PATTERN AND PROCESS OF PLANT INVASION IN AN AFRICAN SAVANNA ECOSYSTEM, WITH EMPHASIS ON MULTIPLE SPATIAL AND TEMPORAL SCALES

By

LLEWELLYN COURTNEY FOXCROFT

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UCDAVIS
UNIVERSITY OF CALIFORNIA

South African
NATIONAL PARKS

UNIVERSITY OF
CAMBRIDGE

Dave and
Shela Nel

C•I•B
DST Centre of
Excellence for
Invasion Biology

IES

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"Respice, adspice, prospice"

"Examine the past, examine the present, examine the future"

"Would it not be good to be able to say, Like John Muir, the Scotsman who became the great American prophet of wilderness conservation:

'To the sane and free it will hardly seem necessary to cross the continent in search of wild beauty, however easy the way, for they will find an abundance of it wherever they chance to be.'
(Elton, quoting Muir, J. 1909. Our National Parks. Boston and New York)

Will we be able to talk like this in fifty years time, as he could do fifty years ago?"

Elton, C. S. 1958.

Since then another fifty years have passed.
2007

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South African National Parks and the Kruger National Park; for logistical and other support and for the opportunity to carry out this research.
The privilege to work in such a place is truly unique and special.

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PREFACE

The broad scope of this thesis, namely, examining the ecology of alien plant invasions in savanna ecosystems, led to interaction and collaboration with a large number of scientists. This collaboration has been extremely beneficial in widening my experience in savanna ecology, invasion biology, plant ecology, conceptual ecology and a number of other sub-disciplines. Further, each chapter was focused on exclusively for a period of time, written and submitted for journal publication when ready. Therefore each chapter in this thesis is in the format of a journal publication. However, for the purposes of this thesis, I have outlined the contribution of the various authors and briefly indicated the aim of the chapter.

Abstract. This was entirely the work of LCF.

Chapter 1- General introduction. This was entirely the work of LCF.
This chapter provides a general overview of the issues that are encompassed in the thesis, discusses the main objectives, and thereby sets the scene for the following chapters.

Chapter 2- Risk assessment of riparian plant invasions into protected areas.
This chapter is based on: Foxcroft L.C., Rouget M. & Richardson D.M. 2007. Risk assessment of riparian plant invasions into protected areas. *Conservation Biology* **21**: 412–421.

LCF designed the framework, and DMR and MR made some suggestions to refine it. LCF carried out all the analysis, and MR provided some limited GIS spatial analysis support. LCF wrote the paper, and DMR and MR provided some support.

This chapter discusses the development of a framework for assessing the risk of alien plant invasion along rivers in a protected area from adjacent watersheds. The framework guides the determination of species distribution and abundance through successive, easily followed steps, providing the means for the assessment of areas of concern. I then applied the framework to Kruger National Park (KNP) in South Africa.

Chapter 3- Ecological, management and monitoring perspectives gained from patterns of alien plant distribution at multiple spatial scales.

This chapter is based: on Foxcroft L.C., Richardson D.M., Rouget M. & MacFadyen S. 2007. Ecological, management and monitoring perspectives gained from patterns of alien plant distribution at multiple spatial scales, in a large national park. To be submitted.

LCF initiated this study, designing the conceptual premise behind the application of scale theory to the dataset. LCF carried out all the spatial analysis and cartography, and MR and SMF provided limited GIS support. LCF wrote the paper, and DMR provided support and comments in writing the paper.

This chapter deals with scale; which is a central issue in ecology, and is critical for understanding and managing biological invasions. In providing direction to managing alien plant invasions, much emphasis is placed on the collection of spatial data. However, too little thought is often given to how the data are to be used, frequently resulting in the incompatibility of the data for different uses. I used data from KNP to explore the role of spatial scale in interpreting, managing, and monitoring alien plant invasions.

Chapter 4- Ornamental plants as invasive aliens: problems and solutions.

This chapter is based on: Foxcroft L.C., Richardson D.M. & Wilson J.R.U. 2007. Ornamental plants as invasive aliens: problems and solutions in Kruger National Park, South Africa. *Environmental Management*, in press.

LCF initiated this study, carried out the field work (with occasional field assistance from various KNP staff). LCF carried out the GIS analysis and the statistical analysis. JRUW suggested additions to the statistical analysis. LCF wrote the paper, and DMR provided some support. LCF also drafted and implemented the KNP policy on which this paper is based.

This chapter deals with the role of ornamental plants as invasive aliens. It is well known that some of the most harmful plant invasions originated from the intentional introduction of plants for horticulture (and other reasons). I explored this global problem in KNP, where large numbers of ornamental plants were introduced over a long period. I also explore the management interventions and approaches.

Chapter 5- Patterns of alien plant distribution in a river landscape following an extreme flood.

This chapter is based on: Foxcroft L.C., Parsons M., McLoughlin C. & Richardson D.M. 2007. Patterns of alien plant distribution in a river landscape following an extreme flood. *South African Journal of Botany*, in press.

LCF designed the conceptual framework for assessing the impact of the flood on invasive alien plants and approached MP to participate in and use the data from the KNP Post Flood Research Programme. CM and MP (and others from the Post Flood Research Programme) collected and maintained the data. MP and CM assisted in sorting the data for this study. MP carried out some exploratory analysis, which LCF revised and furthered with other statistical techniques. LCF wrote the paper, and DMR and MP provided some support in the direction of the study and paper writing.

This chapter discusses the availability of suitable patches and gaps in the landscape as a crucial determinant of invasibility for alien plants. The type and arrangement of patches in the landscape may both facilitate and obstruct alien plant invasions, depending on whether alien species perceive the patches as barriers. In February 2000 tropical weather systems caused an extreme flood with an estimated return interval of 90 to 200 years in the Sabie River, South Africa. The impact of the 2000 flood on the Sabie River landscape provides an array of patches that may provide suitable resources for the establishment of alien plants. This study examines the distribution of alien plants in relation to patchiness of the Sabie River landscape.

Chapter 6- Reconstructing 50 years of *Opuntia stricta* invasion: environmental determinants and propagule pressure.

This chapter is based: on Foxcroft L.C., Rouget M., Richardson D.M. & 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**: 427–437.

LCF initiated this study, designed and carried out the data collection, capture and data analysis. LCF carried out the analysis, and MR provided some support in classification- and regression-tree analysis and SMF in some spatial analysis. LCF wrote the paper, and DMR provided overall guidance and direction in the study, and provided some support in the writing thereof.

This chapter explores factors influencing the spread dynamics and distribution of an invasive alien cactus. Despite progress in unravelling the determinants of invasiveness and invasibility, robust, spatially-explicit predictive models for explaining real-world invasion dynamics remain illusive. Reconstructing invasion episodes is a useful way of determining the roles of different factors in mediating spread and proliferation. I describe the reconstruction of an isolated invasion event from a known source: the 50-year invasion history of *Opuntia stricta* in Kruger National Park. My aim was to explore the relative roles of environment and propagule supply in shaping the invasion pattern.

Chapter 7- What helps *Opuntia stricta* invade Kruger National Park: baboons or elephants?

This chapter is based on: Foxcroft L.C. & Rejmánek M. 2007. What helps *Opuntia stricta* invade Kruger National Park, South Africa: baboons or elephants? *Journal of Applied Vegetation Science* **10**: 265–270.

LCF refined the basic hypothesis, which was suggested in a previous article, from personal experience in the field, and on which this study is based. MR assisted in developing the sampling strategy, and both LCF and MR carried out the field work (with an occasional field assistant). MR carried out most of the statistical analysis. LCF wrote the paper, and MR provided limited support.

This chapter investigates a number of questions and hypothesis regarding the requirements of *Opuntia stricta* at a micro-habitat scale, in the KNP Lowveld where baboons and elephants are regarded as the major vectors. I posed the following questions: Is *Opuntia stricta* more frequent, and its patches larger, under trees suitable for baboon roosting? If so, does it mean that baboons are major dispersal agents and that plants established under these trees are important foci of *Opuntia stricta* spread? I surveyed an area invaded by *Opuntia stricta* in the Skukuza region of KNP in which to explore these questions.

Chapter 8- Beyond filling the gaps: advancing the science of plant invasion ecology using a new conceptual framework.
This chapter is based on: Foxcroft L.C., Pickett S.T.A. & Cadenasso M.L. 2007. Beyond filling the gaps: advancing the science of plant invasion ecology using a new conceptual framework. To be submitted to *Ecosystems*.

LCF initiated the study, sketching various frameworks and drafting ideas for a new conceptual approach to investigating or synthesizing plant invasions. I did this using various literature from the model and framework theory developed by STAP and MLC. LCF then approached STAP and MLC with a view to collaborating on this paper, in view of their considerable expertise in this area. LCF revised the framework and model presented and wrote the paper; MLC and STAP provided support, direction and comments in the writing of the paper. At this time, the paper is essentially completed and will be submitted to the journal *Ecosystems* for consideration.

Although advances have been made in understanding the mechanisms underlying invasions, these are mostly case specific, with little generality. Conceptual frameworks and models have been successfully used in developing new understanding of ecological phenomena such as ecological boundaries and spatial heterogeneity.

In this chapter, I describe a framework and model template that contextualises the key components and linkages in the plant invasion process. The suggested framework provides a structure to facilitate syntheses across scales and situations that might promote generalization. I then use an example from Kruger National Park, South Africa, to further suggest how this framework can guide management response to plant invasions.

Chapter 9- General conclusion. This was entirely the work of LCF.
This chapter briefly summarises the approaches followed and reviews the major findings of this work. I place these insights into context using the general framework derived in chapter 8.

Appendices: The appendix comprises a collection of papers, in which LCF has been either the senior author or intimately involved. The work reported on in the appendices was done in support of the work presented in the thesis. The appendices are arranged in two parts, and contain 1) details of science management linkages, and 2) alien plant species lists.

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ABSTRACT

Pattern and Process of Plant Invasion in an African Savanna Ecosystem, With Emphasis on Multiple Spatial and Temporal Scales. By Llewellyn Courtney Foxcroft, August 2007.

Biological invasions are a significant ecological and economic global crisis. Protected areas also suffer from the increased burden that invasions place on their resources and the impacts placed on the ecosystem. However, management requires an ecological foundation which can inform best practice and optimize its responses. I explored the patterns and processes of invasion in Kruger National Park (KNP), South Africa; a large national park situated in the Lowveld savanna ecosystem.

I used spatially-explicit alien plant data at various scales from: a national database, the whole of KNP, a specific region, river system, and small scale plots in one invaded area of KNP. Using various statistical techniques, primarily classification and regression tree analysis, logistic regression, ANOVA, Nestedness and spatial pattern analysis, I assessed the relationship between the patterns observed at a specific spatial grain and extent, discussing the implications for invasion ecology and management. Using this knowledge and conceptual tools, I developed a new framework and model which contributes to invasion theory.

Scale is a critical component in evaluating alien plant invasions. Without careful consideration of scale, studies from different scenarios cannot be compared and the science of invasion ecology will not advance.

I provide a framework for assessing the risks of plant invasions in a watershed, using both an area- and species-approach, highlighting areas of current and future potential concern. I also explore the role of intentional introduction of ornamental plants and discuss management approaches for dealing with this. Evaluating a riparian system provides insights into how different patches in a landscape are differentially invaded, and how patch type characteristics need to be considered carefully for management and monitoring. I also describe how reconstructing the invasion history of a species, complemented by fine scale assessment, provides insights into species-specific spread models, and also how these types of studies can input into general theories, such as the role of propagule pressure.

These components together provide insight into the dynamics of alien plant invasions in an African savanna and protected area system.

CHAPTER ONE
GENERAL INTRODUCTION

This thesis explores the process of invasion by alien plants in an African savanna ecosystem. I integrate conceptual (for example, conceptual frameworks; Pickett *et al.* 1994) and semi-mechanistic tools (for example, systematic conservation planning; Rouget *et al.* 2003a) from various sub-disciplines in classical ecology and conservation biology, to examine and reveal insights into alien plant invasions.

I start by contextualizing the study area, primarily the Kruger National Park- South Africa's flagship national park- within the broader landscape. I do this to explicitly consider the connectedness between a protected area and the surrounding landscape, and the influences that the wider landscape has on the processes that are internal to the protected area. Thereafter, I focus within the KNP, examining the interplay between features of potentially invasive species and features of the environment. I also incorporated a human dimension, as humans are inextricably linked to the global problem of biological invasions (McNeely 2005), and explored the role between humans and the environment in a protected area, and how this contributes to spreading alien species. I conclude by developing a new conceptual framework and model, suggesting that the framework provides a structure for generalizing across scales and situations, and thus lead to generalization.

I have used scale as the underlying tenet in this thesis in two ways. First, the components or thesis chapters which I present explored alien plant invasions both at an explicit extent and grain (Wiens 1989). It is only by having a scaled understanding of patterns and processes, that ecologists can relate insights from one setting to another, and thus contribute to a general theory for invasion biology. Second, understanding the linkages between ecological scales is the only way in which theory may be applied to real problems (Wiens 1989, O'Neill *et al.* 1991).

In order to organize the thesis in a logical and structured way, I have placed the main objectives in a framework (Fig. 1.1), and to which I refer throughout the thesis.

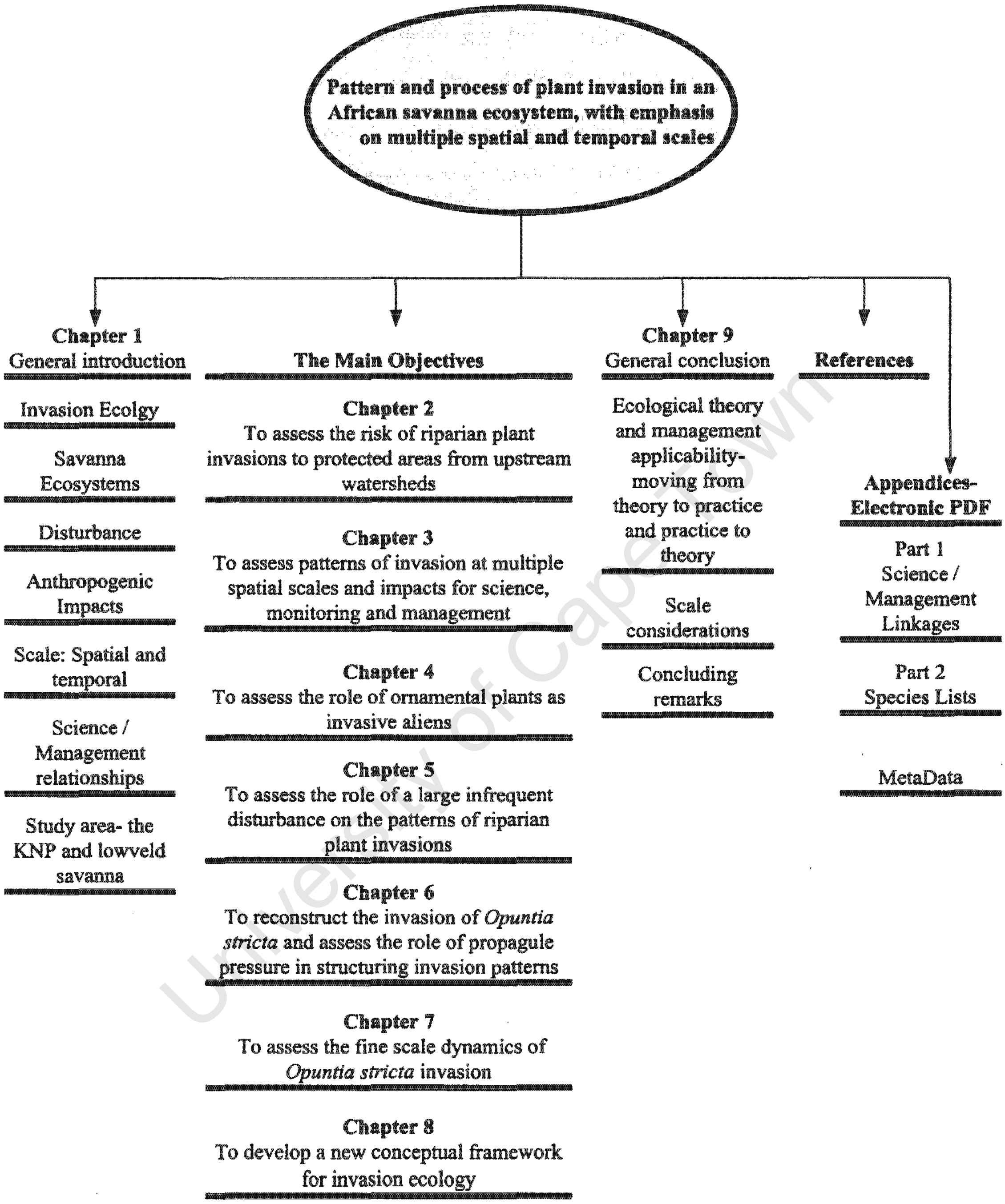

Figure 1.1: A schematic overview of the primary chapters and other important components of the thesis.

Invasion Ecology

The science of invasion ecology is a rapidly growing field (Rejmánek *et al.* 2005); the literature abounds with examples, case studies, syntheses and theories. Although some contributions to understanding invasions by plants were made more than a century ago (De Candolle 1855, Darwin 1859, Hooker 1864, Franchet 1872, Goeze 1882), it was only after the publication of Elton's (1958) seminal volume, did the (sub-) discipline of invasion ecology emerge (Richardson & Pyšek 2007). The field became more prominent with the publication by Drake *et al.* (1989), and continues to attract the attention of leading ecologists globally. The recent publication by Mooney *et al.* (2005) succinctly captures the current wealth of knowledge in *Invasive alien species- a new synthesis*. Of direct relevance to this thesis is the chapter by Rejmánek *et al.* (2005): *Ecology of invasive plants- state of the art*. By adding to and refining the three key questions posed by Drake *et al.* (1989), Rejmánek *et al.* (2005) pose five questions that underpin the science of plant invasion ecology, namely:

- Which taxa invade?
- How fast?
- What makes ecosystems invadible?
- What is the impact?
- How can we control or eradicate harmful invaders?

I have considered these questions in various ways in this thesis.

Although the main questions in the field are well described, numerous attempts to develop general rules for invasion ecology have been largely unsuccessful (Vermeij 1996). This has lead to some authors arguing that expecting such rules to emerge is unrealistic (for example, Crawley 1987, Gilpin 1990, Lodge 1993, Vermeij 1996), beyond trivial correlations which are of limited management use (various authors in Rejmánek *et al.* 2005). One model however has provided substantial benefit in developing a conceptual understanding of invasions; the 'naturalization-transformation' model proposed by Richardson *et al.* (2000; Fig. 1.2), and which has had a profound impact on my conceptual understanding, and further development of my personal theory regarding the ecology of invasions.

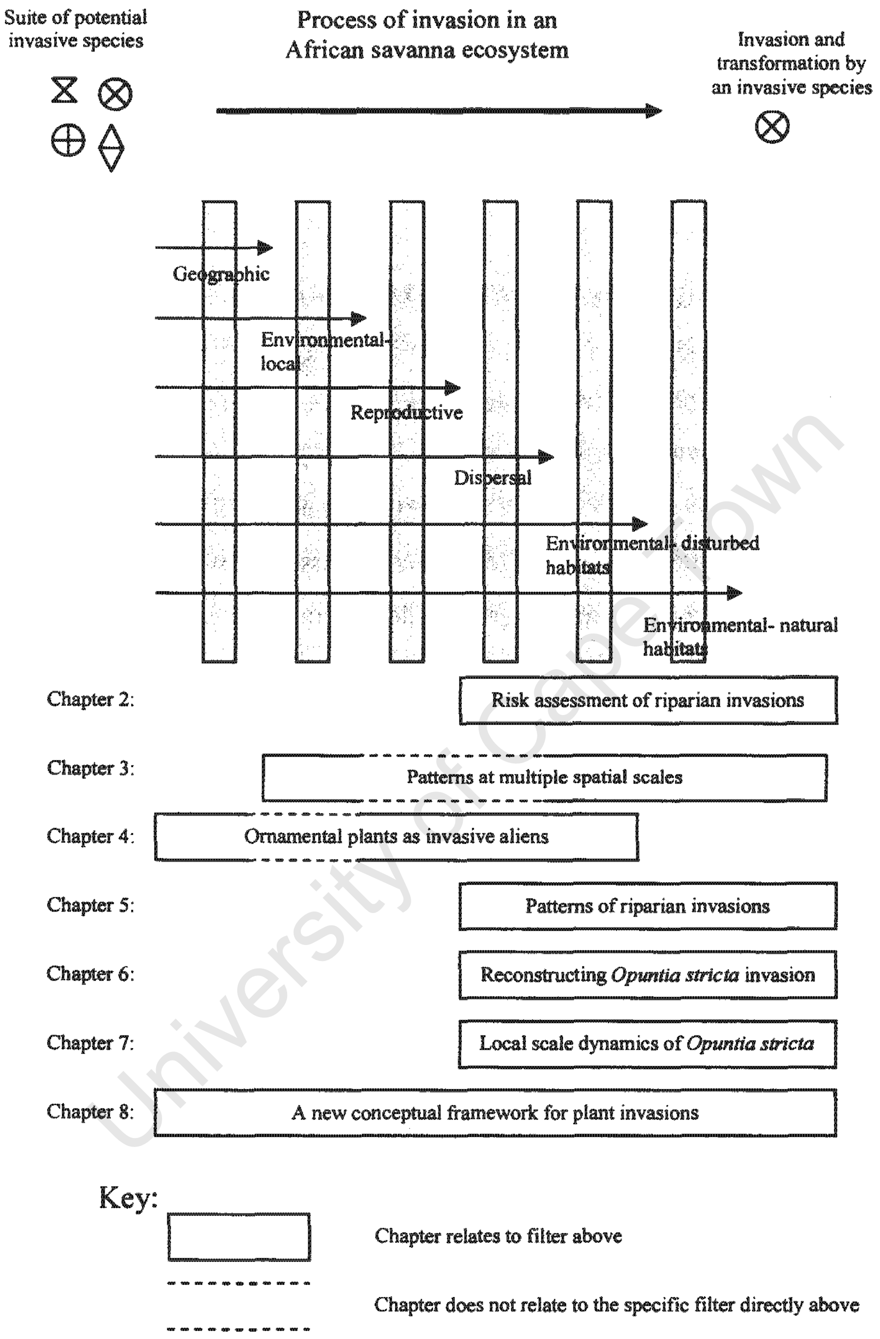

Figure 1.2: The primary thesis chapters in relation to the 'invasion – naturalization' model of Richardson *et al.* (2000).

