nagendra, H. (2016) Remote sensing of invasive plants: incorporating functional traits into the picture. *International Journal of Remote Sensing*, **37**(13), 3074-3085.
- Nkonya, E., Mirzabaev, A. and Von Braun, J. (2013) *Sustainable Development: Economics and Environment in the Third World*. Springer, Cham, Switzerland.
- Noemdoe, S. (2001) Putting people first in a invasive alien clearing programme: Working for Water Programme - are we succeeding. *The Great Reshuffling: Human Dimensions of Invasive Alien Species* (ed McNeely, J.A.), pp. 120-125. IUCN, Gland, Switzerland and Cambridge, UK.
- Ntshotsho, P., Prozesky, H.E., Esler, K.J. and Reyers, B. (2015) What drives the use of scientific evidence in decision making? The case of the South African Working for Water program. *Biological Conservation*, **184**, 136-144.
- Okalebo, J.R., Gathua, K.W. and Woomer, P.L. (2002) *Laboratory Methods of Soil and Plant Analysis: a Working Manual*. Sacred Africa, Nairobi, Kenya.
- Oosting, H.J. (1948) *The Study of Plant Communities: an Introduction to Plant Ecology*. W.H. Freeman, San Francisco, USA.
- Oosting, H.J. (1956) *The Study of Plant Communities: an Introduction to Plant Ecology*. W.H. Freeman, San Francisco, USA.
- Or, K. and Ward, D. (2003) Three-way interactions between *Acacia*, large herbivores and bruchid beetles: a review. *African Journal of Ecology*, **41**(3), 257-265.

- Ordoñez, A., Wright, I.J. and Olf, H. (2010) Functional differences between native and alien species: a global-scale comparison. *Functional Ecology*, **24**, 1353-1361.
- Ostrom, E. (2009) A general framework for analyzing sustainability of social-ecological systems. *Science*, **325**, 419-422.
- Packer, J.G., Meyerson, L.A., Richardson, D.M., Brundu, G., Allen, W.J., Bhattarai, G.P.B., H, Canavan, S., Castiglione, S., Ciccattelli, A. and Čuda, J. (2017) Global networks for invasion science: benefits, challenges and guidelines. *Biological Invasions*, **19**(4), 1081-1096.
- Pammenter, N.W., Drennan, P.M. and Smith, V.R. (1986) Physiological and anatomical aspects of photosynthesis of two *Agrostis* species at a sub-Antarctic island. *New Phytologist*, **102**, 143-160.
- Panetta, F.D. and Gooden, B. (2017) Managing for biodiversity: impact and action thresholds for invasive plants in natural ecosystems. *NeoBiota*, **34**, 53-66.
- Pantone, D.J., Pavlik, B.M. and Kelley, R.B. (1995) The reproductive attributes of an endangered plant as compared to a weedy congener. *Biological Conservation*, **71**, 305-311.
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B.M., Moyle, P.B., Byers, J.E. and Goldwasser, L. (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**(1), 3-19.
- Parker, J.D., Torchin, M.E., Hufbauer, R.A., Lemoine, N.P., Alba, C., Blumenthal, D.M., Bossdorf, O., Byers, J.E., Dunn, A.M., Heckman, R.W., Hejda, M., Jarošík, V., Kanarek, A.R., Martin, L.B., Perkins, S.E., Pyšek, P., Schierenbeck, K.A., Schlöder, C., Van Klinken, R.D., Vaughn, K.J., Williams, W. and Wolfe, L.M. (2013) Do invasive species perform better in their new ranges? *Ecology*, **94**(5), 985-994.
- Parresol, B.R. (1999) Assessing tree and stand biomass: a review with examples and critical comparisons. *Forest Science*, **45**(4), 573-593.
- Pauchard, A. and Alaback, P.B. (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of South-Central Chile. *Conservation Biology*, **18**(1), 238-248.
- Pauchard, A. and Maheu-Giroux, M. (2007) *Acacia dealbata* invasion across multiple scales: conspicuous flowering species can help us study invasion pattern and processes. *Sourcebook on Remote Sensing and Biodiversity Indicators* (eds Strand, H., Höft, R., Strittholt, J., Miles, L., Horning, N., Fosnight, E. and Turner, W.), pp. 168-169. Secretariat of the Convention on Biological Diversity, Montreal, Canada.
- Perkins, L.B. and Nowak, R.S. (2013) Invasion syndromes: hypotheses on relationships among invasive species attributes and characteristics of invaded sites. *Journal of Arid Land*, **5**(3), 275-283.
- Perrings, C., Dalmazzone, S. and Williamson, M. (2005) The economics of biological invasions. *Invasive Alien Species: a New Synthesis* (eds Mooney, H.A., Mack, R.N., McNeely, J.A., Neville, L.E., Schei, P.J. and Waage, J.K.), pp. 16-35. Island Press, Washington, DC, USA.
- Perrins, J., Fitter, A. and Williamson, M.H. (1993) Population biology and rates of invasion of three introduced *Impatiens* species in the British Isles. *Journal of Biogeography*, **20**, 33-44.
- Picard, N., Saint-André, L. and Henry, M. (2012) *Manual for building tree volume and biomass allometric equations: from field measurement to prediction*. Food and Agriculture Organization (FAO), Rome, Italy.
- Pickett, S.T.A. and White, P.S. (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York, USA.
- Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T. and Tsomondo, T. (2000) Economic and environmental threats of alien plant, animal and microbe invasions. *Agriculture, Ecosystems and Environment*, **84**, 1-20.

- Pimentel, D., Zuniga, R. and Morrison, D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, **52**, 273-288.
- Poynton, R.J. (2009) *Tree Planting in Southern Africa Vol 3 - Other Genera*. Department of Agriculture, Forestry and Fisheries, Pretoria, South Africa.
- Praciak, A., Pasiecznik, N., Sheil, D., Van Heist, M., Sassen, M., Correia, C.S., Dixon, C., Fyson, G., Rushford, K. and Teeling, C. (2013) *The CABI Encyclopedia of Forest Trees*. CABI, Oxfordshire, UK.
- Pritchard, B., Vicol, M. and Jones, R. (2017) How does the ownership of land affect household livelihood pathways under conditions of deagrarianization? Hanging in', 'stepping up' and 'stepping out' in two north Indian villages. *Singapore Journal of Tropical Geography*, **38**(1), 41-57.
- Puttick, J.R., Hoffman, M.T. and Gambiza, J. (2011) Historical and recent land-use impacts on the vegetation of Bathurst, a municipal commonage in Eastern Cape, South Africa. *African Journal of Range and Forage Science*, **28**(1), 9-20.
- Pyke, D.A. (1987) Demographic response of *Bromus tectorum* and seedlings of *Agropyron spicatum* to grazing by small mammals: the influence of grazing frequency and plant age. *Journal of Ecology*, **75**(3), 825-835.
- Pyšek, P. and Chytrý, M. (2014) Habitat invasion research: where vegetation science and invasion ecology meet. *Journal of Vegetation Science*, **25**, 1181-1187.
- Pyšek, P., Chytrý, M., Pergl, J., Sadlo, J. and Wild, J. (2012a) Plant invasions in the Czech Republic: current state, introduction dynamics, invasive species and invaded habitats. *Preslia*, **84**(3), 575-629.
- Pyšek, P. and Hulme, P.E. (2005) Spatio-temporal dynamics of plant invasions: linking pattern to process. *Ecoscience*, **12**(3), 302-316.
- Pyšek, P. and Hulme, P.E. (2011) Biological invasions in Europe 50 years after Elton: time to sound the alarm. *Fifty Years of Invasion Ecology: the Legacy of Charles Elton* (ed Richardson, D.M.), pp. 73-88. Blackwell Publishing Ltd, Chichester, UK.
- Pyšek, P., Jarošík, V.K., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U. and Vilà, M. (2012b) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology*, **18**, 1725-1737.
- Pyšek, P. and Richardson, D.M. (2008) Traits associated with invasiveness in alien plants: where do we stand? *Biological Invasions* (ed Nentwig, W.), pp. 97-125. Springer, Berlin, Germany.
- Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G.L., Williamson, M.H. and Kirschner, J. (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon*, **53**(1), 131-143.
- R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Rai, R.K., Scarborough, H., Subedi, N. and Lamichhane, B. (2012) Invasive plants – do they devastate or diversify rural livelihoods? Rural farmers' perception of three invasive plants in Nepal. *Journal for Nature Conservation*, **20**, 170-176.
- Raizada, P., Raghubanshi, A.S. and Singh, J.S. (2008) Impacts of invasive alien plants on soil processes: a review. *Proceedings of the National Academy of Sciences, India - Section B: Biological Sciences*, **78**, 288-298.
- Ramanantoanina, A. and Hull, C. (2016) Formulating spread of species with habitat dependent growth and dispersal in heterogeneous landscapes. *Mathematical Biosciences*, **275**, 51-56.
- Rammel, C., Stagl, S. and Wilfing, H. (2007) Managing complex adaptive systems: a co-evolutionary perspective on natural resource management. *Ecological Economics*, **63**, 9-21.
- Raunkiær, C.C. (1904) *The Life Forms of Plants and Statistical Plant Geography: Being the Collected Papers of C. Raunkiær, etc.* Oxford University Press, Oxford, UK.

- Reaser, J.K., Meyerson, L.A., Cronk, Q., De Poorter, M., Eldrege, L.G., Green, E., Kairo, M., Latasi, P., Mack, R.N., Mauremootoo, J., O'Dowd, D.E., Orapa, W., Sastroutomo, S., Saunders, A., Shine, C., Thrainsson, S. and Vaitu, L. (2007) Ecological and socio-economic impacts of invasive alien species in island ecosystems. *Environmental Conservation*, **34**(2), 1-14.
- Rejmánek, M. (1996) A theory of seed plant invasiveness: the first sketch. *Biological Conservation*, **78**, 171-181.
- Rejmánek, M. and Richardson, D.M. (2013) Trees and shrubs as invasive alien species – 2013 update of the global database. *Diversity and Distributions*, **19**(8), 1093-1094.