The 'naturalization-transformation' model (Richardson *et al.* 2000; Fig. 1.2) describes a series of barriers or filters, through which a species must pass in order to move to the next level in the continuum. Thus, not all species present in a suite of potential invaders will invade and become transformers (a subset of invasive species that alter the character, form or function of the system; Richardson *et al.* 2000). It is this process of invasion, from potential invader to transformer, that attracts my ongoing interest, and particularly, in savanna ecosystems.

Savanna Ecosystems

Seven biomes are recognised in southern Africa (Mucina & Rutherford 2006), of which the savanna biome can broadly be divided into an arid and moist group (Huntley 1982). The savanna biome is characterised by a discontinuous over-story of woody plants and an herbaceous layer dominated by C_4 grasses (Venter *et al.* 2003). Covering 60% of sub-Saharan Africa (Scholes & Walker 1993), savannas constitute 12% of the global land surface (Scholes & Hall 1996). The plant species richness of southern African savannas is high, with about 5,700 plant species being recorded (White 1983).

The interaction of savannas and people dates back a long time. For example, the earlier and middle stone-age people lived in the area that is now KNP for the past 20,000 years (Deacon & Deacon 1999). The combined effect of the main drivers (humans, climate, fire, large herbivores and others) has resulted in the savanna system being ecologically complex and highly heterogeneous (Pickett, Cadenasso & Benning 2003). Additionally, not all patches in the landscape are likely to be equally easily invaded. For example, the riparian habitats in KNP are far more invaded than other habitats (Foxcroft & Richardson 2003). Thus, the ecological template across the African savannas provides a range of opportunities for examining the processes and patterns of invasion. Or alternatively, as Lonsdale (1999) shows African savannas to be less invaded than other parts of the world, perhaps this provides an opportunity to examine the potential biotic resistance to invasions. However, little literature on alien plant invasions emanates from the African savannas.

Disturbance

While disturbance, anthropogenic or natural (Pickett & White 1985), is known to increase opportunities for invasion (Hobbs & Huenneke 1992), disturbance is a regular feature of savannas (du Toit *et al.* 2003). Although studies have investigated the role of resource availability (e.g. Hobbs & Huenneke 1992), and the fluctuating availability of those resources (Davis *et al.* 2000), disturbance regimes (e.g. Hobbs 1989, Grace *et al.* 2001, Brooks & Pyke 2001), and empty niches (e.g. Cannas *et al.*, 2002) in facilitating invasions, I know of only a few studies that have explicitly examined the role of landscape patches in the context of invasibility (With 2002, 2004). The relationship between plant invasions and fire (D'Antonio 2000), floods (Tabacchi *et al.* 1998, Malard *et al.* 2000, Arscott *et al.* 2002, Dixon 2003) and droughts (Davis *et al.* 1998) has been widely explored in various regions of the world, and are also probably the most prevalent, wide scale disturbances featured in the KNP savannas (du Toit *et al.* 2003).

Anthropogenic impacts

The problem of invasive alien species is a human problem (McNeely 2005), and is best captured in the title of a book that explores this subject: *The great reshuffling- human dimensions of invasive alien species* (McNeely 2001). People move things around. Propagules are moved around the world with increasing ease and speed; species seem to more often invade human altered ecosystems (although they are often completely capable of invading natural, well protected ecosystems); many species are intentionally introduced for economic and personal uses; and, the problems with invasions are defined by, and responded to, by humans (McNeely 2005). Even protected areas, mandated with maintaining biodiversity (composition, function and structure, as described by Noss 1990) have problems with, and have to manage invasions that originate from intentional introductions (Foxcroft 2001).

Scale: Spatial and Temporal

Pattern and processes operate over a wide range of scales, and the characteristics observed are scale dependant (Allen *et al.* 1984, Delcourt & Delcourt 1988, Levin 1992, Wessman 1992, Fisher 1993, Wu 1994). Understanding patterns, whether spatial, temporal or functional, is inseparable from scale in theory and practice (Wu & Loucks 1995). The choice of scale acts as a magnifier or blinker, depending on the appropriateness of the observation window to the organisms or function being studied

(Allen & Starr 1982, O'Neill *et al.* 1986). Thus, scale affects the observation of patterns, and therefore must be an integral part of describing patterns (Wu & Loucks 1995).

Although plant ecologists have recognized the importance of sampling scale in their descriptions of dispersal or species distributions (Wiens 1989), invading plants pose further complexity. Consequently, far less attention has been given to scale issues in understanding invasiveness (but see Higgins *et al.* 1996). It may be argued that the reason invasions pose additional layers of complexity to understanding spatial patterns is that most alien plants are still in the process of spreading and have not sampled the full range of available habitats (Rouget *et al.* 2004, Wilson *et al.* 2007). Few studies have studied the processes and patterns of invasion from the initial founder population to the point where all available, susceptible habitats have been sampled (Pyšek & Hulme 2005).

Invading plants also have spatial and temporal dynamics that are difficult to predict (Pyšek & Hulme 2005), frequently expanding their distribution from extremely low numbers of source populations, often through rare dispersal events (Puth & Post 2005). However, the ability to predict ecological phenomena such as patterns of alien plant distribution, and thus infer ecological processes (Turner 1989), depends on the relationship between spatial and temporal scales of variation (Wiens 1989). With an increase in spatial scale, the time scale at which important processes operate is slower, time lags increase, and indirect effects become increasingly important. Further, understanding patterns of invasions is also a function of both the extent and grain of the investigation (Wiens 1989). Extent refers to the overall area of the investigation, while grain refers to the individual units of observation. Therefore, the various components of the scale (time, extent and grain) of the investigation determine the range of patterns that detected and the explanations provided (Dale 1999).

I examined the process of invasion by exploring spatial patterns at a number of scales (Fig. 1.3), ranging from the landscape-level to a plot-level (Table 1.1). Although the KNP is the focal area and the spatial extent of the work in chapters 3-4, I assessed the risks posed by alien plants invasions upriver from the KNP (chapter 2), patterns of riparian plant invasion following a major flood in one large river (chapter 5), reconstructed the invasion of a single species (*Opuntia stricta*) which was well mapped (chapter 6), examined the fine scale dynamics of *O. stricta* (chapter 7), and then provide a new general framework, which may be applied at any scale.

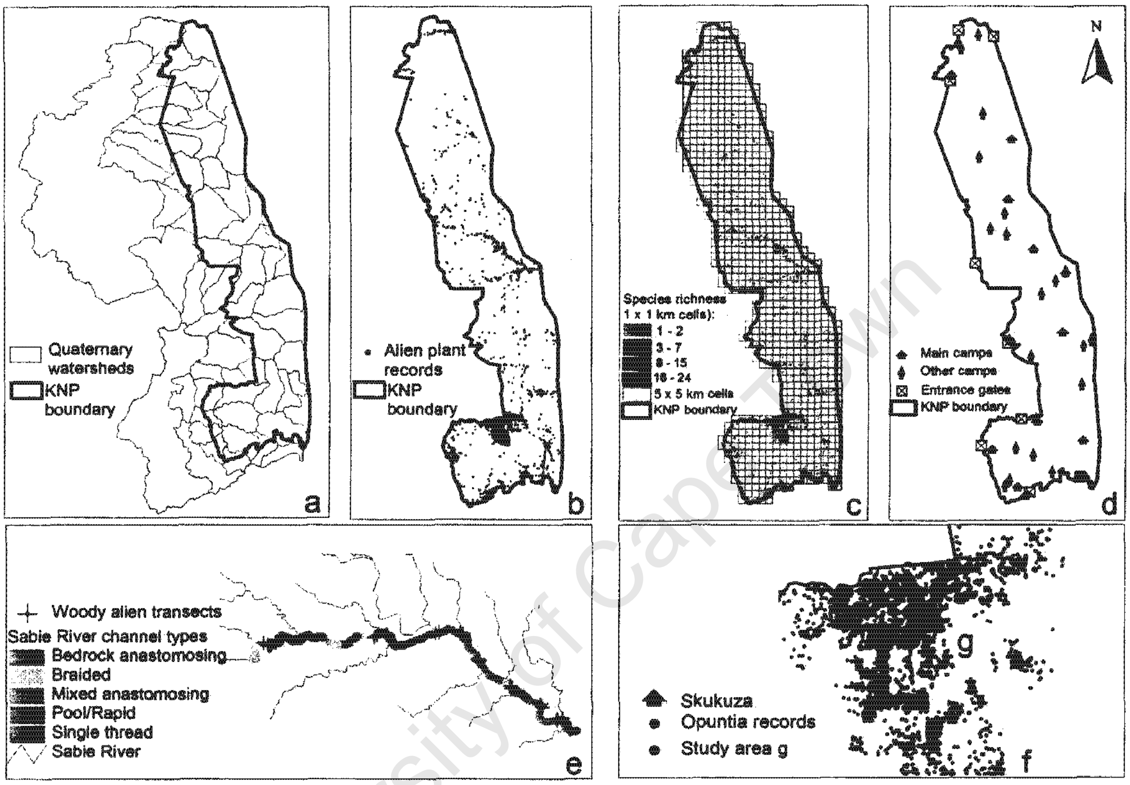

Figure 1.3: The spatial domains of the studies reported on the different chapters of this thesis: (a) Chapter 2, KNP in relation to the wider watershed / river drainage systems to the west; (b) Chapter 3, evaluation of invasive alien plant distribution data across KNP, at various spatial scales, of which 5 x 5 km (larger blue cells) and 1 x 1 km cells (finer red cells) are indicated in (c); (d) Chapter 4, assessing the role of ornamental alien plants as invasive aliens in staff and tourist camps across the KNP landscape; (e) Chapter 5, investigating the distribution of invasive alien plants following a large infrequent flood disturbance in the Sabie River, KNP; (f) Chapter 6, reconstructing the invasion of *Opuntia stricta*, in the Skukuza region of KNP; (g) Chapter 7, assessing local scale dynamics of *O. stricta* invasion in relation to its primary vectors- baboons and elephants.

Table 1.1: The relationship between grain and extent in the primary thesis chapters.

Chapter and short description	**Scale of investigation** **Grain**[1]	 **Extent**[2]
2- Risk assessment of riparian invasions from the upper river basins of rivers draining through the KNP	Quarter degree square (roughly 25 x 27 km), rescaled to the quaternary watershed scale	The entire KNP (20,000 km^2) and westwards, into the upper watershed areas (approx. an additional 20,000 km^2)
3- Patterns of alien plant invasions at multiple spatial scales	Point locality data was evaluated at multiple spatial scales, from 0.1 x 0.1 km, to the quarter degree square	The entire KNP
4- The role of humans and ornamental plants as invasive aliens	36 tourist and staff villages across KNP	The entire KNP
5- Patterns of riparian invasions following a large infrequent flood	For woody species data, 548 plots of 30 x 5 m, and for herbaceous species, 156 plots of 5 x 5 m	The Sabie River, inside the KNP (length approx. 120 km)
6- Reconstructing the invasion of *Opuntia stricta* over 50 years	Point locality data	The Skukuza region of KNP, covering about 66,000 ha
7- Local scale dynamics of *Opuntia stricta* invasion and the role of its vectors- baboons and elephants	Circular plots of diameter of 0.5 to 2.5 m	One patch of *Opuntia stricta* 340 x 380 m
8- A new conceptual framework for plant invasions	The framework is generic in that it can be used to assess the invasion of an alien species at the grain that is relevant to the species and system being investigated	

[1]- Grain refers to the individual units of observation (Wiens 1989)
[2]- Extent refers to the overall area of the investigation (Wiens 1989)

Science / Management Relationships

The general theory of ecosystem heterogeneity (Wu & Loucks 1995) as an alternative paradigm to the 'balance of nature' theory has been embraced in the management of KNP (Pickett *et al.* 2003). In doing so, a new approach to management which caters for continuous flux at multiple space and time scales, was adopted and expressed as the Strategic Adaptive Management process (Biggs & Rogers *et al.* 2003, see appendices 1.3–1.9). In essence, this implies 'learning by doing' and active 'reflection and response' (Rogers 2003), with the intention of achieving integration between ecological science and conservation practice (Biggs 2003).

Rogers (2003) describes three main reasons for science management linkages (or adaptive management). First, if science is not explicit and carefully managed, informal mental models of scientists and managers form self-reinforcing pseudo-facts, which then form the basis of conservation management decisions. Second, because ecosystems are so complex, and the tools of managers somewhat limited (e.g. fire, water, guns, earth moving equipment), much needs to be learned if the products of science are to be turned into achievable goals, and more importantly, implemented. Third, because reports and publications are usually only read by colleagues and scholars, scientists need to make the learning process more explicit and useful to management, and thus turn management decisions into landscape scale experiments, from which we can learn to better manage.

It is thus my fervent hope that the science presented in this thesis is both useful and used, by managers and scientists alike.

Study area- the KNP and Lowveld savanna

The Kruger National Park, situated in South Africa's Lowveld savanna between the Drakensberg escarpment in the west and the extensive coastal plains of Mozambique in the east (Fig. 1.4), is one of the largest protected areas in the world primarily managed for biodiversity conservation. The KNP has over 100 years of formal conservation history and spans about 20,000 km^2. It has a rich natural history which has been both the livelihood of the Hunter-gather and Iron Age (AD 200–1836) eras, and the fascination of the colonial explorers / hunters (1836–1902), game preservation (1902–1925) and formal conservation (1925 onwards) eras. The recent volume: *The Kruger Experience: ecology and management of savanna heterogeneity* (du Toit *et al.* 2003), provides an in-depth discussion of the abiotic template and the biotic interactions.

Due to the spatial arrangement of the focal areas in each chapter, short discussions of the particular areas are given in each chapter. I have tried to reduce duplication, but in providing a necessarily complete description of the study area with reference to the particular study, some overlap between the chapters is inevitable.

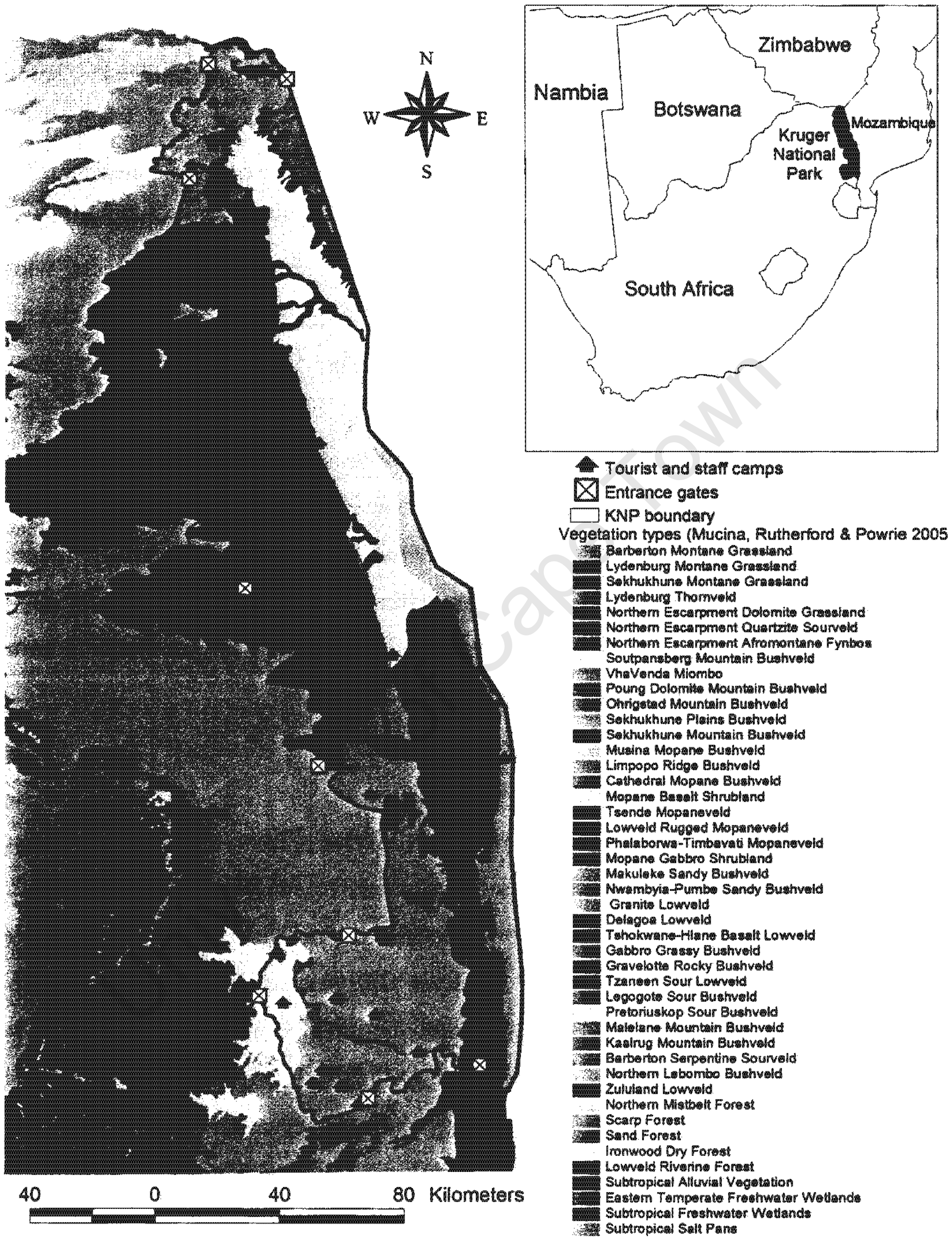

Figure 1.4: The study area, showing the Kruger National Park and Lowveld savanna vegetation types (Mucina, Rutherford & Powrie 2005). The insert places KNP in relation to South Africa.

CHAPTER TWO

RISK ASSESSMENT OF RIPARIAN PLANT INVASIONS INTO PROTECTED AREAS[1]

Abstract

Protected areas are becoming increasingly isolated. River corridors represent crucial links to the surrounding landscape but are also major conduits for invasion of alien species. I developed a framework for assessing the risk of alien plant invasion along rivers in a protected area from adjacent watersheds. The framework combines species- and landscape-level approaches and has five key components: (1) definition of the geographical area of interest; (2) delineation of the domain into ecologically meaningful zones; (3) identification of the appropriate landscape units; (4) categorization of alien species and mapping of their distribution and abundance; and (5) definition of management options. The framework guides the determination of species distribution and abundance through successive, easily followed steps, providing the means for the assessment of areas of concern. I applied the framework to Kruger National Park (KNP) in South Africa.

I recorded 231 invasive alien plant species (of which 79 were major invaders) in the domain. The KNP is facing increasing pressure from alien species in the upper regions of the drainage areas of neighbouring watersheds. Based on climatic modelling, I showed that most major riparian invaders have the ability to spread across KNP should they be transported down the rivers. With this information, KNP managers can identify areas for proactive intervention, monitoring, and wise resource allocation. Even for a very large protected area such as KNP, sustainable management of biodiversity will depend heavily on the response of land managers upstream managing alien plants.

I suggest that this framework is applicable to plants and other passively dispersed species, which invade protected areas situated at the end of a drainage basin.