- Republic of South Africa [RSA] (1983) Conservation of Agricultural Resources Act (CARA; Act No. 43 of 1983, amended 2001). Government Gazette, Pretoria, South Africa.
- Republic of South Africa [RSA] (2004) National Environmental Management: Biodiversity Act (NEMBA; Act No. 10 of 2004). Government Gazette, Pretoria, South Africa.
- Republic of South Africa [RSA] (2014a) NEMBA: Alien and Invasive Species Regulations (GN598). Government Gazette, Pretoria, South Africa.
- Republic of South Africa [RSA] (2014b) NEMBA: Alien and Invasive Species Regulations Listing 1 (GN599). Government Gazette, Pretoria, South Africa.
- Ricciardi, A., Hoopes, M.F., Marchetti, M.P. and Lockwood, J.L. (2013) Progress toward understanding the ecological impacts of non-native species. *Ecological Monographs*, **83**(3), 263-282.
- Richards, J.H. (1984) Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope. *Oecologia*, **64**, 21-25.
- Richardson, D.M. (2011) Invasion science: the roads travelled and the roads ahead. *Fifty Years of Invasion Ecology: the Legacy of Charles Elton* (ed Richardson, D.M.), pp. 397-407. Blackwell Publishing Ltd, Chichester, UK.
- Richardson, D.M., Carruthers, J., Hui, C., Impson, F.A.C., Miller, J.T., Robertson, M.P., Rouget, M., Le Roux, J.L. and Wilson, J.R.U. (2011) Human-mediated introductions of Australian acacias – a global experiment in biogeography. *Diversity and Distributions*, **17**, 771-787.
- Richardson, D.M., Holmes, P.M., Elser, K.J., Galatowitsch, S.M., Stromberg, J.C., Kirkman, S.P., Pyšek, P. and Hobbs, R.J. (2007) Riparian vegetation: degradation, alien plant invasions, and restoration projects. *Diversity and Distributions*, **13**, 126-139.
- Richardson, D.M., Le Roux, J.J. and Wilson, J.R.U. (2015) Australian acacias as invasive species: lessons to be learnt from regions with long planting histories. *Southern Forests: a Journal of Forest Science*, **77**(1), 31-39.
- Richardson, D.M. and Pyšek, P. (2007) Classics in physical geography revisited: Elton, C.S. 1958. the ecology of invasions by animals and plants. *Progress in Physical Geography*, **31**, 659-666.
- Richardson, D.M. and Pyšek, P. (2008) Fifty years of invasion ecology – the legacy of Charles Elton. *Diversity and Distributions*, **14**(2), 161-168.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. and West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93-107.
- Richardson, D.M. and Rejmánek, M. (2011) Trees and shrubs as invasive alien species – a global review. *Diversity and Distributions*, **17**(5), 788-809.
- Richardson, D.M., Van Wilgen, B.W. and Mitchell, D.T. (1987) Aspects of the reproductive ecology of four Australian *Hakea* species (Proteaceae) in South Africa. *Oecologia*, **71**, 345-354.
- Rittel, H.W.J. and Webber, M.M. (1973) Dilemmas in a general theory of planning. *Policy Sciences*, **4**(2), 155-169.
- Robertson, M.P., Villet, M.H., Fairbanks, D.H., Henderson, L., Higgins, S.I., Hoffmann, J.H., Le Maitre, D.C., Palmer, A.R., Riggs, I., Shackleton, C.M. and Zimmermann, H.G. (2003) A proposed prioritization system for the management of invasive alien plants in South Africa: research in action. *South African Journal of Science*, **99**(1-2), 37-43.

- Rodger, J.G. (2012) *Consequences of self-fertilisation for fecundity and progeny performance in invasive plants*. PhD Thesis PhD thesis, University of KwaZulu-Natal, Pietermaritzburg, South Africa.
- Rodger, J.G. and Johnson, S.D. (2013) Self-pollination and inbreeding depression in *Acacia dealbata*: can selfing promote invasion in trees? *South African Journal of Botany*, **88**, 252-259.
- Rodríguez-Echeverría, S., Afonso, C., Correia, M., Lorenzo, P. and Roiloa, S.R. (2013) The effect of soil legacy on competition and invasion by *Acacia dealbata* Link. *Plant Ecology*, **214**, 1139-1146.
- Rodríguez-Echeverría, S., Le Roux, J.J., Crisóstomo, J.A. and Ndlovu, J. (2011) Jack-of-all-trades and master of many? How does associated rhizobial diversity influence the colonization success of Australian *Acacia* species? *Diversity and Distributions*, **17**(5), 946-957.
- Rodríguez, J., Lorenzo, P. and González, L. (2017) Different growth strategies to invade undisturbed plant communities by *Acacia dealbata* Link. *Forest Ecology and Management*, **399**, 47-53.
- Rogers, A.M. and Chown, S.L. (2014) Novel ecosystems support substantial avian assemblages: the case of invasive alien *Acacia* thickets. *Diversity and Distributions*, **20**, 34-45.