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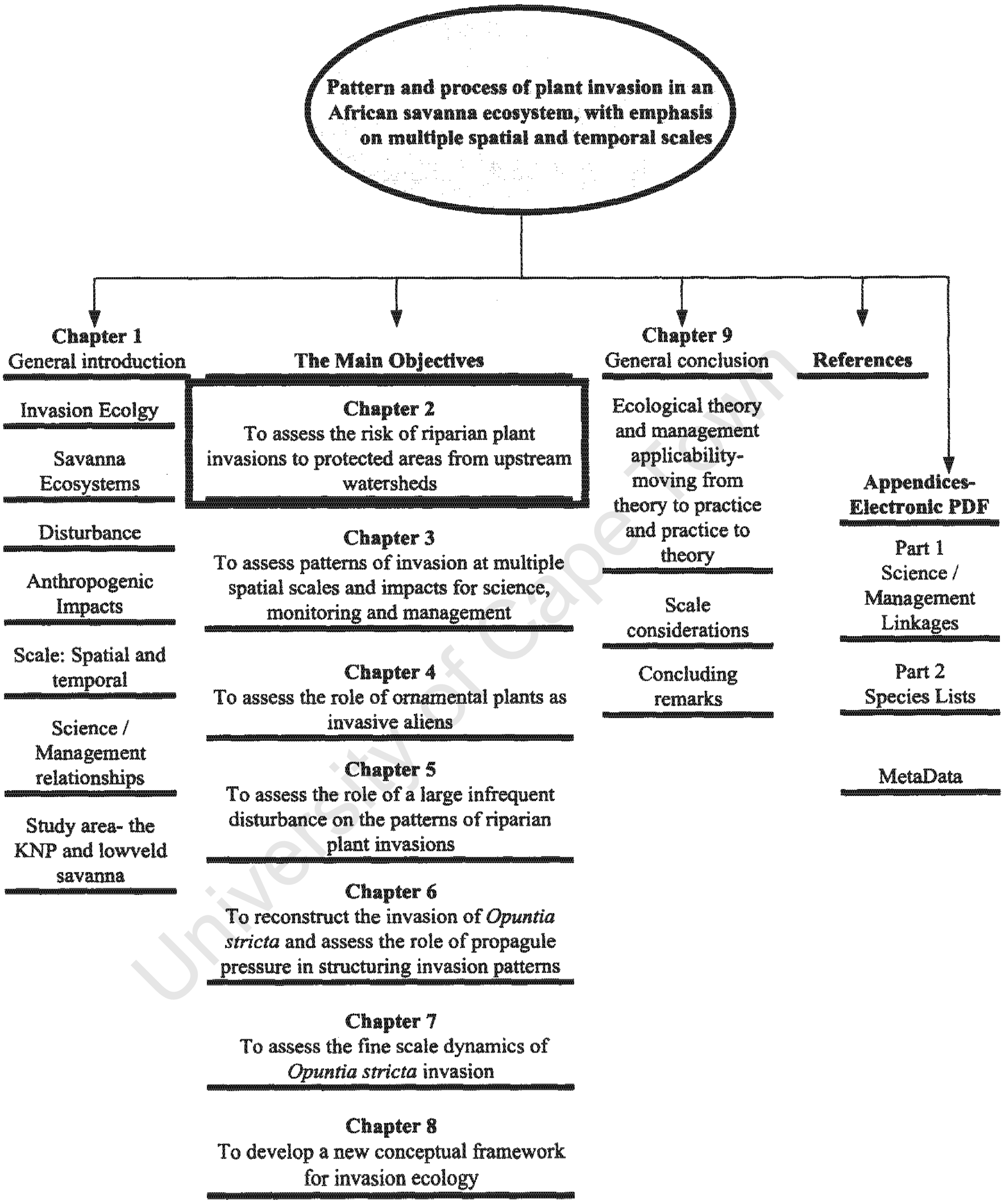
Pattern and process of plant invasion in an African savanna ecosystem, with emphasis on multiple spatial and temporal scales
Chapter 1
General introduction
Invasion Ecolgy
Savanna Ecosystems
Disturbance
Anthropogenic Impacts
Scale: Spatial and temporal
Science / Management relationships
Study area- the KNP and lowveld savanna
The Main Objectives
Chapter 2
To assess the risk of riparian plant invasions to protected areas from upstream watersheds
Chapter 3
To assess patterns of invasion at multiple spatial scales and impacts for science, monitoring and management
Chapter 4
To assess the role of ornamental plants as invasive aliens
Chapter 5
To assess the role of a large infrequent disturbance on the patterns of riparian plant invasions
Chapter 6
To reconstruct the invasion of Opuntia stricta and assess the role of propagule pressure in structuring invasion patterns
Chapter 7
To assess the fine scale dynamics of Opuntia stricta invasion
Chapter 8
To develop a new conceptual framework for invasion ecology
Chapter 9
General conclusion
Ecological theory and management applicability- moving from theory to practice and practice to theory
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Concluding remarks
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Part 1
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Part 2
Species Lists
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Introduction

Protected areas are becoming increasingly isolated, forming islands of relatively intact ecosystems in a matrix of land uses that are often incompatible with biodiversity conservation. The degree to which activities outside protected areas affect the functioning of ecosystems within such areas depends on the geography of the region and numerous socioeconomic factors (Pollard *et al.* 2003). Protected areas are connected with their surroundings in many ways. Besides the many 'edge effects' involving the spill over of human-related activities across the boundaries of protected areas (see references in Alston & Richardson 2006), there are also other important ways that humans impact on protected areas. Roads and rivers are particularly important conduits for the spread of invasive species (Pyšek & Prach 1994) and form links between the protected areas and their surroundings; such links are both beneficial and problematical. Roads allow access for management activities but create openings for the introduction of unwanted organisms (e.g., Lonsdale & Lane 1994, Gelbard & Harrison 2003). Rivers provide corridors and are conveyor belts for the movement of organisms between isolated protected areas (van Wilgen *et al.* 2006). Protected areas are usually too small to contain entire watersheds, but they are linked to surrounding areas via rivers (van Wilgen *et al.* 2006). This linkage adds a level of complexity to the management of protected areas.

Where alien plant species are abundant in the watersheds surrounding a protected area this may provide a continuous source of propagules, greatly complicating long-term control efforts. For example, in South Africa's Kruger National Park (KNP), some of the worst invasive plant species spread into the park along major rivers (Foxcroft & Richardson 2003, appendix 1.2). Given the complex mosaic of land uses and the abundance and diversity of invasive alien plant species in the watersheds drained by the major rivers that flow through KNP (Fig. 2.1a), further incursions of alien species along rivers are a major threat to the biodiversity conservation objectives for the park (KNP 2005).

The KNP objectives hierarchy (KNP 2005, appendix 1.5) guides management policy and strategy. However, physical control interventions are currently mostly *ad hoc* in the absence of a framework to guide actions. Management projects are currently underway to address the invasion of alien species through a number of vectors. For example, management of plants arising from the spread of ornamental plants in tourist villages (Foxcroft 2001) is a major focus of control efforts. Aquatic weeds such as water hyacinth (*Eichhornia crassipes* [Mart.] Solms.) and water lettuce (*Pistia stratiotes* L.) are treated with biological control agents and herbicides. The largest control efforts in KNP have been allocated to managing the invasive cactus, sour prickly pear (*Opuntia stricta* (Haw.) Haw. var. *dillenii* (Ker Gawl.) L. D. Benson), which has invaded more than 80,000 ha (Chapter 6) and to continuous follow-up control against a suite of invasive riparian species by the national Working for Water programme (Foxcroft & Richardson 2003, appendix 1.2, Freitag-Ronaldson & Foxcroft 2003, appendix 1.3).

However, the management of invasive plant species in riparian zones is increasingly seen as a futile task because operations are not planned with due cognizance of the configuration of KNP in relation to propagule sources outside the park. There is an urgent need to assess priorities for management of species that have potential for introduction to the park along rivers. Rivers are a particularly important component of KNP because the entire southern (Crocodile River) and northern (Luvuvhu and Limpopo rivers) and parts of western boundary (Sabie and Nsikazi rivers) are formed by rivers. Even more importantly, seven major rivers flow through the park from drainage areas severely invaded by numerous alien species (Fig. 2.1a & b).

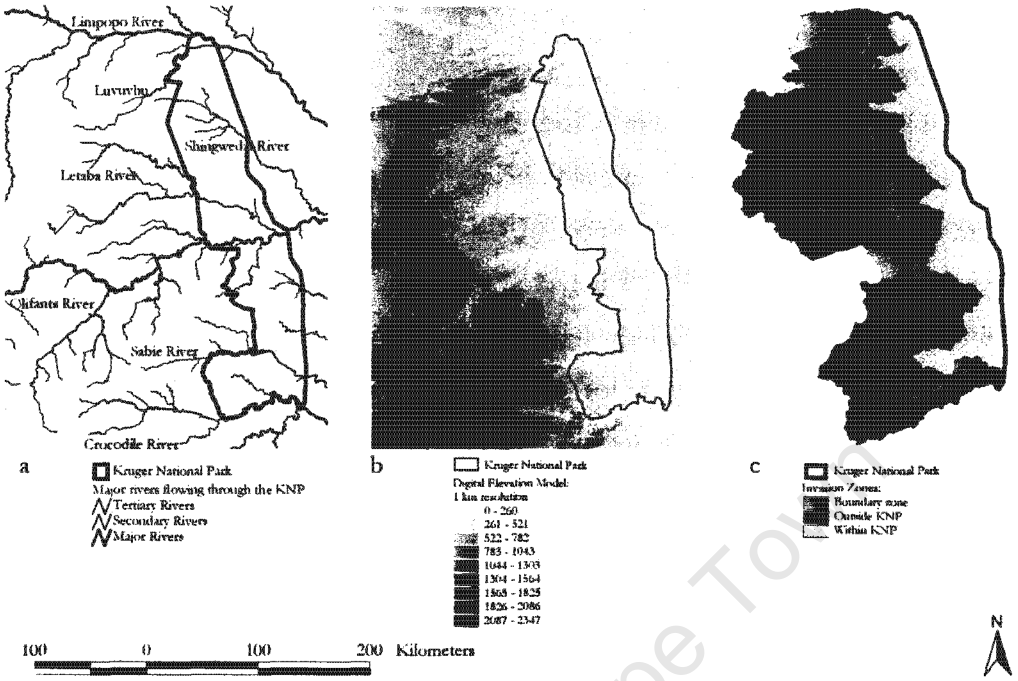


Figure 2.1: Kruger National Park (KNP): (a) the major rivers flowing west to east through KNP, (b) topography of the area showing the higher-elevation areas to the west of KNP, and (c) domain (the entire area, including the protected area and surrounding watersheds) divided into three zones for assessing the risk of plant invasion into KNP.

Although qualitative risk-assessment protocols (e.g., Tucker & Richardson 1995, Pheloung *et al.* 1999, Daehler & Carino 2000) are useful for preventing or reducing introductions of unwanted species, the challenges associated with managing a suite of species already in a particular area are immense. Risk assessment protocols usually aim to identify potentially invasive species based on broad criteria (e.g. previous invasion history) at a regional scale, with some modification for particular areas (Daehler & Carino 2000). An objective assessment of the risk of spread from different watersheds would help managers identify areas where proactive intervention would be most effective and where monitoring for new incursions would be most effective.

I developed a framework for assessing the risk of alien plant invasion along rivers into a protected area from adjacent watersheds. I applied the framework to the KNP situation and discuss how its application could improve conservation management and planning.

Methods

Risk assessment framework

Although qualitative risk assessment is useful at a broad scale, a framework is required for use at a local scale that would provide insights into key species and areas. For the framework to provide a robust assessment of risks posed by alien plants to the protected area from surrounding watersheds, I believed that it had to (1) be specific to the local geography; (2) consider species of special concern (i.e., species known to be aggressive invaders in particular habitats in the area); (4) include abundance or, as a proxy, species richness as a method of incorporating propagule pressure; and (5) be relevant and useful to the management goals of the protected area.

The generic framework (Fig. 2.2) I developed can be applied to other areas in similar situations. There are five key components in the framework (Fig. 2.2).

1. Define the geographical area of interest (i.e., the domain- the entire area including the protected area and surrounding watersheds). The domain includes both the primary area of interest (the protected area) and a much larger surrounding area, including the upstream drainage basins that act as potential sources of invasive alien species. The shape of the protected area within the broader landscape matrix should be considered to ensure adequate inclusion of the areas that may act as sources of propagules.

2. Delineate the domain into zones that are ecologically meaningful and relevant to management so that areas with a high risk of invasion can be identified. I used a zone within the protected area, a transitional zone, and a zone encompassing the remainder of the domain. The transitional zone provided an area for monitoring and implementing early warning or eradication systems because alien plants move passively down the watershed, through the transitional zone and ultimately into the protected area.

3. Identify the appropriate landscape units at which to explore the richness of alien species based on criteria such as the availability and resolution of data and the usefulness of the data to management. The landscape unit selected should be appropriate for studying distinct river systems and allow evaluation and assessment of potential risks posed by certain areas. Depending on the size of the protected area and the rest of the domain as well as resources available to management, the landscape units selected may

be coarser for larger areas and finer in smaller areas, as the smaller areas can be more intensively mapped and monitored.

4. Map the distribution and abundance of alien species. For many areas detailed floristic data are available. Where data need to be collected a number of techniques are available (e.g., see Henderson 1998, 1999, 2001). However, the resolution of the data should be appropriate to the scale of the landscape unit selected (see Chapter 3).

Most approaches for determining species spread and risk focus attention separately on single species (e.g., focus on specific species and identify and manage all known populations) or particular areas (e.g., manage a suite of species in a specially demarcated area to minimize impact) (DoC 2000). My aim, to determine overall management options based on the spatial arrangement of species of primary concern and the invasion foci, called for a combination of these two approaches (species and watershed levels).

4A. In the species-level section of the framework, identify species of primary concern and their distribution. Because certain species are considered more serious invaders than others (e.g., chromolaena, *Chromolaena odorata* [L.] R.M. King & H. Rob., in the KNP context), the presence of one or a few of these requires specific and targeted management action.

4A1. Identify major invader species (i.e., widespread alien plant species or invaders that occur in dense stands). Identification of a subset of major invaders forces managers to consider these species explicitly in formulating management recommendations. This can be done in many ways, for example, by analysis of abundance or expert opinion, but requires that a manageable number of species that are most likely to cause harmful impacts to biodiversity are listed for priority actions.

4A2. Categorize species by habitat preference. Separate alien species into habitat preference categories (i.e., alien plants that predominantly occur in riparian, landscape, or both riparian and landscape areas) in order to focus on those species most likely to be passively dispersed by river flows and floods. I also separated the most widespread and localized species and placed these in a matrix to determine the species risk categories. From this, appropriate management intervention, such as early detection, eradication, or biological control, is determined.

4A3. Categorize species by zone. Separate the species into the three zones determined in component 2 to assess the species that occur in the protected area, adjacent to it, or in the upper basin of the protected area.

4B. Assess sources of propagule pressure outside the protected area and map areas of high invasion risk within the protected areas.

4B1. Record current alien species richness. Determine the current species richness (for all recorded alien species) per landscape unit (watershed) and per zone. Species richness is used to provide a measure of the availability and size of the propagule pool and is used as a proxy for species abundance data, which is often unavailable.

4B2. Record potential alien species richness. To account for future risks consider the current distribution of alien plants in the landscape units and predicted species distribution of the major invaders. Various approaches are now available for predicting species distributions (e.g. Thuiller 2003, Guisan & Thuiller 2005). The potential species distribution is useful because including species likely to be present in the future extends the lifespan of the framework in terms of its relevance to managers in the medium term (5 to 10 years).

Furthermore, because the predicted distribution of the major species "fills in" or supplements the data, databases for invasive species are frequently incomplete due to the rapidly changing nature of invasions.

5. Define management options. In the final step, assess both the species' risk category and the watershed risk index. The species risk category assesses the threat that specifically selected species pose to the protected area based on their distribution and proximity to the protected area. The watershed risk index delineates the threat posed by the current (and predicted) pools of high propagule supply and the proximity of the threat to the protected area. The species risk category and the watershed risk index provide an understanding of the combined effects of the number and species of alien invaders. Species are categorized into manageable groups and suitable management recommendations are provided per group.

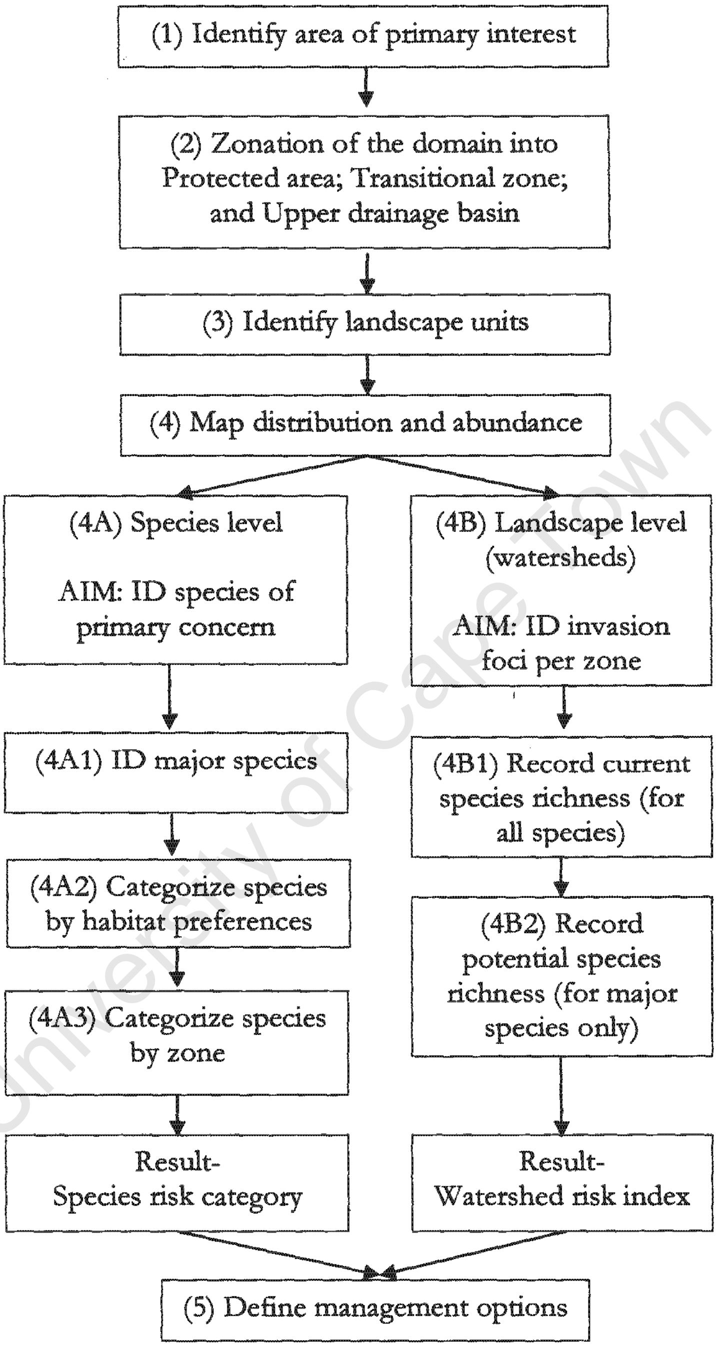


Figure 2.2: A framework for assessing the risk of alien plant invasion into a protected area that combines species- and landscape-level considerations.

Case Study of Kruger National Park

I used Kruger National Park (KNP) as a case study through which to evaluate the framework. The discussion is arranged numerically to correspond with the numbered components above and in Fig. 2.2.

1. KNP covers an area of 20,000 km² in the north-eastern corner of South Africa. Its entire eastern boundary borders on Mozambique. It extends 360 km north to south and 90 km east to west at its widest point. Located in the mid-reaches of an extensive drainage basin that arises in the higher-elevation areas to the west (Fig. 2.1b), KNP comprises mostly gently undulating landscapes (Gertenbach 1983). Elevation in the domain (i.e., the entire area including the protected area and surrounding watersheds) varies from 2253 m asl (Table 2.1) in the west to 104 m asl in KNP. The study area includes KNP within the broader landscape context. The landscape contains quaternary watersheds up to approximately 140 km west of the KNP boundary. Of the seven main river systems, KNP only manages a small proportion of each. The Crocodile River, which is 316 km long, has only 36% under formal protection in KNP. The Letaba, 481 km, 26%; Limpopo, 736 km, 4%; Luvuvhu, 225 km, 35%; Olifants, 704 km, 14%; Sabie, 178 km, 57% and the Shingwedzi, 159 km, 63%; respectively, are protected in KNP. I was interested only in the upstream basin because alien plants largely enter KNP through dispersal of propagules in water. I paid no attention to areas downstream of KNP in Mozambique because there is no evidence suggesting the passive dispersal of alien plants upstream into KNP.

Table 2.1: Environmental and land-use variables used to characterize the watersheds in Kruger National Park (KNP), including a summary of 20 features for the overall domain (the entire area, including the protected area and surrounding watersheds) and each of the three alien plant management zones.

Category	*Domain*	*Upper basin*	*Transitional zone*	*Within KNP*
Alien plant species richness				
All aliens	231	192	165	97
Major invaders	79	72	66	45
Riparian invaders	185	153	138	88
River length				
Total length of all segments (km)	7437	2158	3559	1720
Mean length / segment (km)	19	19	22	17
Watershed				
Area (km^2)	52 169	14 259	25 771	12 139
Ave watershed size (km^2)	462	264	572	551
Size of largest watershed (km^2)	1 249	759	1 249	927
Size of smallest watershed (km^2)	47	47	254	182
Ave mean annual runoff (mm)	21	39	17	6
Primary land-use types				
Cultivated (%)	11	21	12	0.1
Degraded (%)	5	7	6	0.08
Mines (%)	0.1	0.02	0.2	0.00
Natural (%)	75	50	78	99
Plantations (%)	6	19	1	0.00
Urban (%)	2	3	2	0.03
Water bodies (%)	0.1	0.2	0.1	0.05
Topography				
Mean elevation (m asl)	561	892	468	323
Max elevation (m asl)	2 253	2 253	1 501	700
Min elevation (m asl)	104	419	122	104

Riparian aliens are primarily introduced into KNP through dispersal of propagules along rivers. Thus, it may be argued that the simplest framework for controlling riparian alien plants from spreading into KNP would be to focus simply on rivers that have the highest runoff rates. To ascertain that the species richness in the watersheds was not correlated simply to water runoff, I carried out linear regression to determine whether I could predict species richness as a function of mean annual runoff.

2. Based on elevation and broad biophysical criteria (moisture and vegetation gradients), I determined three zones through which to evaluate the proximity and potential risk of each of the zones to the KNP: (1) within the protected area (KNP), where the watershed is contained completely within the KNP, (2) transitional zone, where the KNP boundary falls within the particular watershed, and (3) the upper drainage basin, representing the uppermost watersheds in the river system, bounded by the top of the tertiary watershed. In some cases I adjusted the zones slightly to make the zone more continuous along the length of the KNP boundary (Fig. 2.2c).

3. Due to the large area covered, I worked at the scale of quaternary watersheds (quaternary catchments are nested subdivisions within primary, secondary, and tertiary catchments). Quaternary catchments are used for regional-scale planning for many environmental initiatives in South Africa, such as the national Working for Water programme (invasive alien plant control programme). The study area contained 121 quaternary watersheds, ranging in size from 1249 km^2 to 47 km^2. I believed that the quaternary watersheds provided an appropriate scale against which to determine the species richness. This was based on the size of the entire domain and the resolution of the data. Furthermore, because I was interested in the potential of alien species to invade down the major rivers into KNP, I believed that the watershed approach provided the appropriate landscape unit for this study.