- Rutherford, M.C., Powrie, L.W. and Husted, L.B. (2013) Herbivore-driven land degradation: consequences for plant diversity and soil in arid subtropical thicket in south-eastern Africa. *Land Degradation and Development*, **25**(6), 541-553.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N. and Weller, S.G. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305-332.
- Saner, M.A., Clements, D.R., Hall, M.R., Doohan, D.J. and Crompton, C.W. (1995) The biology of Canadian weeds. 105. *Linaria vulgaris* Mill. *Canadian Journal of Plant Science*, **75**, 525-537.
- Sanon, A., Beguiristain, T., Cebron, A., Berthelin, J., Ndoeye, I., Leyval, C., Sylla, S. and Duponnois, R. (2009) Changes in soil diversity and global activities following invasions of the exotic invasive plant, *Amaranthus viridis* L., decrease the growth of native sahelian *Acacia* species. *FEMS Microbiology Ecology*, **70**(1), 118-131.
- Sax, D.F. and Brown, J.H. (2000) The paradox of invasion. *Global Ecology and Biogeography*, **9**, 363-371.
- Schepker, H. and Kowarik, I. (1998) Invasive North American blueberry hybrids (*Vaccinium corymbosum* x *angustifolium*) in northern Germany. *Plant Invasions: Ecological Mechanisms and Human Responses* (eds Starfinger, U., Edwards, K., Kowarik, I. and Williamson, M.H.), pp. 253-260. Backhuys Publishers, Leiden, Netherlands.
- Schierenbeck, K.A., Mack, R.N. and Sharitz, R.R. (1994) Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology*, **75**(6), 1661-1672.
- Schoeman, F., Newby, T.S., Thompson, M.W. and Van den Berg, E. (2010) *South African National Land Cover Change Map*. Agricultural Research Council (ARC), Pretoria, South Africa. Unpublished Report No GW/A/2010/47
- Schweitzer, J.A. and Larson, K.C. (1999) Greater morphological plasticity of exotic honeysuckle species may make them better invaders than native species. *Journal of the Torrey Botanical Society*, **126**(1), 15-23.
- Scoones, I. (1998) *Sustainable Rural Livelihoods: a Framework for Analysis*. Institute of Development Studies, University of Sussex, Sussex, UK.
- Searle, S.D. (1997) *Acacia mearnsii* De Wild. (Black Wattle) in Australia. *Black Wattle and its Utilization* (eds Brown, A.G. and Ko, H.C.), pp. 1-13. Rural Industries Research and Development Corporation, Canberra, Australia.
- Searle, S.D. and Owen, J.V. (2005) Variation in basic wood density and percentage heartwood in temperate Australian *Acacia* species. *Australian Forestry*, **68**(2), 126-136.

- Seastedt, T.R. (2015) Biological control of invasive plant species: a reassessment for the Anthropocene. *New Phytologist*, **205**(2), 490-502.
- Seath, J.L. (2017) *The effects of different patch sizes of Acacia dealbata on avifauna diversity in montane grassland*. Unpublished Honours dissertation, Rhodes University, Grahamstown, South Africa.
- Semenya, S.S., Tshisikhawe, M.P. and Potgieter, M.T. (2012) Invasive alien plant species: a case study of their use in the Thulamela Local Municipality, Limpopo Province, South Africa. *Scientific Research and Essays*, **7**(27), 2363-2369.
- Shackleton, C.M., McGarry, D., Fourie, S., Gambiza, J., Shackleton, S.E. and Fabricius, C. (2007) Assessing the effects of invasive alien species on rural livelihoods: case examples and a framework from South Africa. *Human Ecology*, **35**(1), 113-127.
- Shackleton, C.M. and Shackleton, R.T. (2016) Knowledge, perceptions and willingness to control designated invasive tree species in urban household gardens in South Africa. *Biological Invasions*, **18**, 1599-1609.
- Shackleton, C.M. and Shackleton, S.E. (2004) The importance of non-timber forest products in rural livelihood security and as safety nets: a review of evidence from South Africa. *South African Journal of Science*, **100**(11-12), 658-664.
- Shackleton, R.T., Le Maitre, D.C. and Richardson, D.M. (2015a) Stakeholder perceptions and practices regarding *Prosopis* (mesquite) invasions and management in South Africa. *Ambio*, **44**(6), 569-581.
- Shackleton, R.T., Le Maitre, D.C., Van Wilgen, B.W. and Richardson, D.M. (2015b) Use of non-timber forest products from invasive alien *Prosopis* species (mesquite) and native trees in South Africa: implications for management. *Forest Ecosystems*, **2**(1), 1-11.
- Shackleton, R.T., Le Maitre, D.C., Van Wilgen, B.W. and Richardson, D.M. (2016) Identifying barriers to effective management of widespread invasive alien trees: *Prosopis* species (mesquite) in South Africa as a case study. *Global Environmental Change*, **38**, 183-194.
- Shackleton, R.T., Shackleton, C.M., Shackleton, S.E. and Gambiza, J. (2013) Deagrarianisation and forest revegetation in a biodiversity hotspot on the Wild Coast, South Africa. *PloS ONE*, **8**(10).