4. Data on the current distribution of invasive alien plants in the domain was provided by the Southern African Plant Invaders Atlas (SAPIA; Henderson 1998, 1999, 2001). The SAPIA database has more than 50,000 geo-referenced records based on a quarter-degree grid-square system (15' latitude x 15' longitude), representing roughly 25 x 27 km. Although relatively coarse, the SAPIA data is the best available alien plant distribution data for southern Africa (Richardson *et al.* 2005). The data was collected over many

years, with a number of participants, and data collection is still ongoing. Also, as I was assessing alien plant distribution at a large scale, (i.e. the watershed), I felt that this data was appropriate for this purpose (see Nel *et al.* 2004, for a discussion on this dataset). I rescaled the current distribution of species to quaternary watersheds. Coverage's for quarter-degree squares (QDS) and watersheds were overlaid in a geographic information system (GIS), and I listed all species currently occurring in each watershed by overlapping species distribution from SAPIA at the QDS scale and watershed boundaries.

4A1. I selected records of species considered to be major invaders as defined by Nel *et al.* (2004). These were widespread alien plant species or invaders that occur in dense stands. I decided to focus on the major invaders for the purposes of predicting the potential distribution of "transformer species" (terminology following Richardson *et al.* 2000).

4A2. Alien plants were categorized into riparian or landscape species depending on the type of habitat they invade. I considered species riparian or landscape if more than 75 % of their records from SAPIA fell into the respective category. If < 75 % the records fell into either riparian or landscape category, then I designated the species an invader of both riparian and landscape habitats. I was primarily interested in "riparian" and "riparian and landscape" invaders, given that my main interest was in species with propagules that can be dispersed along rivers. I considered landscape invaders if they had a high probability of invading up the catena into the drier upland areas, once having established along the riparian zones.

4A3. For each zone I summed the number of watersheds that the major species occurred in based on the current species distribution (Table 2.2). For species already in the KNP, I used the KNP alien plant list (Foxcroft *et al.* 2003, appendix 2.3) as the best available plant list.

4B1. I used the number of invasive alien species (species richness) in the watersheds to quantify the potential risk that each watershed poses to the lower river reaches. The best measure for this would be the abundance of species in the watersheds, but I did not have this data available. My rationale was that the higher the alien species richness in a watershed, the more likely the watershed could act as a source of propagules to initiate an invasion downstream.

4B2. I assessed the number of watersheds each major invader could potentially invade. Assessing the potential distribution of invasive species can be problematic because invasive species are seldom in equilibrium with the environment (Rouget *et al.* 2004, Jimenez-Valverde & Lobo 2006). Nevertheless, climatic envelope modelling provides a useful tool to assess potential distribution of a species. I rescaled the potential distribution of species to quaternary watersheds. Using existing models for predicting the potential distribution of invasive plants in South Africa (Rouget *et al.* 2004) I determined the potential distribution of the 79 major invaders with a variant of climatic envelope models (CEMs) based on the Mahalanobis distance. To further explain and determine the potential distribution of the species in the watersheds, I derived potential species richness for all alien species. This was done by determining whether a potential invader could invade a given watershed. After evaluating the distribution maps for a number of species, I decided to use a 10 % rule to determine whether the species would fall into a particular watershed. Where the species was observed to potentially invade ≥10 % of the area of the watershed, the species was recorded as present in that watershed (Rouget *et al.* 2004). I was then able to assess potential species richness per watershed and the number of watersheds invaded by each species.

Table 2.2: Species richness of major invaders (i.e., widespread alien plant species or invaders that occur in dense stands) for each of the three alien plant management zones in Kruger National Park (KNP).

Zone	*Distribution*[A]	*KNP presence*[B]	
		Yes	*No*
Within KNP[C]	Localized	41	-
	Widespread	5	-
Transition[D]	Localized	25	17
	Widespread	17	0
Upper basin[E]	Localized	25	17
	Widespread	18	5

[A] Localized if the species occurred in < 50% of the watersheds within the particular zone.

[B] The number of species recorded in KNP according to Foxcroft *et al.* (2003).

[C] 'Within KNP' refers to the zone that is included within KNP

[D] 'Transition' refers to the zone where the KNP boundary falls within the particular watershed

[E] 'Upper basin' refers to the uppermost watersheds in the river system, bounded by the top of the tertiary watershed.

Results

Species risk category

I recorded 231 species in the domain: 191 species in the upper basin, 165 in the transitional zone, and 97 in KNP. Seventy-nine species were major invaders. Seventy-two, 66, and 45 species occurred in each zone respectively.

Within KNP (Table 2.2) most species were still localized (e.g., giant reed, *Arundo donax* L. and bugweed, *Solanum mauritianum* Scop.), and a small number were widespread (e.g., lantana, *Lantana camara* L. and castor-oil plant, *Ricinus communis* L.). Of the 79 major invasive species, 45 occurred in KNP. In the transition zone only 17 species were not recorded in KNP (e.g., black wattle, *Acacia mearnsii* De Wild.), whereas 42 species were present. A similar pattern held for the upper basin, with only 22 species not yet in KNP and 43 species present in KNP.

Watershed risk index

The high species richness in the upper basin (192 species) represented a substantial source of invasion for KNP (Fig. 2.3a). The invasion of the upper basin and transitional zone appeared to be substantially worse than in KNP, but with pathways of spread linking these areas with KNP (Fig. 2.3a, b & c). There are two main pathways of spread into KNP. In the central part of the domain the Letaba and Olifants river systems provide the links, and in the southern parts the links are provided by the Sabie and Crocodile rivers. In the northern part of the domain, the link between the upper catchments and KNP via the Luvuvhu and Limpopo rivers appears to form a less important conduit (Fig. 2.3b & c). City and town development, commercial plantation forestry, and the associated transformation of natural vegetation appear to have taken place later in comparison with the more developed southern region. Also, the region through which the Limpopo and Luvuvhu rivers flow is more arid than farther south; thus, the invasion is still at an early stage and less pronounced. However, the distribution of major riparian weeds (Fig. 2.3c) along the corridor suggests that some species have the ability to overcome these potentially limiting barriers and become just as important in linking KNP to the upper basin.

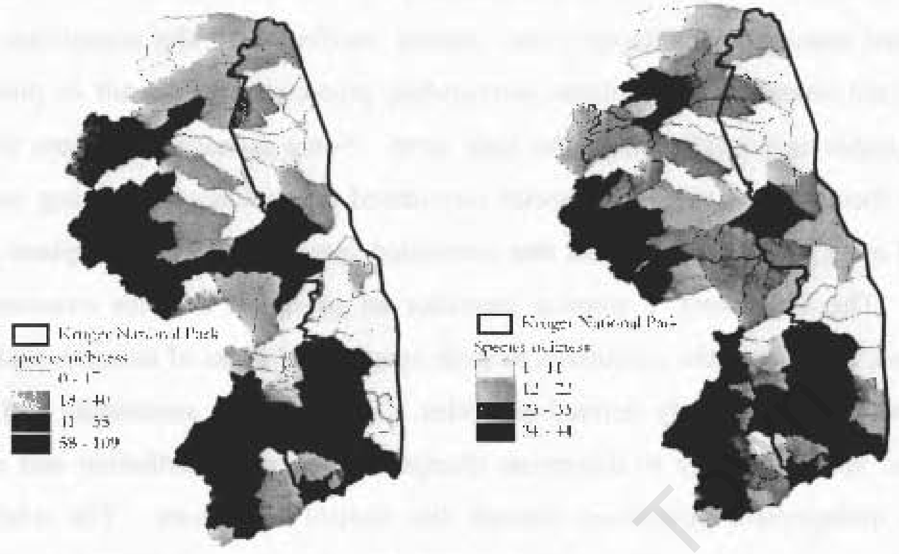
The predicted species distribution map (Fig. 2.3d) indicates the ability of major riparian species to spread across KNP should they be transported down the rivers. This distribution also places the likely source for propagules closer to KNP.

In the linear regression between mean annual runoff and species richness, I found a significant (P=5.045e-008) but relatively weak correlation (multiple R^2 = 0.2217) between riparian species richness and mean annual runoff. Therefore, although there is a significant relationship, the relatively weak correlation cannot simply be used as a predictor of plant invasion along rivers for management purposes.

Based on my assessment, the following management recommendations can be made. Species localized in the upper basin and transitional zone, but are not yet present in KNP, should be targeted for eradication. This includes for example, pom pom weed (*Campuloclinium macrocephalum* [Less.] DC.), inkberry (*Cestrum laevigatum* Schlehtd), and pepper tree (*Schinus molle* L).

Species widespread in the upper zone and only occurring occasionally in the transition zone and not yet recorded in KNP, such as black wattle, should be eradicated immediately when detected in KNP, contained where it occurs in the transitional zone and managed at acceptable levels in the upper zone.

Within the KNP, widespread species, such as lantana and castor-oil plant should be managed at acceptable tolerable levels. Localized species such as parthenium (*Parthenium hysterophorus* L.) and giant reed must at minimum be contained in the present sites, and eradicated where feasible. This will mainly depend on the area of the invasion of the specific species. Chromolaena might also be considered in this context, but the species level assessment of the framework categorizes chromolaena as a major invader, warranting 'species specific' targeted action.



a) all invasive species

b) all riparian invaders

c) major riparian invaders

d) major riparian invaders (predicted)

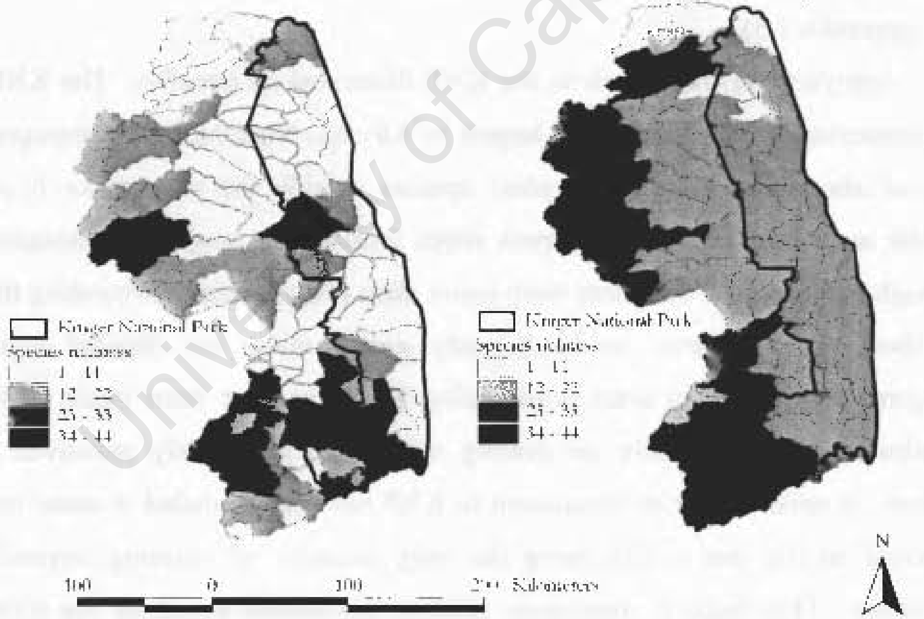


Figure 2.3: Watershed-risk index: the potential risk that each watershed poses to the lower river reaches, based on species richness of (a) all invasive alien species (based on 231 species), (b) riparian invasive alien species (based on 185 species), (c) major riparian species (based on 55 species), and (d) predicted distribution of major riparian species (based on 79 widespread alien plant species or invaders that occur in dense stands).

Discussion

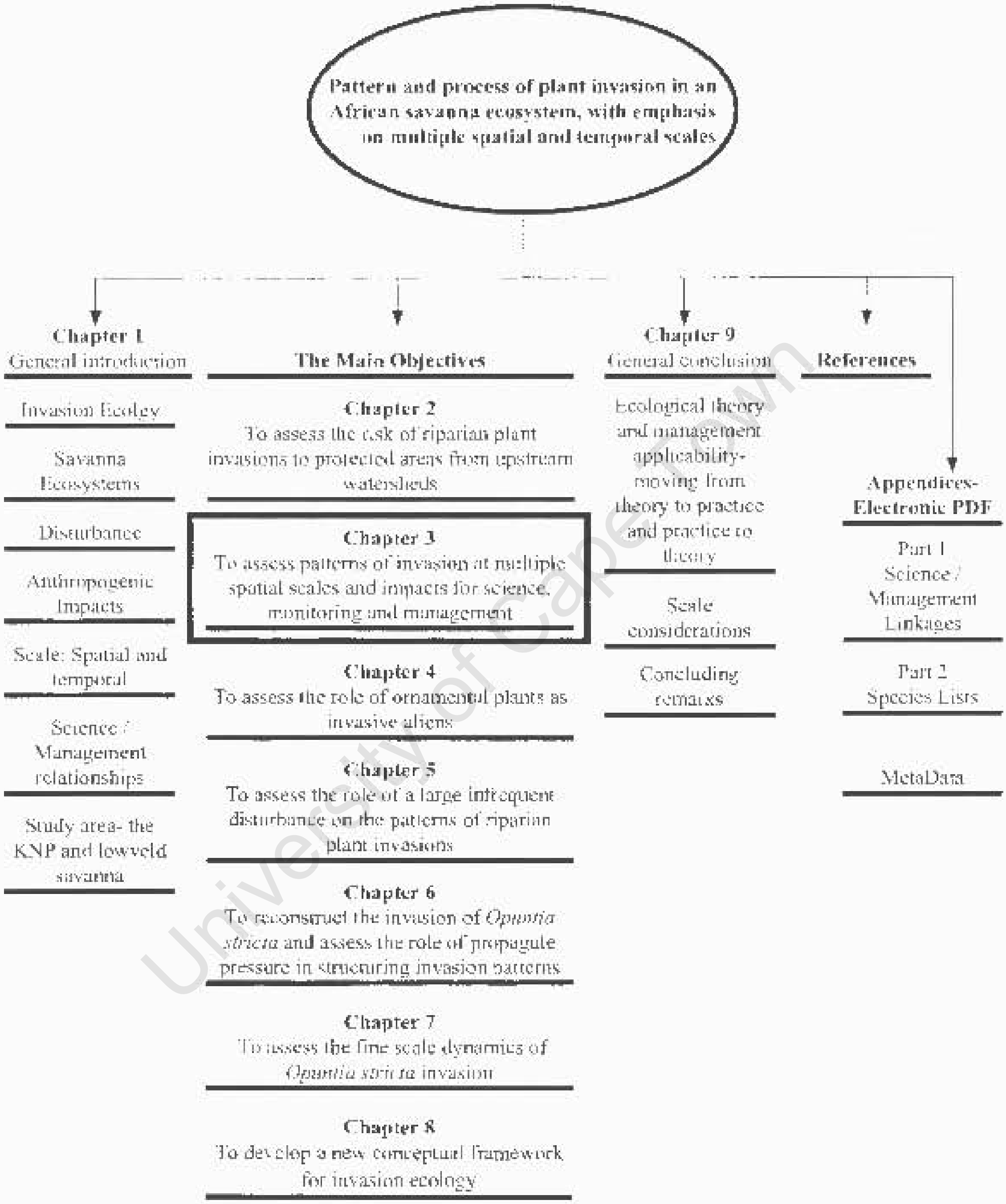
Protected areas are influenced substantially by threats beyond their borders, and traditional management strategies are usually ineffective. The complicated land-use pattern and enormity of problems surrounding protected areas result in plans that are unsustainable and inefficient in the long term. Some management plans for invasive species focus on one or a few species considered particularly threatening, neglecting a suite of other species and the fact that controlled species are likely to replace other alien plants. The framework I propose provides an objective tool for overcoming these problems, organizing the evaluation of both species and areas of concern, and providing managers with objectively defined priorities. This is a first assessment and should be followed up periodically to determine changes in species' distribution and abundance, and as management progresses through the control operations. The whole process requires ongoing monitoring and adaptation to changing conditions, as is currently applied in KNP's strategic adaptive management process (Freitag-Ronaldson & Foxcroft 2003, appendix 1.3).

Applying the framework to the KNP illustrated its benefits. The KNP is a very large conservation area (one of the largest in Africa). Nonetheless the topography, land-use, and abundance of invasive plant species outside the park make it essential to consider areas upstream from the park when formulating long-term management plans. Although it is accepted that there were many alien plant species surrounding the park and that these pose a threat to biodiversity conservation, no detailed evaluation of management priorities in areas surrounding KNP has ever been made. Management activities have focused only on dealing with species currently perceived as serious invaders. A small buffer zone adjacent to KNP has been included in some management operations in the past - this being the only example of working beyond the KNP boundaries. This focus is inadequate because the threats posed by the distribution of alien plant species in the broader watershed areas are not considered. The transition zone requires substantially more attention to lessen the effects of future invasions. For example, 17 species not yet recorded in KNP are still localized and should be targeted for management. Twenty-two invasive species that occur in the upper basin are not yet present KNP. Seventeen of these 22 are localized, and all efforts should be made by the provincial authorities to target these species.

River corridors provide links between the heavily invaded upper basin and the largely un-invaded lower reaches of the watershed. These corridors facilitate the spread of invasive species throughout KNP and warrant targeted and specific action. The riparian areas are also reasonably well delineated, requiring only a narrow zone parallel to the river to be considered in clearing efforts, providing species have not yet moved into the broader landscape. However, where the plants have already spread into the broader landscape, the assessment of plant distribution in the quaternary watershed provides good management unit boundaries for plant control operations.

What does the framework provide beyond traditional approaches to invasive species management? First, the framework assists in objective prioritization of species and areas, based on the current and future potential threat of invasion. This means planning is based on invasiveness, rather than according to frequently used criteria such as resources, funding, and logistical considerations. Second, separating the area- and species-led approaches is often based on managerial bias, experience, and knowledge of species and systems because the approaches are seen as mutually exclusive. I see the two aspects as complementary and integrated. Finally, the framework guides the assessment of management priorities in a logical and structured way and provides insights into the problems and solutions to managing alien plant invasions in a large landscape, in a clear, meaningful manner.

Depending on the scale and extent at which spatial data on alien plant invasions are evaluated, substantially different perspectives are gained; this has implications for understanding ecological processes, for management applications, and for defining effective monitoring strategies. Quarter-degree grids and quaternary watersheds are most useful at a regional or national scale. Grid cells of 1 to 5 km in size are generally useful for guiding priorities and planning management interventions. Fine scale data are useful for management areas which are small in extent, but provide good detail with which to assess patterns and rates of invasion.


Pattern and process of plant invasion in an African savanna ecosystem, with emphasis on multiple spatial and temporal scales
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Savanna Ecosystems
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Introduction

The negative impacts of biological invasions are among the foremost concerns facing conservation managers (Mooney *et al.* 2005). In an effort to provide strategic direction to management interventions, much emphasis is placed on the collection of spatial data (Ewel *et al.* 1999, Wittenberg & Cock 2005, Hulme 2003, Dark 2004, Guisan & Thuiller 2005). Unfortunately, in many cases insufficient attention is given to how the data is to be used (Pyšek & Hulme 2005). The result is that the spatial resolution and scale of data collection may be inappropriate for particular uses.

Although plant ecologists have recognized the importance of sampling scale in their descriptions of dispersal or species distributions (Wiens 1989), with much attention being paid to scale in understanding rarity (Hartley & Kunin 2003), invading plants pose further complexity. Consequently, far less attention has been given to scale issues in understanding invasiveness (but see Higgins, Richardson & Cowling 1996).

Invasions (range expansion) are in many respects the opposite of rarity (range contraction; Van Kleunen & Richardson 2007). Considerable insights for allocating conservation priorities have emerged from studies of scale dependency of rarity and extinction risk (Hartley & Kunin 2003). Similar insights are needed for managing invasive species, where management options depend on various features in the range structure, some of which may only be detected at a certain grain.

It may be argued that the reason invasions pose additional layers of complexity to understanding spatial patterns is that most alien plants are still in the process of spreading and have not sampled the full range of available habitats (Rouget *et al.* 2004, Wilson *et al.* 2007). Few studies have studied the processes and patterns of invasion from the initial founder population to the point where all available, susceptible habitats have been sampled (Pyšek & Hulme 2005). Further, only 10% of studies focus on the initial stages of dispersal while the remainder focus on widespread and advanced invasions (Puth & Post 2005). Invading plants also have spatial and temporal dynamics that are difficult to predict (Pyšek & Hulme 2005), frequently expanding their distribution from extremely low numbers of source populations, often through rare dispersal events (Puth & Post 2005). However, the ability to predict ecological phenomena such as patterns of alien plant distribution, and thus infer ecological processes (Turner 1989), depends on the relationship between spatial and temporal scales of variation (Wiens 1989). With an increase in spatial scale, the time scale at which important processes operate is slower, time lags increase, and indirect effects become increasingly important. Further, understanding patterns of invasions is also a function of both the extent and grain of the investigation (Wiens 1989). Extent refers to the overall area of the investigation, while grain refers to the individual units of observation (grid cells; Turner *et al.* 1989). Therefore, the various components of the scale (time, extent and grain) of the investigation determine the range of patterns that detected and the explanations provided.

Studies on biological invasions that integrate across different scales are rare (Pyšek & Hulme 2005) because of the difficulty of collecting sufficient data over a sufficiently large area, and to capture infrequent, long-distance dispersal events, with which to explore these problems (see also Richardson, Rouget & Rejmánek 2004). Invasive species rarely disperse across the landscape in a continuous front (Pyšek & Hulme 2005), and opportunistic dispersal events, or secondary invasion foci are frequently disproportionally important in driving spatial expansion (Chapter 6). If distributions are mapped at fine grain, such small outlying patches, which may be important invasion foci, can potentially be identified, whereas at a coarse grain such crucial resolution is lost (Wiens 1989, Rouget & Richardson 2003). Although much information is available at different spatial scales, there is no obvious way for insights to be readily transferred from one spatial scale to another. Consequently, such collections of information are of limited use to managers, planners and policy makers (Rouget & Richardson 2003, Barnett *et al.* 2007).