- Shackleton, S.E., Kirby, D. and Gambiza, J. (2011) Invasive plant friends or foe? Contribution of prickly pear to livelihoods in Makana municipality, Eastern Cape, South Africa. *Development Southern Africa*, **28**, 177-193.
- Shea, K. and Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution*, **17**(4), 170-176.
- Sheppard, A.W., Shaw, R.H. and Sforza, R. (2006) Top 20 environmental weeds for classical biological control in Europe: a review of opportunities, regulations and other barriers to adoption. *Weed Research*, **46**(2), 93-117.
- Sholto-Douglas, C., Shackleton, C.M., Ruwanza, S. and Dold, T. (2017) The effects of expansive shrubs on plant species richness and soils in semi-arid communal lands, South Africa. *Land Degradation and Development*, **28**(7), 2191-2206.
- Siemann, E., DeWalt, S.J., Zou, J. and Rogers, W.E. (2017) An experimental test of the EICA hypothesis in multiple ranges: invasive populations outperform those from the native range independent of insect herbivore suppression *AoB PLANTS*, **9**(plw087), 1-13.
- Simberloff, D. (2009) The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 81-102.
- Simberloff, D. (2011) Charles Elton: neither founder nor siren, but prophet. *Fifty Years of Invasion Ecology: the Legacy of Charles Elton* (ed Richardson, D.M.), pp. 11-24. Blackwell Publishing Ltd, Chichester, UK.
- Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E. and Vilà, M. (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology and Evolution*, **28**(1), 58-66.
- Simberloff, D. and Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21-32.

- Sitters, J., Edwards, P.J. and Venterink, H.O. (2013) Increases of soil C, N, and P pools along an *Acacia* tree density gradient and their effects on trees and grasses. *Ecosystems*, **16**, 347-357.
- Smith, H.G., Sheridan, G.J., Lane, P.N.J., Snyman, P. and Haydon, A. (2011) Wildfire effects on water quality in forest catchments: a review with implications for water supply. *Journal of Hydrology*, **396**(1-2), 170-192.
- Souza-Alonso, P., González, L. and Cavaleiro, C. (2014a) Ambient has become strained: identification of *Acacia dealbata* Link volatiles interfering with germination and early growth of native species. *Journal of Chemical Ecology*, **40**(9), 1051-1061.
- Souza-Alonso, P., Guisandre-Collazo, A. and González, L. (2015) Gradualism in *Acacia dealbata* Link invasion: impact on soil chemistry and microbial community over a chronological sequence. *Soil Biology and Biochemistry*, **80**, 315-323.
- Souza-Alonso, P., Novoa, A. and González, L. (2014b) Soil biochemical alterations and microbial community responses under *Acacia dealbata* Link invasion. *Soil Biology and Biochemistry*, **79**, 100-108.
- Souza-Alonso, P., Rodríguez, J., González, L. and Lorenzo, P. (2017) Here to stay. Recent advances and perspectives about *Acacia* invasion in Mediterranean areas. *Annals of Forest Science*, **74**, 1-20.
- Stafford, L. and Blignaut, J. (2017) Reducing landscape restoration costs: feasibility of generating electricity from invasive alien plant biomass on the Agulhas Plain, South Africa. *Ecosystem Services*, **27**, 224-231.
- Stafford, W., Birch, C., Etter, H., Blanchard, R., Mudavanhu, S., Angelstam, P., Blignaut, J., Ferreira, L. and Marais, C. (2017) The economics of landscape restoration: benefits of controlling bush encroachment and invasive plant species in South Africa and Namibia. *Ecosystem Services*, <http://dx.doi.org/10.1016/j.ecoser.2016.11.021>.
- Statistics South Africa (2011) Stats SA 2011 Census. [Online] Available at: http://www.statssa.gov.za/?page_id=964 [Accessed 18 November 2017].
- Statistics South Africa (2012) Census 2011: Population Dynamics. [Online] Available at: <http://www.statssa.gov.za/publications/Report-03-01-67/Report-03-01-672011.pdf> [Accessed 27 July 2016].
- Statistics South Africa (2014) Census 2011 Provincial Profile: Eastern Cape. [Online] Available at: <http://www.statssa.gov.za/publications/Report-03-01-71/Report-03-01-712011.pdf> [Accessed 27 July 2016].
- Stephens, P.A., Sutherland, W.J. and Freckleton, R.P. (1999) What Is the Allee effect? *Oikos*, **87**(1), 185-190.
- Steyn, C.G., M, Robertson, M.P., Kalwij, J.M. and Le Roux, P.C. (2017) Alien plant species that invade high elevations are generalists: support for the directional ecological filtering hypothesis. *Journal of Vegetation Science*, **28**(2), 337-346.
- Stickler, M.M. and Shackleton, C.M. (2015) Local wood demand, land cover change and the state of albany thicket on an urban commonage in the Eastern Cape, South Africa. *Environmental Management*, **55**(2), 411-422.
- Stone, G.N., Raine, N.E., Prescott, M.N. and Willmer, P.G. (2003) Pollination ecology of acacias (Fabaceae, Mimosoideae). *Australian Systematic Botany*, **16**(1), 103-118.
- Strum, S.C., Stirling, G. and Mutunga, S.K. (2015) The perfect storm: land use change promotes *Opuntia stricta*'s invasion of pastoral rangelands in Kenya. *Journal of Arid Environments*, **118**, 37-47.
- Sukopp, H. (1962) Neophyten in natürlichen Pflanzengesellschaften Mitteleuropas. *Berichte der Deutschen Botanischen Gesellschaft*, **75**, 193-205.
- Sundaram, B., Krishnan, S., Hiremath, A.J. and Joseph, G. (2012) Ecology and impacts of the invasive species, *Lantana camara*, in a social-ecological system in South India: perspectives from local knowledge. *Human Ecology*, **40**(6), 931-942.
- Taylor, C.M. and Hastings, A. (2004) Finding optimal control strategies for invasive species: a density-structured model for *Spartina alterniflora*. *Journal of Applied Ecology*, **41**(6), 1.

- Teixeira, Z., Teixeira, H. and Marques, J.C. (2014) Systematic processes of land use/land cover change to identify relevant driving forces: Implications on water quality. *Science of the Total Environment*, **470-471**, 1320-1335.
- Theoharides, K.A. and Dukes, J.S. (2007) Plant invasion across space and time: factors affecting non-indigenous species success during four stages of invasion. *New Phytologist*, **176**, 256-273.
- Thiele, K.R., Funk, V.A., Iwatsuki, K., Morat, P., Peng, C.I., Raven, P.H., Sarukhán, J. and Seberg, O. (2011) The controversy over the retypification of *Acacia* Mill. with an Australian type: a pragmatic view. *Taxon*, **60**(1), 194-198.
- Thomson, G.M. (1922) *The Naturalization of Animals and Plants in New Zealand*. Cambridge University Press, Cambridge, UK.
- Tizora, P., Le Roux, A., Mans, G. and Cooper, A. (2016) Land use and land cover change in the Western Cape Province: quantification of changes and understanding of driving factors. *7th Planning Africa Conference 2016 – Making Sense of the Future: Disruption and Reinvention 4-6 July 2016* (eds Ogra, A., Nkoane, I., Lodi, J., Mohan, K. and Minyuku, N.), pp. 108-125. South African Planning Institute (SAPI), Johannesburg, South Africa.
- Tobin, P.C., Berec, L. and Liebhold, A.M. (2011) Exploiting Allee effects for managing biological invasions. *Ecology Letters*, **14**(6), 615-624.
- Trueman, M., Standish, R.J., Orellana, D. and Cabrera, W. (2014) Mapping the extent and spread of multiple plant invasions can help prioritise management in Galapagos National Park. *NeoBiota*, **23**, 1-16.
- Tsoar, A., Shohami, D. and Nathan, R. (2011) A movement ecology approach to study seed dispersal and plant invasion: an overview and application of seed dispersal by fruit bats. *Fifty Years of Invasion Ecology: the Legacy of Charles Elton* (ed Richardson, D.M.), pp. 103-119. Blackwell Publishing Ltd, Chichester, UK.
- Turner, M.G. (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics*, **20**, 171-197.
- Turner, M.G. and Gardner, R.H. (2015) *Landscape Ecology in Theory and Practice: Pattern and Process*. Springer, New York, USA.
- Turpie, J.K., Heydenrych, B.J. and Lamberth, S.J. (2003) Economic value of terrestrial and marine biodiversity in the Cape Floristic Region: implications for defining effective and socially optimal strategies. *Biological Conservation*, **112**(1), 233-251.
- Turpie, J.K., Marais, C. and Blignaut, J.N. (2008) The Working for Water programme: evolution of a payments for ecosystem services mechanism that addresses both poverty and ecosystem service delivery in South Africa. *Ecological Economics*, **65**(4), 788-798.
- Van Wilgen, B.W., Cowling, R.M., Marais, C., Esler, K.J., McConnachie, M. and Sharp, D. (2012a) Challenges in invasive alien plant control in South Africa. *South African Journal of Science*, **108**, 8-11.
- Van Wilgen, B.W., Dyer, C., Hoffmann, J.H., Ivey, P., Le Maitre, D.C., Moore, J.L., Richardson, D.M., Rouget, M., Wannenburgh, A. and Wilson, J.R.U. (2011) National-scale strategic approaches for managing introduced plants: insights from Australian acacias in South Africa. *Diversity and Distributions*, **17**(5), 1060-1075.
- Van Wilgen, B.W., Forsyth, G.G., Le Maitre, D.C., Wannenburgh, A., Kotzé, J.D., Van den Berg, E. and Henderson, L. (2012b) An assessment of the effectiveness of a large, national-scale invasive alien plant control strategy in South Africa. *Biological Conservation*, **148**(1), 28-38.
- Van Wilgen, B.W., Reyers, B., Le Maitre, D.C., Richardson, D.M. and Schonegevel, L. (2008) A biome-scale assessment of the impact of invasive alien plants on ecosystem services in South Africa. *Journal of Environmental Management*, **89**, 336-349.