Unfortunately there are few areas which lend themselves to assessing plant invasions at multiple spatial scales. This is because most systems are fragmented, with complicated patterns of anthropogenic influence which substantially increase the complexity of understanding invasions through affecting the distribution patterns of plants. Therefore large protected areas provide a useful arena in which to test the problem of scale generally (Turner *et al.* 1989), and in understanding invasions (Vitousek *et al.* 1996). However, few areas have been suitably mapped at a sufficiently fine grain, over a large extent. I thus propose that this paper is uniquely positioned to explore the pattern and scale issues of invasive alien plants, for a number of reasons. I use a dataset from the Kruger National Park (KNP), one of the largest national parks in the world that is actively managed for biodiversity conservation, and for which I have a spatially explicit dataset for nearly 27,000 alien plant records over an area of nearly 20,000 km^2. I believe that combining this data, with the setting and inherent attributes of KNP, provided me with an excellent opportunity to explore these issues. I suggest that only by carefully assessing spatial patterns of plant invasion at scales ranging from a plot to the landscape and to the region can we understand the full range of processes that interact to structure the distribution of invading plants (Rouget & Richardson 2003, Richardson, Rouget & Rejmánek 2004). Further, effective management of plant invasions demands accurate spatial data on the overall distribution within an area, the patterns of presence/absence and abundance across the area, and the co-occurrence with other invasive species. Such information is crucial for planning management interventions, setting realistic targets, and to monitor the success of control operations.

My aims were therefore to assess the implications of scale in developing an understanding of the distribution of IAPs (Invasive alien plants), to 1) propose important features of scale that need forethought in collecting and managing invasive alien plant data for holistic management interventions, and 2) assess whether I could determine the minimum grain of data that is required to fulfil the above requirements.

Materials and Methods

Study area and priority species

Protected areas are habitat islands: natural landscapes and habitats surrounded by various culturally modified systems (Pickett & Thompson 1979). KNP (Fig. 3.1a), while a large protected area, is thus functionally a habitat island. KNP also shares the increasing global concerns over invasive alien species (IAS; Rejmánek *et al.* 2005), to the point where IAS are now regarded as one of the greatest threats to the biodiversity of the park (Freitag-Ronaldson & Foxcroft 2003, appendix 1.3). A number of pathways of plant invasion have been described in detail for KNP specifically, including rivers (Chapter 2) and intentional introductions for ornamentation in staff villages and tourist accommodation (Chapter 4). In other protected areas, vehicles (Lonsdale & Lane 1994) and roads (Bennet 1991, Gelbard & Belnap 2003) have also been shown to be important pathways of invasion. Both are implicated in the spread of invasive species in KNP (Freitag-Ronaldson & Foxcroft 2003, appendix 1.3) but have not been studied in detail.

KNP is situated in the mid-reaches of seven extensive drainage systems (namely the Limpopo, Luvuvhu, Shingwedzi, Letaba, Olifants, Sabie, Crocodile Rivers), flowing from the higher lying reaches in the west, to Mozambique in the east. All the watersheds are invaded to some extent, with 192 invasive alien plant species being recorded in the upper watersheds of KNP (Chapter 2). To date 372 alien plant species have been recorded in KNP (Foxcroft *et al.* 2003, appendix 2.3), including ornamental aliens, ruderal species and widespread invasive aliens.

While management has evolved and priorities have changed over time (see Foxcroft & Freitag-Ronaldson 2007, appendix 1.9, for a synopsis), recent efforts have focused on chemical and later biological control of *Opuntia stricta* (Haw.) Haw. var. *dillenii* (Ker Gawl.) L. D. Benson (Cactaceae; sour prickly pear), mechanical/chemical control of riparian species (such as *Lantana camara* L.; Verbenaceae; common lantana), and removal of ornamental alien plants in staff and tourist villages. Although good progress has been made, if KNP is to be successful in the long-term, a more holistic, proactive approach is required. Hopefully, the sentiments embodied in the objectives that have been developed for KNP (KNP 2005, appendix 1.5), and which include best practice theory (Wittenberg & Cock 2005) and ecological understanding (such as gained from these insights), will provide a framework to achieve this.

Data collection

Alien plant records and distribution data have accumulated over a long period and from several different sources. The first seven records of alien plants in KNP were made in 1937 (Obermeijer 1937). Although early records were accompanied by general descriptions of localities, the advent of increasingly accurate Global Positioning Systems (GPS) has led to increasingly precise locality data. The three main sources of data are: (1) the records of the KNP alien biota section (Fig. 3.1b); (2) a species-specific (*Opuntia stricta*) data set (Fig. 3.1c); and (3) a large set of locality-precise data collected by park rangers on their patrols (CT: Fig. 3.1d and Table 3.1). The data from the KNP alien biota section comprise mainly *ad hoc* records collected during various field trips and from herbarium and other records. The species-specific distribution data on *O. stricta* was collected over the entire range of that species in KNP, to guide management strategies (Foxcroft *et al.* 2007a,b) and for research on the spread dynamics of the species (Chapter 6). The CyberTracker system (see http://www.cybertracker.org) was developed for application in conservation management, as a user-friendly interface for PalmOS computers linked to GPS units (see also DiPietro *et al.* 2002, McNaught *et al.* 2006). The system allows personnel (including semi-literate field workers) to record customized observations with GPS co-ordinates. The potential use of the CyberTracker system for collecting ecological data in KNP was recognized in 2000 and the system was incorporated into KNP procedures for testing and further development. Up to 120 CyberTracker units are currently deployed on daily patrols across the KNP. Observations, including animal and plant sightings, water and fire management records and other types of data are recorded on each patrol. Rangers then email data files to the central KNP Geographic Information Systems (GIS) Lab where the data are collated, cleaned, summarized and made accessible to users. The KNP CyberTracker data currently comprises over 1.9 million records collected between 2004 and 2006. Almost the entire KNP has been sampled at least once, with priority areas (in terms of rangers patrol requirements) being sampled much more often (Fig. 3.2).

Table 3.1: Sources of alien plant distribution data for the Kruger National Park

Source database	Number of records	Number of alien species	Years covered	Data type	Method of collection
KNP CyberTracker	2982 (pres) 1965910 (abs)	8[#]	2004-2006	P/A	GPS/Palm (CyberTracker); ranger patrols
Opuntia stricta	19849	1	2000-2003	P	GPS/Palm (CyberTracker); GPS records manually captured. Systematic survey, described in Foxcroft *et al.* (2004)
General IAS	4118	162[#]	1974-2005	P	GPS records manually captured. *Ad hoc* data from KNP alien biota section, herbarium, rangers, field guides. Some of this data is described in Foxcroft *et al.* (2003)

[#] includes some "spp" records, for example "*Opuntia* spp."

Data type - whether data includes presence and absence points or presence records only

Table 3.2: Summary of attributes per grid cell size. There are a total of 26,949 alien plant records and 1,965,910 absence points for the KNP.

Cell size (km)[1]	Cell area (km^2)	Total number of cells in KNP	% of cells invaded	% cells occupied by 4 main species[4]	Mean (Max) species richness / cell	StdDev species richness / cell	Mean number records / cell (incl. absence)
0.1	0.01	1904673	0.41	0.33	0.005 (23)	0.08	1.03
0.25	0.06	306222	1.35	0.99	0.02 (23)	0.2	5.20
0.5	0.25	77162	3.11	2.00	0.04 (23)	0.3	25.48
1	1	19602	7.18	4.12	0.1 (24)	0.7	100.29
2	4	5053	16.03	8.41	0.4 (31)	1.4	389.06
5	25	872	41.97	20.07	1.5 (49)	3.8	2254.48
QW[2]	ave 551	49	91.84	81.63	12.8 (71)	13.4	38263.76
QDS[3]	675	51	90.20	72.55	11.4 (72)	13	39905.86

[1] Cell size- indicates the length of the cell side. for example 1 x 1 km

[2] QW- Quaternary watershed (quaternary watersheds are nested subdivisions within primary, secondary, and tertiary watersheds and are used for regional-scale planning for many environmental initiatives in South Africa, such as the national Working for Water programme which is responsible for invasive alien plant control. The average size of the QW in the KNP is 551 km^2 (Chapter 2)

[3] QDS- Quarter-degree square (15′ latitude × 15′ longitude, representing roughly 25 × 27 km at the latitude of the study area, Rouget *et al.* 2004)

[4] The four most abundant species (number of records) in the KNP include *Opuntia stricta* (20029 records), *Lantana camara* (2059 records), *Chromolaena odorata* (302 records) and *Parthenium hysterophorus* (204 records).

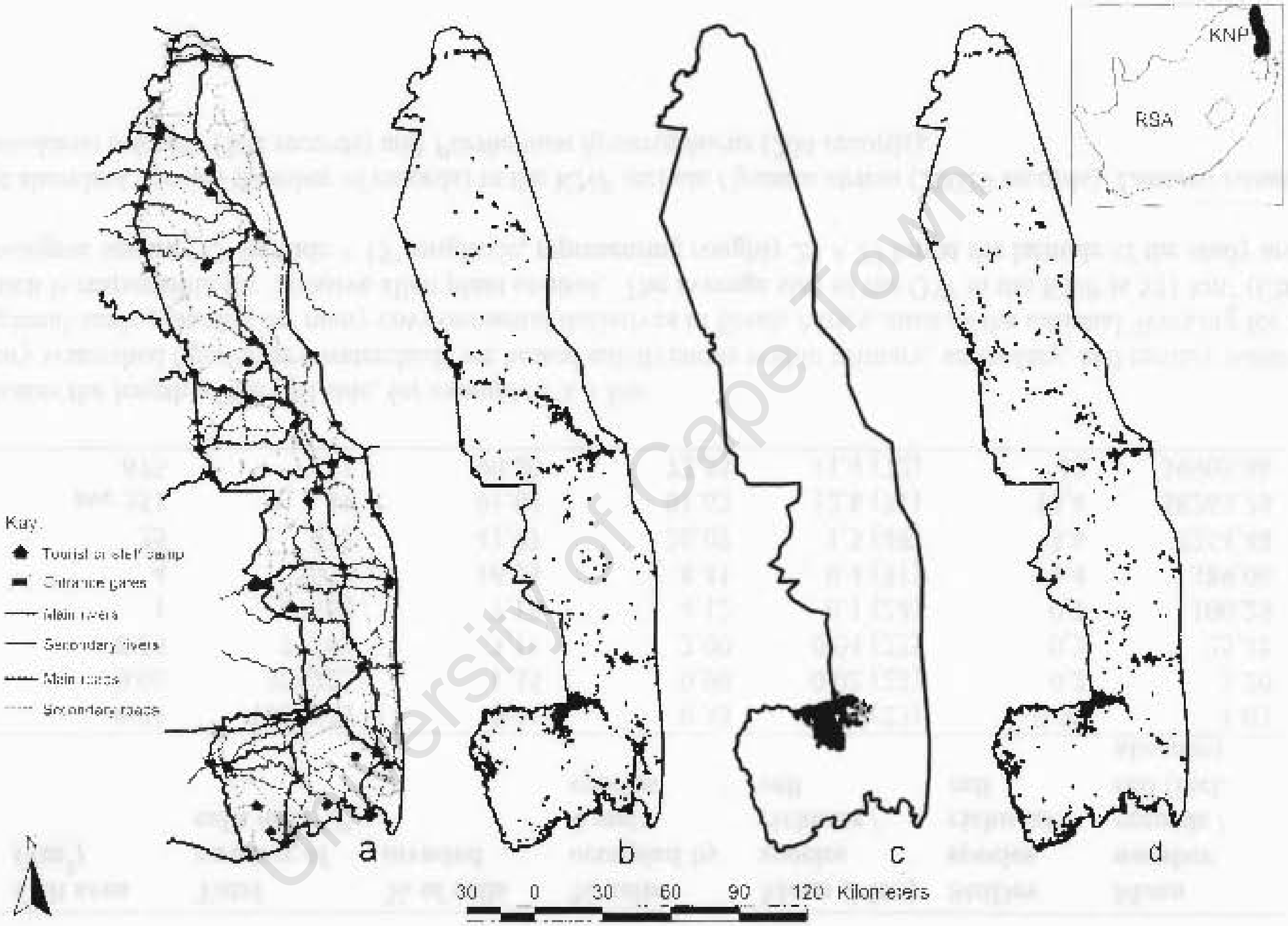

Figure 3.1: Sources of alien plant distribution data; (a) in relation to KNP infrastructure and rivers, (b) KNP alien biota section alien plant distribution data, (c) *Opuntia stricta* distribution data, and (d) alien plant distribution data from the CyberTracker programme. The insert places KNP in relation to the rest of South Africa.

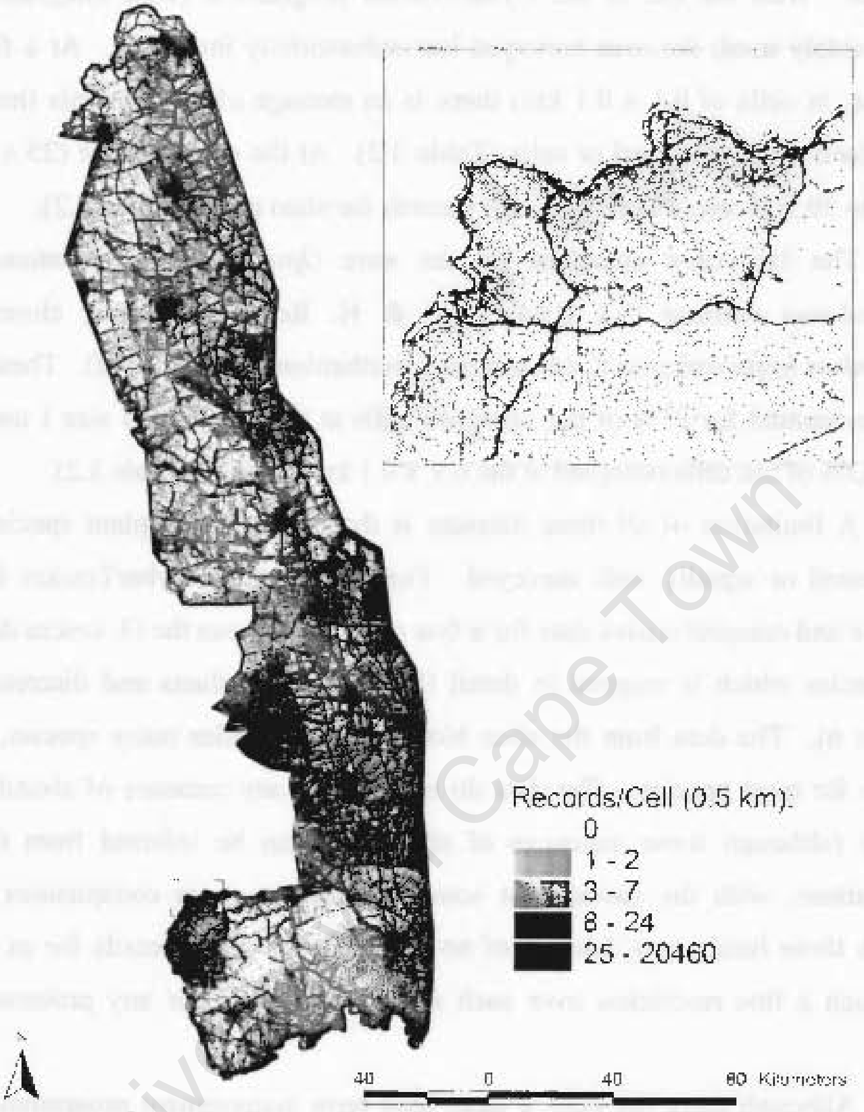

Figure 3.2: Distribution of KNP CyberTracker data plotted as records / 0.5 x 0.5 km cell. This data is collected by KNP rangers, on aspects such as water, fire and poaching management (amongst others), and are used as absence (null) records for assessing alien plant distribution. The insert shows a detailed view of the point records.

The combined alien plant distribution data amounts to 26,949 records (Table 3.1). Although the data includes 162 species, 70% of the records are for a single species, *Opuntia stricta*, which was systematically collected for a specific purpose (Chapter 6). The earliest records with detailed locality data date from 1974 (*Salvinia molesta* D.S. Mitch., Salviniaceae, Kariba Weed), while most of the data was collected from 2000 onwards. With the use of the CyberTracker programme (with integrated GPS units) being widely used, the area surveyed has substantially increased. At a fine grain (for example, in cells of 0.1 x 0.1 km) there is an average of 1.03 records (null records for alien plants) per watershed or cells (Table 3.2). At the coarser scale (25 x 27 km) there are up to 39,900 records per cell (null records for alien plants; Table 3.2).

The four most abundant species were *Opuntia stricta*, *Lantana camara* L., *Chromolaena odorata* (L.) R.M. King & H. Rob (Asteraceae, chromolaena) and *Parthenium hysterophorus* L. (Asteraceae, parthenium) (Fig. 3.3a–d). These four species alone accounted for 81% of the occupied cells at the largest cell size I used (551 km^2), and 0.33% of the cells occupied at the 0.1 x 0.1 km cell size (Table 3.2).

A limitation of all three datasets is that not all alien plant species are equally represented or equally well surveyed. For example, the CyberTracker has extremely accurate and comprehensive data for a few species, whereas the *O. stricta* data focuses on one species which is mapped in detail (i.e. individual plants and discrete patches, see Chapter 6). The data from the alien biota section includes many species, but with few records for most species. The data do not include any measure of abundance for each locality (although some measures of abundance can be inferred from the density of observations, with the caveat that some species are more conspicuous than others). Despite these limitations, I know of no other dataset with records for as many species with such a fine resolution over such an extensive area for any protected area in the world.

Although there has been a large long-term management programme (Foxcroft & Freitag-Ronaldson 2007, appendix 1.9), no populations of alien plants are known to have been eradicated. In the best-case scenario, some alien plant populations have been reduced in abundance / density. I am therefore confident that the data is representative of the real situation in KNP and that ongoing clearing programmes have not had a substantial influence on the distribution patterns.

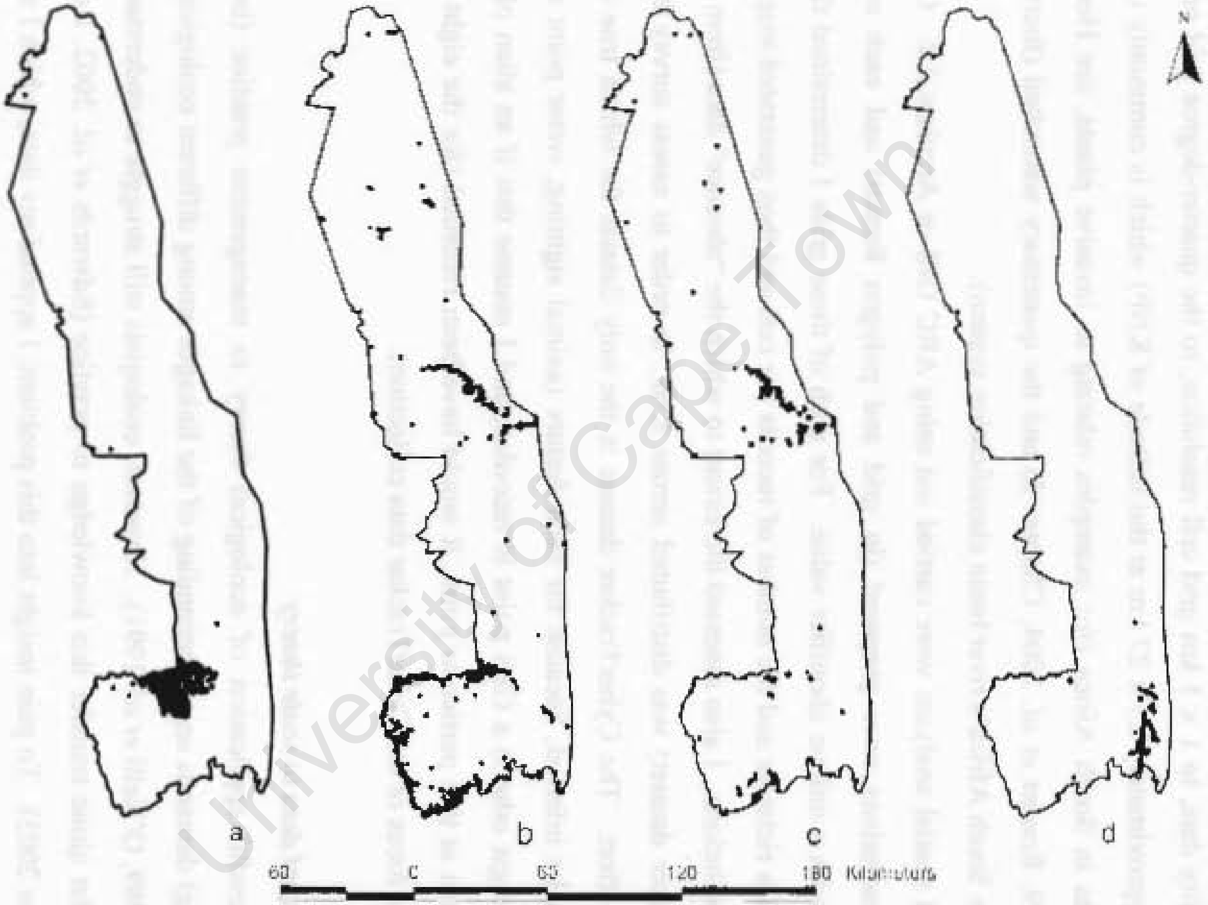

Figure 3.3: The distribution of the four most abundant alien plant species in KNP; (a) *Opuntia stricta*, (b) *Lantana camara*, (c) *Chromolaena odorata*, and (d) *Parthenium hysterophorus*.

Mapping alien plants at multiple spatial scales

As I was interested in understanding perspectives of alien plant invasions at various scales and making recommendations for management and monitoring, I mapped the alien plant species distribution at nine different levels of grain (Table 3.2). This ranged from point locality data, to 1 x 1 km grid cell resolution, to the quarter-degree grid reference system (approximately 25 x 27 km at the latitude of KNP) which is commonly used for survey data in South Africa (for examples relating to invasive plants, see Henderson 1998, 1999, Rouget *et al.* 2004, Chapter 2) and the quaternary watershed (fourth level category in South Africa's river basin classification system).

All spatial analyses were carried out using ARC GIS or Arcview 3.2. Grids of various resolutions were prepared (in grid and polygon format) and each cell was provided with a unique identifier value. For each of these grids I determined the alien plant species richness and the number of records per cell and then generated maps at the various resolutions. I also assessed the extent to which the "absence" data (from the full CyberTracker dataset) was distributed across KNP, in order to assess survey bias and sampling effort. The CyberTracker dataset is the only dataset for which true absence points can be inferred, because for each feature (animal sighting, water point and fire scars, amongst others) a GPS point is recorded, and I assume that if an alien plant had been present at that particular point, it would have been recorded (for the eight species that are the focus of the CyberTracker data collection).

Applying real data to scale theory

The successful application of ecological theory to management practice (including monitoring) demands an understanding of the linkages among different ecological scales (Wiens 1989, O'Neill *et al.* 1991). However, ecologists still struggle to understand these linkages, let alone transfer this knowledge to practice (Edwards *et al.* 2002, Rouget & Richardson 2003). To gain insight into this problem, I applied my data, which I assessed at nine different scales, to the hierarchical patch dynamic model of Kotliar & Wiens (1990). This model was developed to provide a framework for classifying patch structure across a range of scales. Although the model was explored using foraging theory as an example, it is abstract enough so that the principles can be applied to other areas of ecology. I randomly selected one quaternary watershed with high alien species richness and one quaternary watershed with low species richness, with which to contrast insights gained from assessing the different scales. Within each of these units one cell at a finer scale was selected, for both high and low species richness respectively. I then discuss the implications for understanding ecological processes in the invasion process, managing and monitoring plant invasions.

Results

Mapping alien plants at multiple spatial scales

A frequency distribution diagram (Fig. 3.4a–h) provides interesting insight into the pattern of species richness per cell. The quarter-degree cell and quaternary watershed scale (Fig. 3.4a and b), not surprisingly, show similar (normal) distribution patterns, as they are similar in extent (675 km^2 and 551 km^2, respectively). However, it is important to note that although the quaternary watershed scale varies slightly, it is more ecologically meaningful when considering functions related to rivers or riparian corridors. The 5 x 5 km cell, 2 x 2 km cell and 1 x 1 km cell (Fig. 3.4c–e) have similar shape distribution curves, while cells at the 0.5 x 0.5 km, 0.25 x 0.25 km, and 0.1 x 0.1 km resolution (Fig. 3.4f–h) have similar patterns. I thus infer that similar insights into understanding alien plant patterns may be gained from working at three broadly similar units, namely, 500–700 km^2, 1–25 km^2 and 0.01–0.25 km^2 (Table 3.2).

The range of cell sizes I selected corresponds to a substantial difference in the number of cells across the KNP. For example, at the 0.1 x 0.1 km cell size, there are 1,9 million cells in KNP, while there are only 51 cells at the scale of quarter-degree grid cells (Table 3.2). This corresponds to a range of 0.4% and 90% of the cells being invaded, respectively, substantially altering the perceived level of invasion across the landscape.

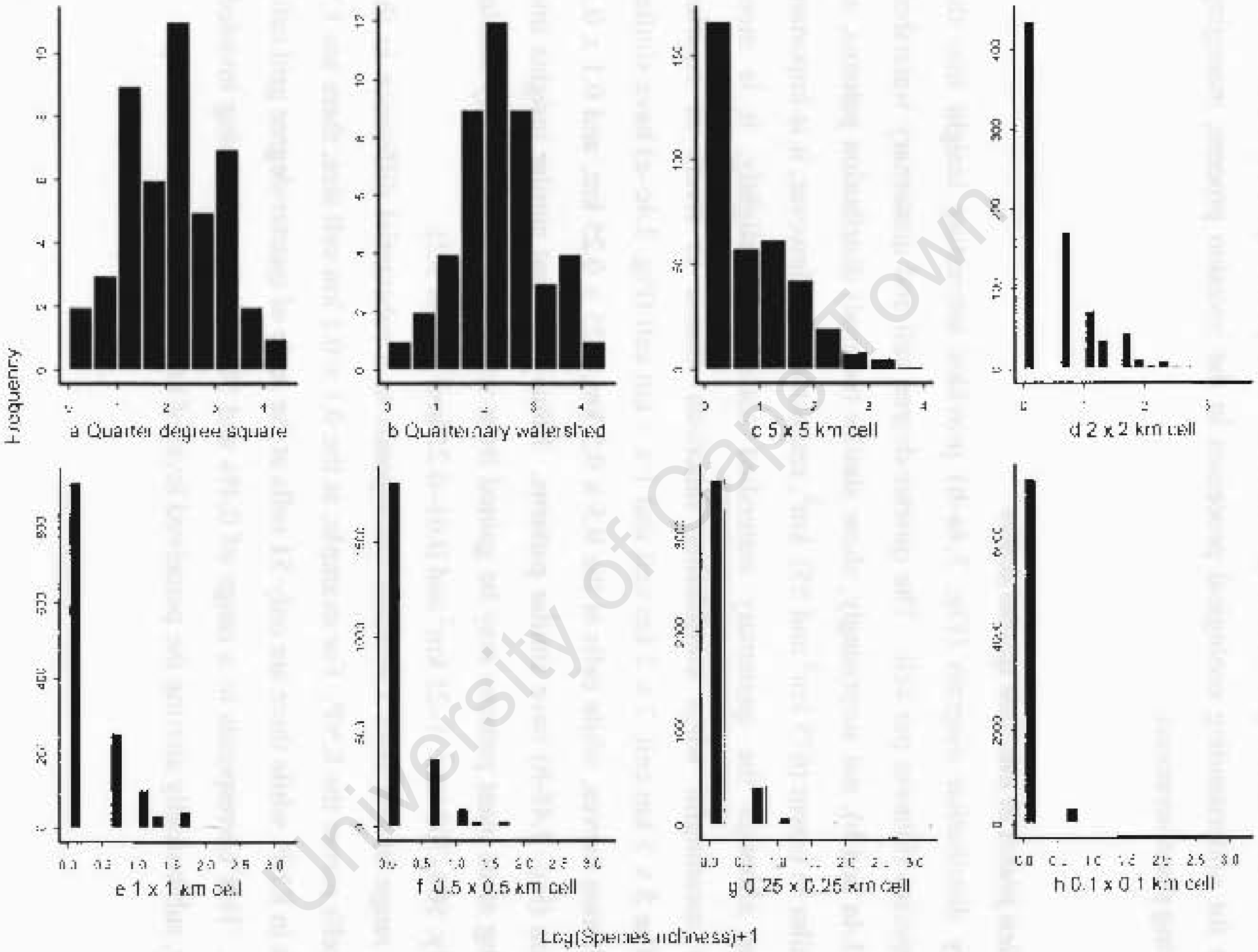

Figure 3.4: Frequency distribution of alien plant data in the Kruger National Park at eight scales of resolution.

The CyberTracker database presents an unparalleled spatial dataset, covering an extensive area. The full richness of the dataset will only emerge over time as the data is explored from a number of perspectives. I used the full dataset to represent absence (null) records for alien plants and to show whether there were any areas that had been substantially under- or over-surveyed. While there is an average of 39,000 records for the QDS scale, more importantly, there is a mean of 1.03 records per cell for the 0.1 x 0.1 km cell size (Table 3.2). This indicates that at the finest scale of resolution for which I evaluated alien plant richness data, that almost every cell was visited at least once.

I plotted the alien plant species richness for each cell size in order to assess the spatial patterns (Fig. 3.5–3.7). Although the pattern of invasion is similar across the 0.1 to 0.5 km scales (Fig. 3.5a–c), this differs substantially from those of 1–5 km (Fig. 3.6a–c), altering the perceived level of invasion in KNP. The level of invasion suggested by two vastly different scales, for example, 0.1 x 0.1 km cells (Fig. 3.5a) and 5 x 5 km cells (Fig. 3.6c), would leave the reader with the impression that the southern KNP is either hardly, or severely invaded. The loss of resolution is also clear as the size of the cells increase, loosing crucial information about specific outlying populations. Consider for example, the straight line of records running north-south in the south eastern KNP, where in Fig. 3.5a–c (0.1 to 0.5 km cells), the distribution of the patches is clearly distinguished, but completely lost in Fig. 3.6b–c (1 to 5 km cells).

Working at a scale of a quatemary watershed or quarter-degree cell (Fig. 3.7a–b) substantially altered perceptions of the level of invasion in the KNP, although the shape of the watersheds provides some insights into which river systems or catchments are priority areas generally. However, comparing the patterns in Fig. 3.7c and Fig. 3.5a clearly shows that much information is lost about the detailed nature of the invasion.

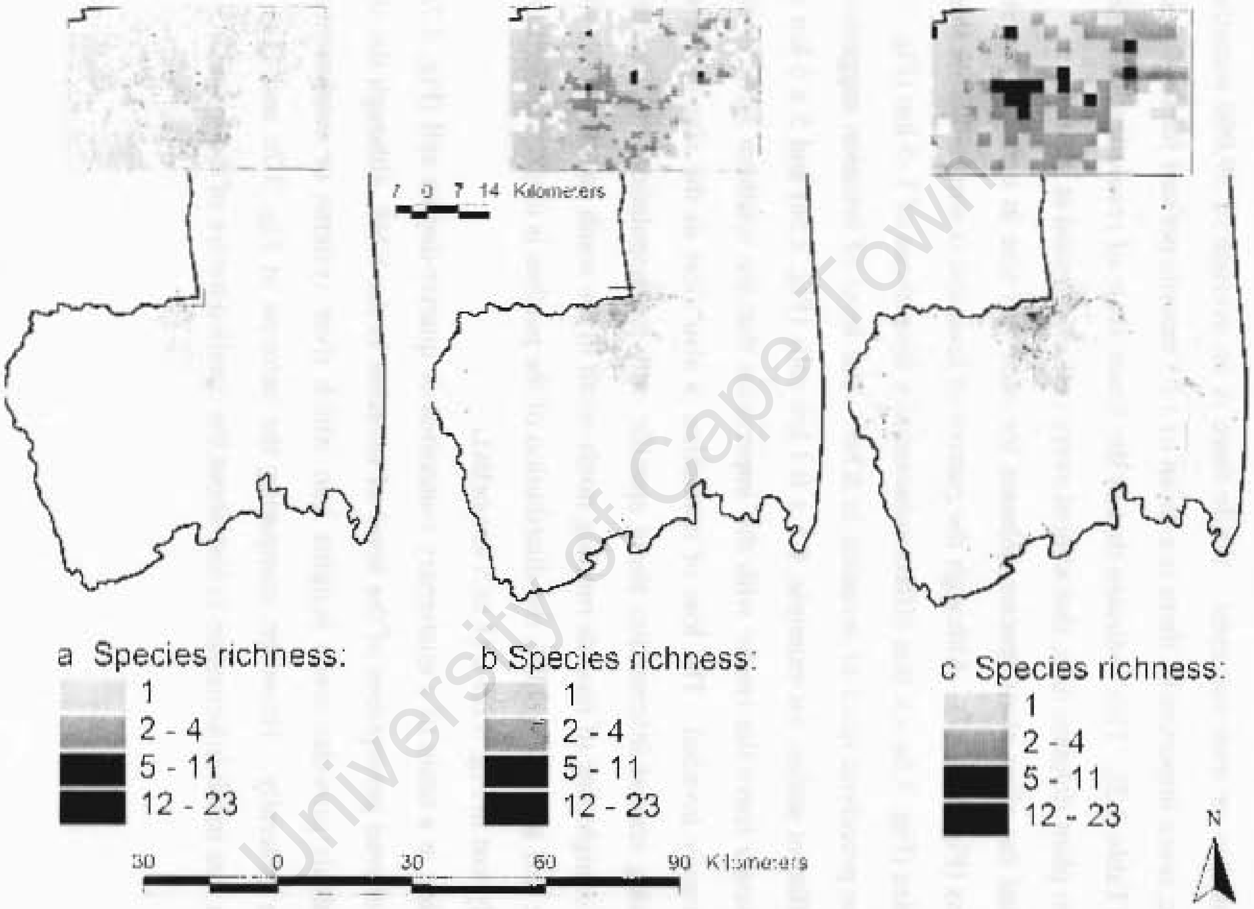

Figure 3.5: Alien plant richness data, for the southern Kruger National Park, at (a) 0.1 x 0.1 km scale, (b) 0.25 x 0.25 km scale and (c) 0.5 x 0.5 km scale. The inserts provide a more detailed view of the data for each scale.

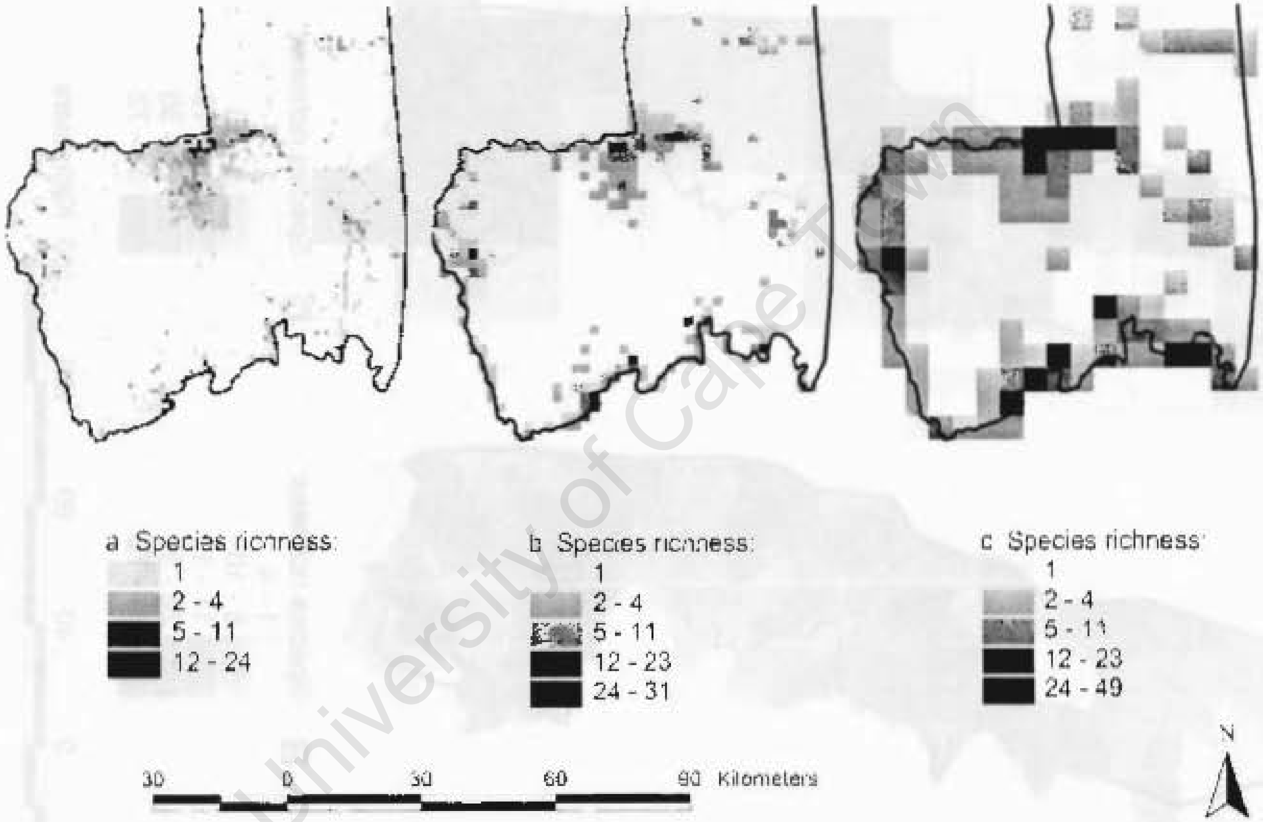

Figure 3.6: Alien plant richness data, for the southern Kruger National Park, at (a) 1 x 1 km scale, (b) 2 x 2 km scale and c) 5 x 5 km scale.

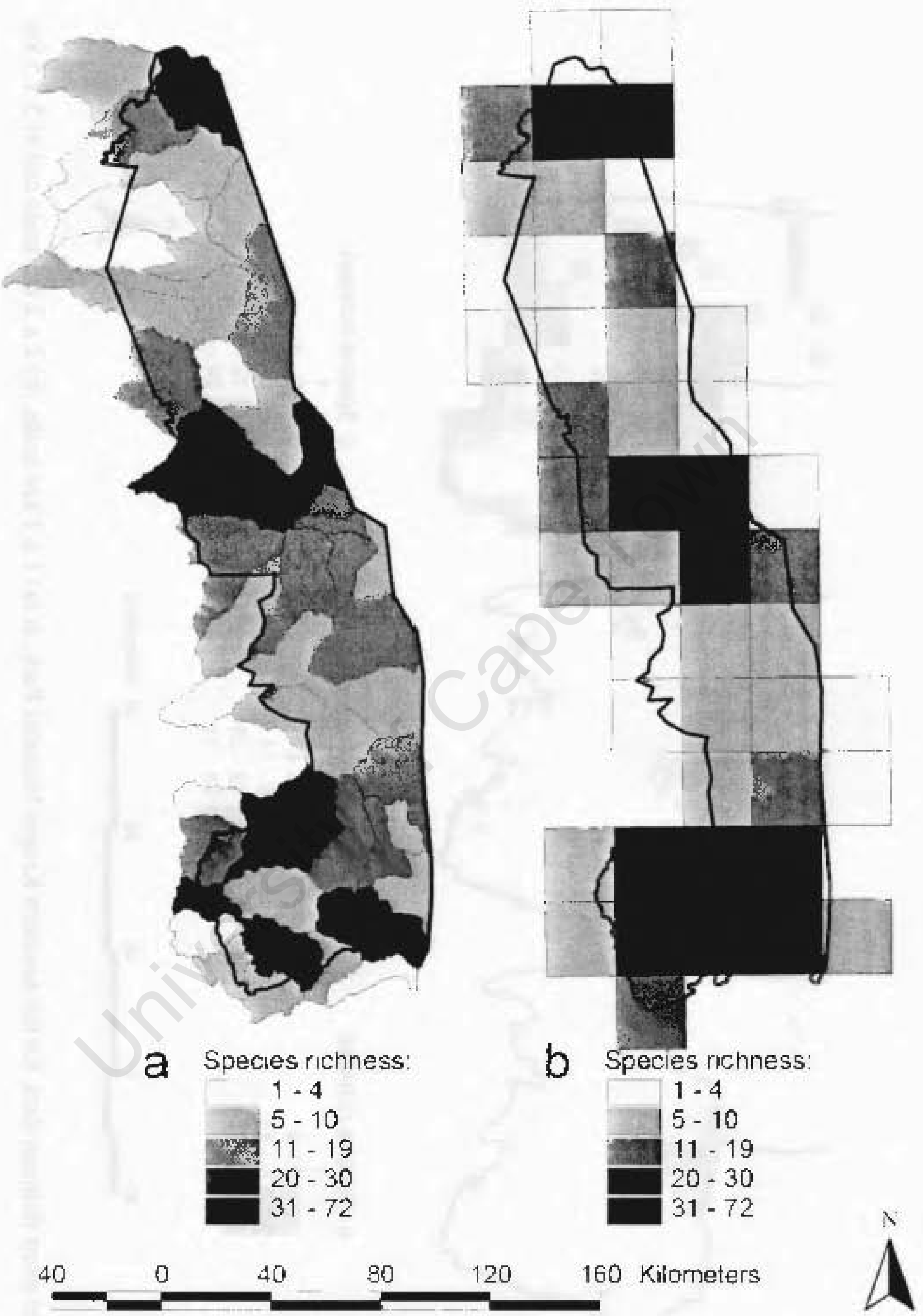

Figure 3.7: Alien plant richness data for the Kruger National Park, at (a) the quaternary watershed scale, and (b) the quarter-degree cell scale.

Applying real data to scale theory

By applying my alien plant distribution data to ecological theory (Kotliar & Wiens 1990), in which the various levels of grain are nested within each other (Fig. 3.8 and 3.9), I gained insights for three important aspects of plant invasions: ecological understanding, monitoring and management (Table 3.3). As each cell is sequentially examined at a finer scale, nested within the next, the usefulness of the particular scale for any of the three components (ecology, monitoring and management) emerges. The management and ecological usefulness of each scale are usually opposite. Coarser scales are generally more useful for directing management interventions (Table 3.3, level a and b), and finer scales more useful for research into aspects such as examining plant distribution patterns and predictive distribution modelling, where features of the environment can be closely related to the distribution patterns of the plants (Table 3.3, level e and f). However, due care is also required here. In Fig. 3.9, I selected a quaternary watershed with low species richness, indicating that although present in low numbers, the entire watershed appears invaded to some degree. However, at a finer level of resolution (Fig. 3.9e) it is evident that there are very low numbers of plant records, which define the category for the entire watershed at a coarser level.

Determining the scale at which monitoring– referred to here as the ability to detect changes in species distribution and species density/abundance over time– should take place is more difficult and relates to the extent of the area. At the extent of KNP, general changes in density can be detected at coarser scales (Table 3.3, level a and b), but it is unlikely that good information can be gained for changes in species distribution at these scales. In areas of smaller extent, surveying at fine resolution will provide detailed insight into both changes in abundance and distribution.