- Van Wilgen, B.W. and Richardson, D.M. (2012) Three centuries of managing introduced conifers in South Africa: benefits, impacts, changing perceptions and conflict resolution. *Journal of Environmental Management*, **106**, 56-68.
- Van Wilgen, B.W. and Richardson, D.M. (2014) Challenges and trade-offs in the management of invasive alien trees. *Biological Invasions*, **16**, 721-734.

- Van Wilgen, B.W., Richardson, D.M. and Higgins, S. (2000) *Integrated control of invasive alien plants in terrestrial ecosystems*. The Working for Water Programme, Cape Town, South Africa.
- Van Wilgen, B.W. and Wannenburgh, A. (2016) Co-facilitating invasive species control, water conservation and poverty relief: achievements and challenges in South Africa's Working for Water programme. *Current Opinion in Environmental Sustainability*, **19**, 7-17.
- Van Wyk, B. and Van Wyk, P. (2013) *Field Guide to Trees of Southern Africa*. Struik Nature, Cape Town, South Africa.
- Vaz, A.S., Kueffer, C., Kull, C.A., Richardson, D.M., Schindler, S., Muñoz-Pajares, A.J., Vicente, J., Martins, J., Hui, C., Kühn, I. and Honrado, J. (2017) The progress of interdisciplinarity in invasion science. *Ambio*, **46**, 428-442.
- Venables, W.N. and Ripley, B.D. (2002) *Modern Applied Statistics with S*. Springer, New York, USA.
- Vermeiji, G.J. (1996) An agenda for invasion biology. *Biological Conservation*, **78**, 3-9.
- Versfeld, D.B., Le Maitre, D.C. and Chapman, R.A. (1998) *Alien invading plants and water resources in South Africa: a preliminary assessment*. Report No. TT 99/98. Water Research Council, Pretoria, South Africa.
- Vicente, J., Randin, C.F., Gonçalves, J., Metzger, M.J., Lomba, Â., Honrado, J. and Guisan, A. (2011) Where will conflicts between alien and rare species occur after climate and land-use change? A test with a novel combined modelling approach. *Biological Invasions*, **13**(5), 1209-1227.
- Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D. and Hulme, P.E. (2009) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment*, **8**(3), 135-144.
- Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y. and Pyšek, P. (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, **14**, 702-708.
- Vilà, M. and Ibáñez, I. (2011) Plant invasions in the landscape. *Landscape Ecology*, **26**, 461-472.
- Vilà, M., Weber, E. and D'Antonio, C.M.D. (2000) Conservation implications of invasion by plant hybridization. *Biological Invasions*, **2**, 207-217.
- Vivanco, J.M., Bais, H.P., Stermitz, F.R., Thelen, G.C. and Callaway, R.M. (2004) Biogeographical variation in community response to root allelochemistry: novel weapons and exotic invasion. *Ecology Letters*, **7**(4), 285-292.
- Von Holle, B.M. and Motzkin, G. (2007) Historical land use and environmental determinants of nonnative plant distribution in coastal southern New England. *Biological Conservation*, **136**, 33-43.
- Wang, H. and Fang, Y. (1991) The history of acacia introduction to China. *Advances in Tropical Acacia Research* (ed Turnbull, J.W.), pp. 64-66. Bangkok, Thailand.
- Wang, Y., Bai, S., Binkley, D., Zhou, G. and Fang, F. (2016) The independence of clonal shoot's growth from light availability supports moso bamboo invasion of closed-canopy forest. *Forest Ecology and Management*, **368**, 105-110.
- Warren, C.R. (2007) Perspectives on the 'alien' versus 'native' species debate: a critique of concepts, language and practice. *Progress in Human Geography*, **31**(4), 427-446.
- Wickham, H. (2009) ggplot2: Elegant Graphics for Data Analysis. R package Springer-Verlag, New York, USA.
- Williams, B. and Van't Hof, S. (2014) *Wicked Solutions: a Systems Approach to Complex Problems*. Bob Williams, Wellington, New Zealand.
- Williamson, M.H. (1996) *Biological Invasions*. Chapman & Hall, London, UK and New York, USA.

- Williamson, M.H., Pyšek, P., Jarošík, V. and Prach, K. (2005) On the rates and patterns of spread of alien plants in the Czech Republic, Britain, and Ireland. *Ecoscience*, **12**(3), 424-433.
- Wilson, J.R.U., Dormontt, E.E., Prentis, P.J., Lowe, A.J. and Richardson, D.M. (2009) Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology and Evolution*, **24**, 136–144.
- Wilson, J.R.U., Gaertner, M., Griffiths, C.L., Kotzé, I., Le Maitre, D.C., Marr, S.M., Picker, M.D., Spear, D., Stafford, L., Richardson, D.M. and Van Wilgen, B.W. (2014) Biological invasions in the Cape Floristic Region: history, current patterns, impacts, and management challenges. *Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region* (eds Allsopp, N., Colville, J.F. and Verboom, G.A.), pp. 273-298. Oxford University Press, Oxford, UK.