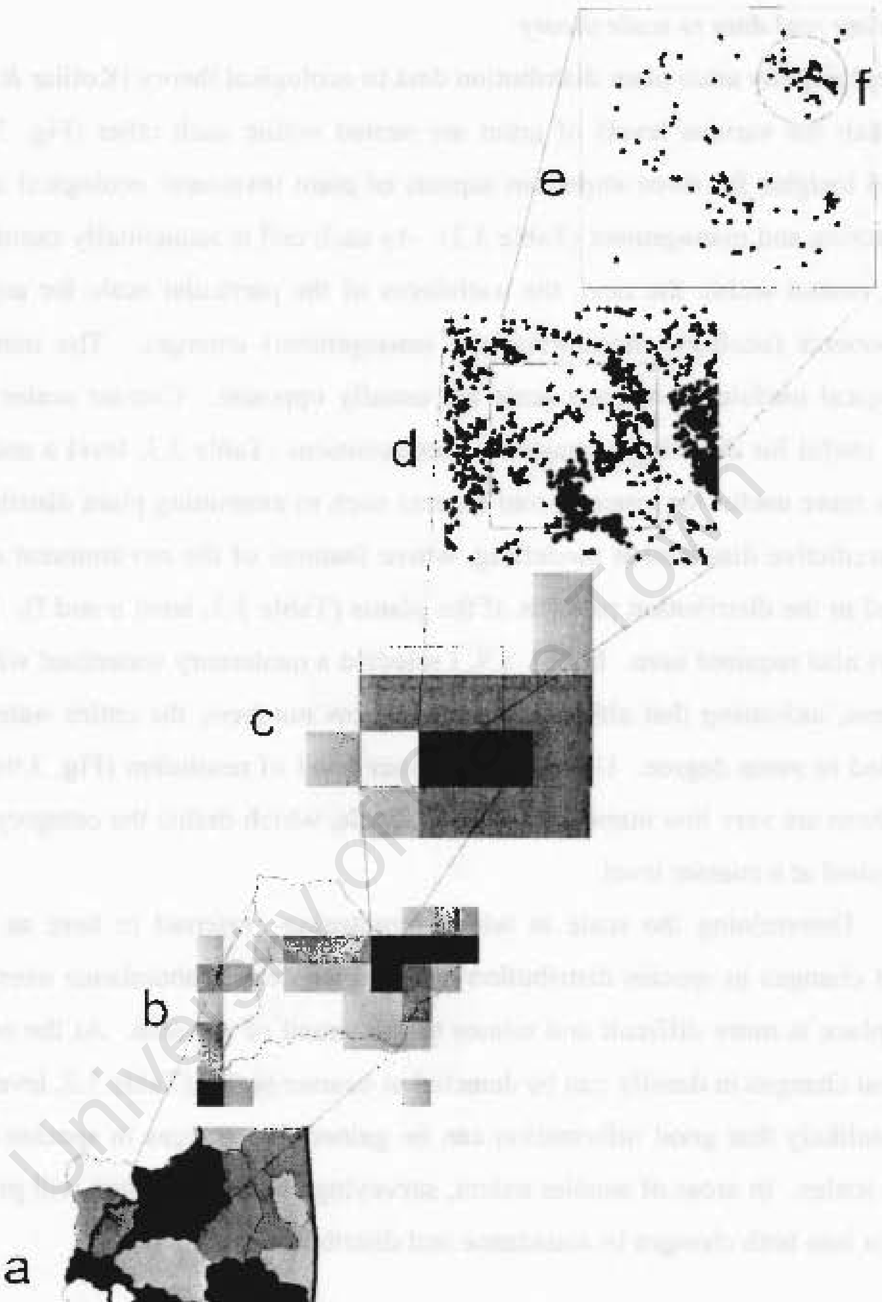

Figure 3.8: Alien plant richness data from Kruger National Park, applied to the hierarchical patch dynamic principle of Kotliar & Wiens (1990). The letters at each scale of resolution cross-reference to Table 3.3. The dots in (d) and (e) are individual alien plant records.

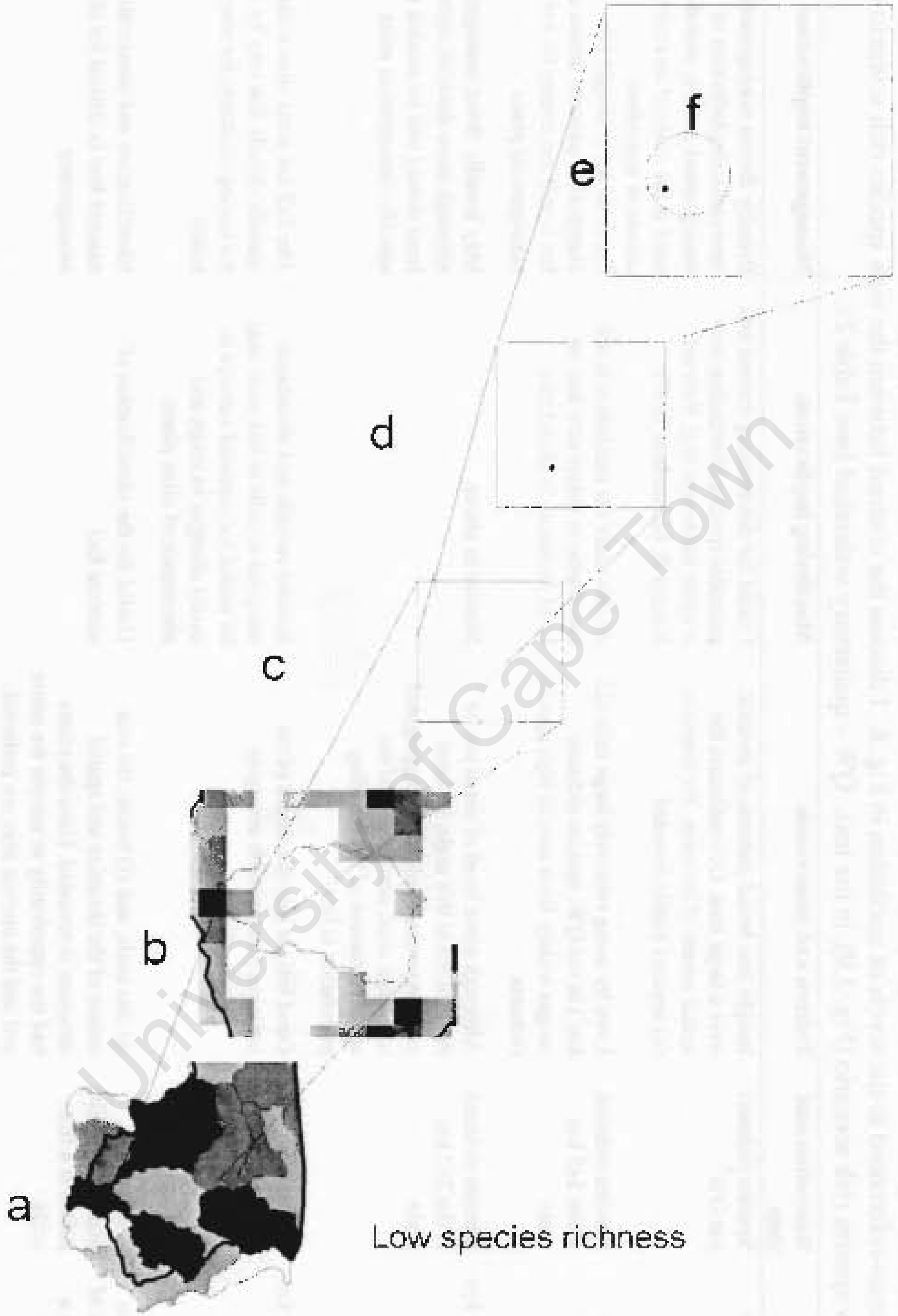

Figure 3.9: Alien plant data from the Kruger National Park applied to the hierarchical patch dynamic principle of Kotliar & Wiens (1990). The dots in (d) and (e) are individual alien plant records.

Table 3.3: Perspectives gained from changing spatial scales of alien plant distribution data in Kruger National Park. The implications indicated are cross-referenced to the levels of resolution in Fig. 8. I discuss the contrast between the high species rich scenario (in this table), to a low species rich scenario (Fig. 3.9), in the text. QW – quaternary watershed (see Table 2).

Level	Extent	Resolution and data	Pattern and observation	Monitoring implications	Management implications
a	Southern KNP	Species richness per QW^2	Insight into broad patterns of invasion over a large area. Overestimates the actual extent of invasion, for example (a) appears highly invaded	Useful for determining current and potential species distribution over a wider landscape (e.g. Foxcroft, Rouget & Richardson 2007)	Broadly directs management interventions (definition of management zones): probably best used at the scale of an entire river course or watershed
b	One QW	Species richness at the 5x5 km scale	Even by using relatively large cells (25 km^2) in the QW, species richness ranges widely from zero to high species richness	At this scale the resolution is still too coarse to detect new foci or local increases in abundance	Provides some insight into distribution patterns across a QW, but is still too coarse for use in management plans
c	One 5x5 km cell	Species richness at the 2x2 km scale	Although some level of detail can be determined at this scale, isolated patches or single plants are aggregated to a large area: perspective of the spatial structure of the invading population is lost	Similar to above	May broadly direct management, although more detailed units (next level down) will be needed for specific management units
d	One 2x2 km cell	Actual alien plant distribution	Good insight into the extent of the invasion pattern starts emerging	Species records and abundance assigned to cells at this scale may be useful for repeated surveys to detect changes in range and abundance of alien plants	The 2x2 km scale shows site specific details that may be useful for setting contracts for management teams
e	A random selection of points in a cell of < 1x1 km	A sample of plant distribution points at a finer scale	At this scale, and (f) below, the true nature of the invasion and spatial structure is revealed. Have the plants had the opportunity to sample the entire cell and the current sites are preferred, or is the invasion still expanding?	Useful for the identification of nascent foci	Identification and demarcation of nascent foci is critical for effective management
f	A random selection of points in a radius of < 250 m	Patchiness and distribution of a small cluster of alien plants	At these scale, including (e) above, insights into the spread dynamics and ecology of the species may be determined	In a small region, mapping of individual points or patches will facilitate detailed monitoring of range expansion, increases in abundance and efficacy of management interventions	Probably only useful for management in a small, well demarcated area, where individual plants and patches can be targeted for control

Discussion

The spatial scales at which data on alien plant invasions are assessed clearly affect the perceptions and insights that can be gleaned (Wiens 1989). The grain (cell size) also substantially alters the overall perceived level of invasion across an area, where for example, I show the southern KNP to be highly invaded when assessed at a quaternary watershed level, while the 0.1 x 0.1 km scale indicates the real pattern of the invasion.

Both a quarter-degree grid system and tertiary watershed scale provide a distorted assessment of invasion levels when used at an extent of the KNP. However, when considered nationally (e.g. Rouget *et al.* 2004) or regionally (e.g. Chapter 2) these scales are useful in broadly guiding management, and perhaps monitoring, activities. The quaternary watershed is probably also useful as a scale at which species lists can be compiled, and used in broad scale risk and priority assessment. The 0.1 x 0.1 km and 0.25 x 0.25 km scales are most useful for ecological studies, and where the overall extent is limited, for example a small nature reserve, can probably be used for planning management interventions and monitoring programmes. However, as Barnett *et al.* (2007) point out, the real benefit of mapping will only be realised when combined with plot-based techniques; an issue which is being explored by KNP.

Up-scaling diffuses abundance and distribution patterns, resulting in scattered patchy distribution patterns becoming continuous blocks of invaded areas. Similarly, even at fine scales, cells with a single record have the same effect. However, having data available at a fine resolution (point data) allows up-scaling (Pyšek & Hulme 2005), which may be useful when comparing to other data which was collected at a coarser resolution (for example, remote sensing data; Edwards *et al.* 2007).

Although not all species received the same level of effort in mapping, assessing the distribution of the most abundant species provides interesting insights. For example, when assessed at a fine scale, the distribution of *O. stricta* can be clearly related to the Skukuza village, and insights into the invasion process gained (Chapter 6). *Parthenium hysterophorus* can be clearly associated with roads at a fine scale, but the strength of this association is lost at coarser scales, which is crucial for understanding invasions. The same association is observed between *L. camara* and rivers in KNP.

An additional strength of the CyberTracker dataset is the large number of records that may be used as absence data or null records in assessing and modelling plant invasions. Although a number of techniques are being developed to use presence only data for predictive distribution modelling (Robertson, Villet & Palmer 2004 and references therein, Tsoar *et al.* 2007), methods using pseudo-absence points appear to be more accurate than presence only models (Elith *et al.* 2006). Thus the large number of absence points is a distinct advantage and facilitates accurate niche-based modelling, providing opportunities for accurately modelling potential species distribution at a specific spatial extent, for example, KNP.

CHAPTER FOUR

ORNAMENTAL PLANTS AS INVASIVE ALIENS: PROBLEMS AND SOLUTIONS[3]

Abstract

The most widespread invasive species in South Africa's Kruger National Park (KNP) were either introduced unintentionally along rivers and roads, or intentionally for use as ornamentals. I examine the spatial dimensions of ornamental alien plants in KNP, including the distribution of foci of species richness, links between human population size and history and species richness, and the nestedness of foci in terms of species presence. Results are used to assess whether past management actions have been appropriately directed.

Two hundred and fifty eight alien species have been recorded in the 36 tourist camps and staff villages. The number of staff housed in villages explains much of the diversity of cultivated alien plant species. Older camps also tend to have more cultivated alien plant species. However, the lack of a strong link between camp age and number of cultivated species suggests that ornamental plants have been widely spread around KNP by humans. I also show that increased camp activity (either size or age) has lead to more ornamental species, while, with the notable exception of Skukuza, camp activity has had a much smaller effect on the number of non-cultivated species. Non-cultivated species tend to be naturally dispersed, as opposed to being directly spread by humans between camps.

Past management focused on species prioritised on the basis of their potential to invade KNP and prevailing national legislation. These species were removed manually and follow-up control was carried out. Once the priority species were deemed to be under control, less invasive species were targeted. All alien species were removed from vacated houses, regardless of the potential invasiveness of the species.

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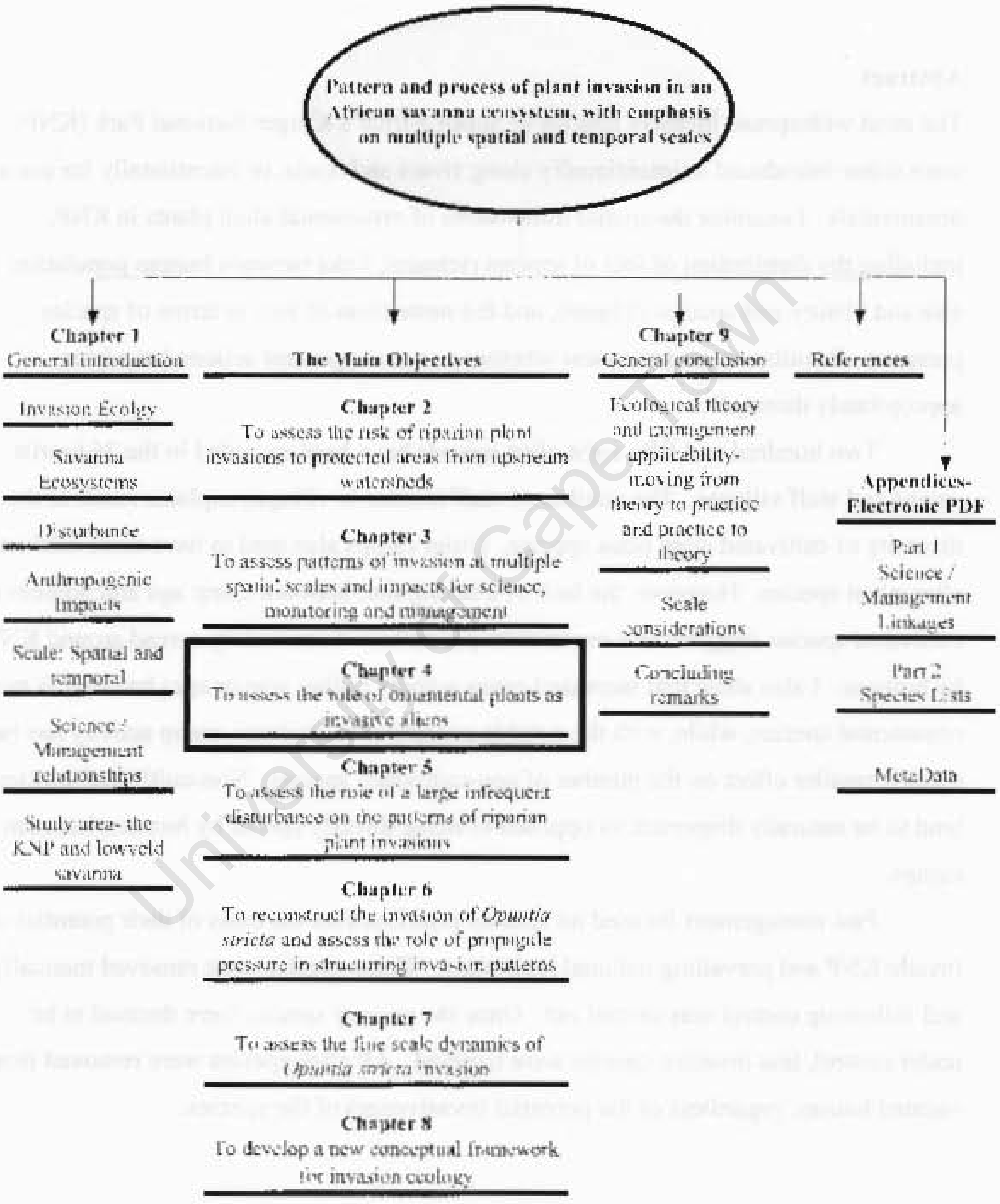
[3] Publication status: Foxcroft, L.C., Richardson, D.M., Wilson, J.R.U. 2007. Ornamental Plants as Invasive Aliens: Problems and Solutions in Kruger National Park, South Africa. *Environmental Management*, In press.


Pattern and process of plant invasion in an African savanna ecosystem, with emphasis on multiple spatial and temporal scales
Chapter 1
General introduction
Invasion Ecolgy
Savanna Ecosystems
Disturbance
Anthropogenic Impacts
Scale: Spatial and temporal
Science / Management relationships
Study area- the KNP and lowveld savanna
The Main Objectives
Chapter 2
To assess the risk of riparian plant invasions to protected areas from upstream watersheds
Chapter 3
To assess patterns of invasion at multiple spatial scales and impacts for science, monitoring and management
Chapter 4
To assess the role of ornamental plants as invasive aliens
Chapter 5
To assess the role of a large infrequent disturbance on the patterns of riparian plant invasions
Chapter 6
To reconstruct the invasion of *Opuntia stricta* and assess the role of propagule pressure in structuring invasion patterns
Chapter 7
To assess the fine scale dynamics of *Opuntia stricta* invasion
Chapter 8
To develop a new conceptual framework for invasion ecology
Chapter 9
General conclusion
Ecological theory and management applicability- moving from theory to practice and practice to theory
Scale considerations
Concluding remarks
References
Appendices- Electronic PDF
Part 1
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Part 2
Species Lists
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Introduction

Alien plant invasions are a major threat to the conservation of biodiversity in many parts of the world (Rejmánek *et al.* 2005a). They affect biodiversity in many ways, notably by altering nutrient cycling and disturbance regimes (e.g. Vitousek 1990; Brooks *et al.* 2004), disrupting naturally occurring mutualisms (Travaset & Richardson 2006), consuming excessive amounts of water, light and oxygen, donating limiting resources, promoting or suppressing fire and stabilizing sand or promoting erosion (Rejmánek *et al.* 2005b). No areas, however isolated, are totally spared from human-assisted introduction, establishment, and proliferation of alien species (Chapter 2). Even protected areas – parcels of land set aside for the conservation of natural and semi-natural ecosystems and the processes that sustain biodiversity within them – are increasingly affected by biological invasions. Consequently, managing invasive species is a growing challenge in protected areas. Successful management involves education, prevention, detection/early warning, eradication, containment, and other forms of intervention (Wittenberg & Cock 2001, 2005).

A large proportion of invasive alien species worldwide were intentionally introduced to the areas where they are currently invasive, and many were widely disseminated once introduced to provide some value to humans (Ewel *et al.* 1999, Pyšek *et al.* 2002b, Williams & Cameron 2006). In the USA, more than 100 new floriculture species (flowering or potted plants, cut flowers, and herbaceous perennials) were introduced by amateur or professional plant breeders in the last decade alone (Anderson *et al.* 2006). Unfortunately, plant breeders frequently select plants for introduction based on the same traits that are associated with invasion potential, such as fruit production, high germination and growth rate, and tolerance to a wide range of environmental conditions (Anderson *et al.* 2006). Therefore, it is not surprising that a large proportion of invasive alien plants were first introduced to their adventive range for ornamental use (Binggeli 2001, Reichard & White 2001, Baskin 2002, Wittenberg & Cock 2005). Species introduced intentionally appear to be quicker to naturalize and invade, at least in Central Europe, than is the case for accidentally introduced species (Pyšek *et al.* 2003).