- Wilson, J.R.U., Gairifo, C., Gibson, M.R., Arianoutsou, M., Bakar, B.B., Baret, S., Celesti-Grapow, L., DiTomaso, J.M., Dufour-Dror, J.M., Kueffer, C., Kull, C.A., Hoffmann, J.H., Impson, F.A.C., Loope, L.L., Marchante, E., Marchante, H., Moore, J.L., Murphy, D.J., Tassin, J., Witt, A., Zenni, R.D. and Richardson, D.M. (2011) Risk assessment, eradication, and biological control: global efforts to limit Australian acacia invasions. *Diversity and Distributions*, **17**(5), 1030-1046.
- Wilson, J.R.U., García-Díaz, P., Cassey, P., Richardson, D.M., Pyšek, P. and Blackburn, T.M. (2016) Biological invasions and natural colonisations are different – the need for invasion science. *NeoBiota*, **31**, 87-98.
- Wilson, J.R.U., Ivey, P., Manyama, P. and Nänni, I. (2013) A new national unit for invasive species detection, assessment and eradication planning. *South African Journal of Science*, **109**(5-6), 1-13.
- Wilson, J.R.U., Richardson, D.M., Rouget, M., Procheş, Ş., Amis, M.A., Henderson, L. and Thuiller, W. (2007) Residence time and potential range crucial considerations in modelling plant invasions. *Diversity and Distributions*, **13**, 11-22.
- Wise, R.M., Van Wilgen, B.W. and Le Maitre, D.C. (2012) Costs, benefits and management options for an invasive alien tree species: the case of mesquite in the Northern Cape, South Africa. *Journal of Arid Environments*, **84**, 80-90.
- Wiser, S.K., Allen, R.B., Clinton, P.W. and Platt, K.H. (1998) Community structure and forest invasion by an exotic herb over 23 years. *Ecology*, **79**(6), 2071-2081.
- With, K.A. (2002) The landscape ecology of invasive spread. *Conservation Biology*, **16**(5), 1192-1203.
- Witkowski, E.T. and Garner, R.D. (2008) Seed production, seed bank dynamics, resprouting and long-term response to clearing of the alien invasive *Solanum mauritanum* in a temperate to subtropical riparian ecosystem. *South African Journal of Botany*, **74**(3), 476-484.
- Witt, A.B.R., Kiambi, S., Beale, T. and Van Wilgen, B.W. (2017) A preliminary assessment of the extent and potential impacts of alien plant invasions in the Serengeti-Mara ecosystem, East Africa. *Koedoe*, **59**(1), 1-16.
- Wood, A.R. and Morris, M.J. (2007) Impact of the gall-forming rust fungus *Uromycladium tepperianum* on the invasive tree *Acacia saligna* in South Africa. *Biological Control*, **41**, 68-77.
- Woodford, D.J., Richardson, D.M., MacIsaac, H.J., Mandark, N.E., Van Wilgen, B.W., Wilson, J.R.U. and Weyl, O. (2016) Confronting the wicked problem of managing biological invasions. *NeoBiota*, **31**, 63-86.
- Wu, J. and David, J.L. (2002) A spatially explicit hierarchical approach to modeling complex ecological systems: theory and applications. *Ecological Modelling*, **153**, 7-26.
- Xiang, W.-N. (2013) Working with wicked problems in social-ecological systems: awareness, acceptance, and adaptation. *Landscape and Urban Planning*, **110**, 1-4.
- Yannelli, F.A., Koch, C., Jeschke, J.M. and Kollmann, J. (2017) Limiting similarity and Darwin's naturalization hypothesis: understanding the drivers of biotic resistance against invasive plant species. *Oecologia*, **183**(3), 775-784.

- Young, J.C., Marzano, M., White, R.M., McCracken, D.I., Redpath, S.M., Carss, D.N., Quine, C.P. and Watt, A.D. (2010) The emergence of biodiversity conflicts from biodiversity impacts: characteristics and management strategies. *Biodiversity and Conservation*, **19**(14), 3973-3990.
- Zachariades, C., Paterson, I.D., Strathie, L.W., Hill, M.P. and Van Wilgen, B.W. (2017) Assessing the status of biological control as a management tool for suppression of invasive alien plants in South Africa. *Bothalia*, **47**(2), 1-19.
- Zalba, S.M. and Villamil, C.B. (2002) Woody plant invasion in relictual grasslands. *Biological Invasions*, **4**, 55-72.
- Zengeya, T., Ivey, P., Woodford, D.J., Weyl, O., Novoa, A., Shackleton, R.T., Richardson, D.M. and Van Wilgen, B.W. (2017) Managing conflict-generating invasive species in South Africa: challenges and trade-offs. *Bothalia*, **47**(2), 1-11.
- Zhang, H., Qi, Z., Ye, X., Cai, Y., Ma, W. and Chen, M. (2013) Analysis of land use/land cover change, population shift, and their effects on spatiotemporal patterns of urban heat islands in metropolitan Shanghai, China. *Applied Geography*, **44**, 121-133.
- Zweig, C.L. and Newman, S. (2015) Using landscape context to map invasive species with medium-resolution satellite imagery. *Restoration Ecology*, **23**(5), 524-530.