Problems arising from invasive ornamental plants lead to conflicts of interest between horticulturalists, landowners, and conservationists. Various initiatives in different parts of the world aim to reduce the use of known invasive species in horticulture - for example, the St. Louis Declaration on Invasive Plant Species in North America (Baskin 2002), the New Zealand Pest Plant Accord (http://www.biosecurity.govt.nz/pests-diseases/plants/accord.htm). and the Scottish Horticulture Code of Practice (http://www.scotland.gov.uk/Topics/Environment/Wildlife-habitats/InvasiveSpecies/HCOP). In South Africa, there is a cooperative agreement between the Nurserymen's Association and the Working for Water programme (the national agency responsible for managing invasive alien plants; a part of the Department of Water Affairs and Forestry). Although schemes such as these may assist in minimising future invasions by promoting the use of indigenous species, the problem of ornamental species used previously and which are now widely planted, remains a major challenge for conservation biologists. Besides the encouraging schemes mentioned above, I know of no formal strategies for dealing with the problem of invasive ornamental plants for any major protected area.

Ornamental plants are most likely to invade at the urban/wild land interface, where human habitation borders on natural vegetation. The cultivation and tending of plants in gardens produces high propagule pressure (i.e. many seeds and other propagules can spread into the surrounding natural vegetation). This then increases the likelihood and rate of any particular species invading natural and semi-natural ecosystems (e.g. Sullivan *et al.* 2004, 2005, Alston & Richardson 2006, Sullivan *et al.* 2006, Milton *et al.* 2007).

This paper presents perspectives on invasive ornamental plants in one of the world's largest areas managed primarily for biodiversity conservation: South Africa's Kruger National Park. I discuss the emergence of the problem of invasive alien ornamental species in KNP, the evolution of the current approach to managing the problem, describe and analyse a survey for ornamental species, and combine the previous experience and results of my work to suggest a way forward for the control of ornamentals in KNP, and in protected areas in general.

The problem and work conducted so far

The study area

The Sabie Game Reserve (southern third of the current KNP) was proclaimed in 1898, and the remaining area was proclaimed in 1926. Most of KNP (Fig. 4.1) has therefore been under formal protection for 80–100 years (du Toit *et al.* 2003). However, the infrastructure in KNP has recently expanded rapidly with the growth in tourism and consequent increase in staff numbers (Freitag-Ronaldson & Foxcroft 2003, appendix 1.3). For example, KNP currently maintains about 885 km of paved roads, 1,700 km of gravel roads open to tourists, and 737 km of gravel roads for park management (Freitag-Ronaldson & Foxcroft 2003, appendix 1.3).

As of 2006, about 3687 staff members were housed in KNP. Skukuza, the largest tourist village and administrative headquarters, comprises about 250 staff houses, various recreational and sporting amenities, and living quarters for general workers, amounting to about 2347 staff members. There are also five large tourist camps with between 100–200 staff members each, and about 36 smaller camps and ranger outposts most of which are substantially smaller with fewer than 20 staff members each (Table 4.1). Many staff members are involved in administrative and maintenance jobs, some of them with little knowledge of general conservation issues, including the threats posed by alien plant invasions (Foxcroft 2001).

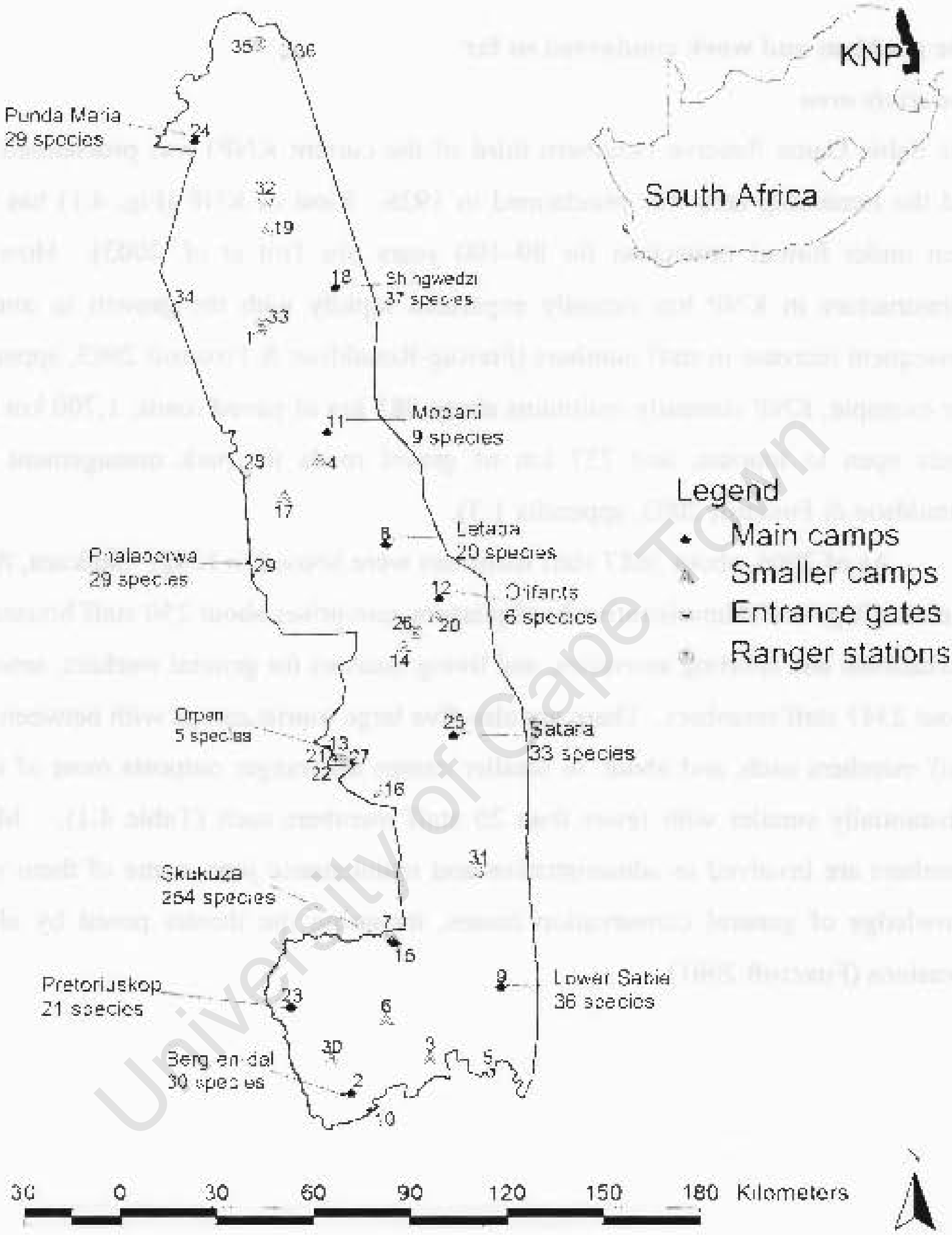

Figure 4.1: The Kruger National Park, indicating the main tourist camps. The inset shows the KNP in relation to the rest of South Africa. Species numbers refer to the number of alien species recorded per camp. The numbers next to each symbol cross-reference to the camps listed in Table 4.1.

Table 4.1: Tourist camps and staff villages in Kruger National Park, indicating the number of alien species recorded therein, the date of establishment of the camp and the number of resident staff per camp. Camp numbers cross-reference to Figure 4.1.

Camp number	Camp	Date Est.	Number staff	Number of alien plant species recorded	Camp situated on river
20	Balule	1930	2	0	No
1	Bataleur	1988	8	3	No
2	Berg-en-Dal	1983	124	30	tributary
3	Biyamiti	1990	12	0	No
4	Boulders	1985	10	0	No
5	Crocodile Bridge	1930	59	4	main river
26	Houtboschrand ranger	1982	14	7	tributary
6	Jock of the Bushveld	1970	11	9	No
27	Kingfisherspruit ranger	1954	14	8	tributary
8	Letaba	1927	140	20	main river
9	Lower Sabie	1902	42	36	main river
28	Mahlangeni ranger	1958	14	1	main river
10	Malelane	1924	6	1	main river
21	Marula	1973	8	0	No
11	Mopani	1991	63	9	tributary
12	Olifants	1959	113	6	main river
13	Orpen	1932	5	5	tributary
35	Pafuri ranger	1973	17	3	main river
29	Phalaborwa	1960	26	29	No
23	Pretoriuskop	1924	63	21	No
24	Punda Maria	1919	96	29	No
14	Roodewal	1983	8	0	No
25	Satara	1908	183	33	No
34	Shangoni ranger	1938	21	7	No
17	Shimuweni	1990	9	0	main river
18	Shingwedzi	1934	122	37	main river
19	Sireni	1990	12	0	Tributary
15	Skukuza	1902	2347	254	main river
30	Stolznek ranger	1976	17	3	No
16	Talamati	1991	14	7	No
22	Tamboti	1995	8	0	No
36	TEBA- Pafuri	1920	17	16	No
7	Tinga Legends	1990	10	0	main river
31	Tshokwane ranger	1928	44	11	No
32	Vlakteplaas ranger	1978	14	7	No
33	Woodlands ranger	1982	14	8	main river

The role of villages and camps in plant invasions

The villages and camps in KNP are all landscaped to varying degrees. Until recently, landscaping typically involved the use of many alien species (Foxcroft 2001). As was the case elsewhere in South Africa, despite the rich local flora, alien plant species were very often favoured over indigenous species for use as ornamentals (Richardson *et al.* 2003; Fig. 4.2).

Three factors are important in connection with the role of the villages/camps in KNP as foci for the spread of introduced plants. These include the large number of mammalian and avian seed dispersers, the proximity of the tourist camps and staff villages to the rivers, and the fact that the camps are evenly distributed across the entire KNP landscape.

First, since many of the introduced ornamental species have fleshy fruits, the availability of potential dispersal agents provides a means for effective dissemination of propagules from the foci created by plantings in the villages/camps. Although most of the villages/camps are fenced to exclude dangerous mammals such as buffalos, elephants, hippopotamus, hyenas, lions, leopards and rhinoceros, the fences are still permeable to mammals that are potential dispersers of alien plant propagules. Even elephants gain entry to some of the villages occasionally, and thus have access to alien plants growing along fences around villages. KNP also has a rich avifauna, including many species of frugivorous birds (Sinclair & Whyte 1992) and at least three species of frugivorous bats (G. Zambatis pers. comm.). Added to this is the disposal of garden refuse and cuttings, from which the ornamental plants can escape the demarcated dumpsites or compost heaps.

Second, most tourist villages and camps are located near major rivers (Table 4.1). Rivers provide important conduits for the dispersal of alien plants in KNP (Foxcroft & Richardson 2003, appendix 1.2, Chapter 2). Dispersal from villages may be facilitated by bird or animal movement between the rivers and villages, or through dumping of garden refuse in compost heaps from where plants may disperse. Dispersal may also occur directly, through extreme floods. For example, the extreme flood event of 2000 (see Heritage *et al.* 2001, Parsons *et al.* 2005, Parsons *et al.* 2006) inundated about 70 personnel gardens in Skukuza and large portions of other tourist camps, thereby spreading propagules of various species.

The third important factor in connection with the invasion of ornamental alien plants from camps and villages is the distribution of the camps themselves. Although KNP covers a large area (360 km along its longest axis), the camps are distributed fairly evenly over the area; consequently no natural area is far removed from a source of potential invasive plants cultivated in the camps.

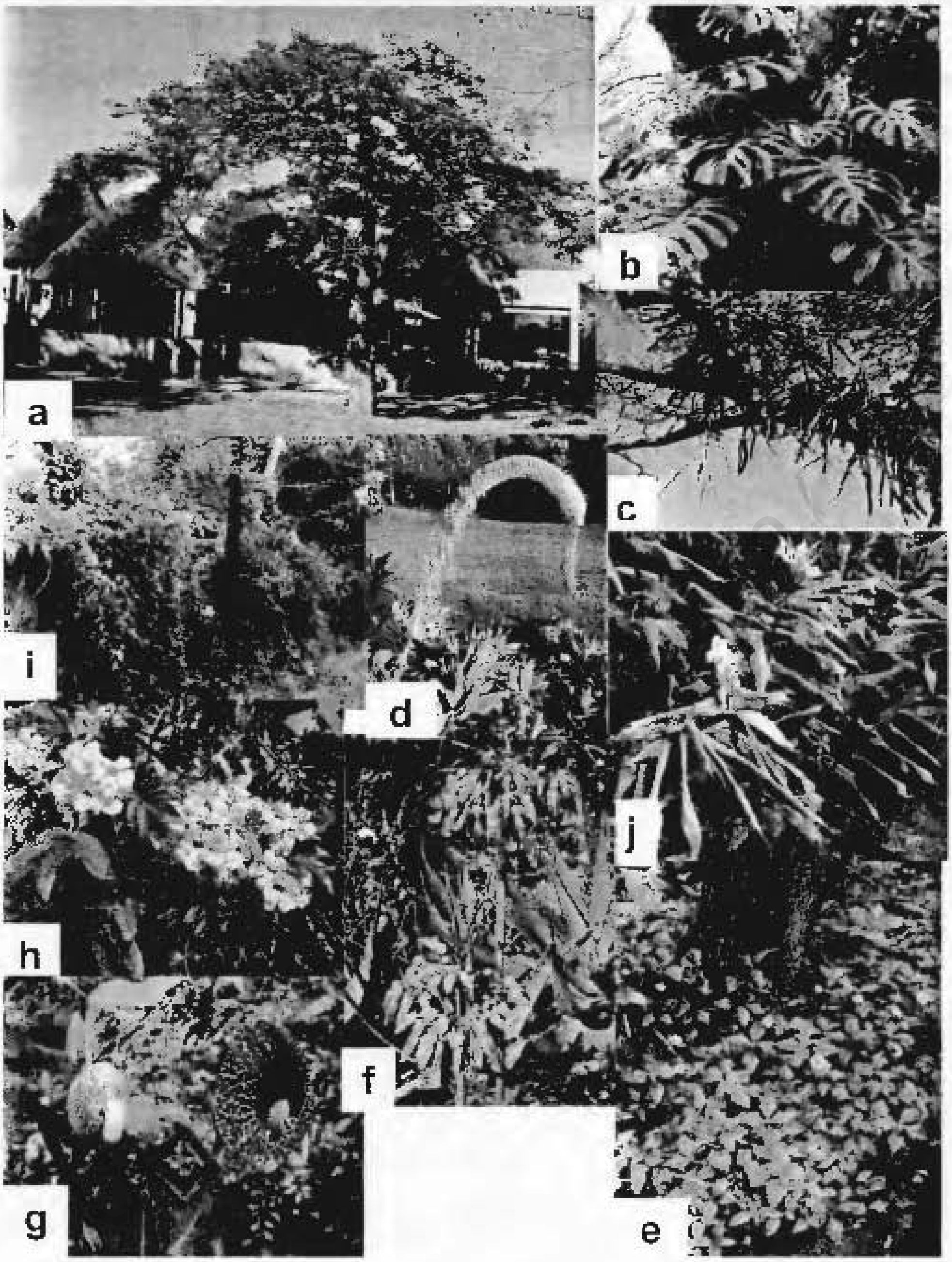

Figure 4.2: Examples of alien plants used in Kruger National Park for shade, ornamentation and hedging. The illustrated species are: (a) *Delonix regia* (Fabaceae; flamboyant), (b) *Monstera deliciosa* (Araceae; delicious monster), (c) *Hylocereus undatus* (Cactaceae; night-blooming cereus), (d) *Agave attenuata* (Agavaceae; soft-leaved agave), (e) *Sphagneticola trilobata* (Asteraceae; Singapore daisy), (f) *Bryophyllum delagoense* (Crassulaceae; mother of millions), (g) *Aristolochia elegans* (Aristolochiaceae; Dutchman's pipe), (h) *Tecoma stans* (Bignoniaceae; yellow bells), (i) *Antigonon leptopus* (Polygonaceae; coral creeper), (j) *Alpinia zerumbet* (Zingiberaceae; shell ginger). (Photographs: (a) V. Mngomezulu, (c,d,h) G.R. Nichols, others: L.C. Foxcroft).

History and evolution of strategies for ornamental aliens

Following the promulgation of the Sabie Game Reserve in 1898, access to the area now comprising KNP was considerably limited. It may be safely assumed that the intentional introduction of alien plants was thus also limited. I could find records of only two alien plant species that were introduced before proclamation of the KNP. *Arundo donax* L. was planted in the Phabeni Gate area (west of Skukuza) between 1845 and 1847, and about nine eucalyptus trees (*Eucalyptus camphora* R.T. Baker) were planted at Gomondwane (southern KNP) between 1892 and 1898 (Pienaar 1990). There is no record of either species becoming invasive from these introductions, although *A. donax* is now invasive from another source of introduction.

Between 1935 and 2006, the issue of invasion or control of ornamental alien plants was formally raised on at least 10 occasions (Joubert 1986). This included suggestions and recommendations from the KNP Warden, recommendations by the SANParks Board, as well as national legislation, from which internal KNP policy/management plans were later derived. However, the problem steadily deteriorated and only in 2005, some 70 years after the first objections to the use of alien trees in tourist camps, did KNP manage to start reversing the problem through the implementation of a systematic management programme.

Following the realisation of the seriousness of the risk posed to KNP ecosystem by many of the species recorded, and from experiences of species having escaped from cultivation in KNP already, management focused on actively removing potentially invasive ornamental plants. Although support and advances have fluctuated over the past decade, with a notable upward trend recently, tremendous progress has been made. Certainly, there has been a considerable reduction in the abundance of potentially invasive species in all staff and tourist villages.

The history of efforts at managing invasive alien plants in KNP, starting in 1958, was reviewed by Foxcroft & Richardson (2003, appendix 1.2) and Freitag-Ronaldson & Foxcroft (2003, appendix 1.3). Here, I give further details on efforts to deal with ornamental alien plants in the tourist villages and camps. Management of ornamental alien plants started in the Skukuza village in the mid 1980s. This initiative was not well supported by staff, and resulted in continuous resistance from residents towards the alien plant control team. As a result, less effort was placed on preventative control measures in the village and work continued on other alien plant species that had already escaped into the surrounding areas (mainly *Opuntia stricta* and *Lantana camara*). From the early 1980s until the mid 1990s the alien plant control team focused on about 30 well-known alien plants (such as *Lantana camara* and species of Cactaceae), and allowed the use of numerous other potential alien species to continue, for example *Sphagneticola trilobata* (Singapore daisy) and *Alpinia zerumbet* (shell ginger). Following the 1999 survey of alien plants in the villages, KNP management approved a new policy (see appendix 1.1: Policy / standard operating procedure regarding alien plants in the staff villages and tourist camps of the KNP, 4th revision), and a substantial, coordinated programme was launched to remove the alien species. Because of continuing opposition to the policy from some residents and staff, attention was initially given to only the most serious invasive species. Considerable effort was also invested in extension and education of residents regarding the damage caused by invasive alien species. This included some species present in these villages and not yet invasive in South Africa but invasive elsewhere in the world. Despite this, problems were still experienced when scheduling removal of established alien plants from gardens; especially well-established or large plants that formed prominent features in gardens (e.g. *Alpinia zerumbet* [shell ginger], *Hedychium gardenarium* [kahili ginger lily], *Nephrolepis exaltata* [sword fern], and *Sphagneticola trilobata* [Singapore daisy]). Consequently, more effort was placed on removing all alien plants from gardens that were vacated when staff relocated. This approach was preferred by the management team, as it avoided conflicts with residents and proved a better use of resources. However, it is too early to say whether any species have been eradicated from the KNP through this programme.

Following the amendments to the Conservation of Agricultural Resources Act (Act 43 of 1983) (CARA; http://www.nda.agric.za/docs/act43/eng.htm) in 2001, the KNP policy was revised in order to ensure that the KNP complied with the new national legislation. According to the revised CARA legislation, 198 alien plant species were divided into three categories, based on their invasion potential and economic use in South Africa. These include 'Category 1 - declared weeds' which are prohibited; 'Category 2 - declared invaders' that are typically commercial plantation species and may only be grown under permit (therefore excluding the KNP); and 'Category 3 - declared invaders', which may not be propagated or intentionally disseminated, but which may be left until they senesce (although sub-regulations require their removal in some cases, e.g. when planted close to streams and rivers). In applying the legislation in KNP, all declared weeds and invaders are regarded as prohibited species that require control. In the revised KNP policy on the management of alien species, all species listed in the CARA act were flagged as top-priority species (prohibited), requiring immediate removal from all gardens and tourist camps. All alien plants would still, however, be removed from vacant gardens and tourist camps. During this period, a heightened appreciation of the problem was also observed (L. Foxcroft pers. obs.). The alien plant team was frequently requested by staff to clear their gardens ahead of the scheduled clearing (L. Foxcroft pers. obs.), requesting that all alien plants (including non-invasive ornamentals) be removed, as the residents planned to re-landscape their gardens using indigenous plants only. By 2003, all gardens and areas surrounding Skukuza had been cleared at least once. Regular follow-up operations are still carried out.

In 2004 the National Environmental Management: Biodiversity Act (Act 10 of 2004) ("NEMBA") was promulgated. This was followed by the regulations and species listing process in 2005-2006 (finalization of the regulations is still in progress in mid-2007). The draft NEMBA regulations list 381 plant taxa, with a further list of 92 taxa still under consideration. Invasive taxa are placed under five categories in the regulations, ranging from those species that require compulsory control, to those species under surveillance.

The latest version (Ver. 4) of the KNP policy/ Standard operating procedure (appendix 1.1) on alien species management accommodates the new regulations by including the plant lists, and managing these as first priority species in KNP. Most policies and strategies in KNP have a life span of five years, after which a formal management review is required. However, these policies will also be updated more frequently in order to take account of changes in national policy and legislation as well as advances in international best practice.

Survey of the extent of the problem

I had four main aims for surveying the tourist camps. First, I wanted to identify the scale and spatial spread of ornamental plantings across the park so that the size of the problem could be assessed and control measures targeted. Second, I wanted to identify factors affecting ornamental species richness at any particular camp to derive predictors of risk and as a basis for evaluating the efficiency of past strategies. Thirdly, I examined how the alien flora varies between camps, to see whether ornamental floras simply reflect patterns of planting or the ability of species to grow in certain areas of the park. Finally, I wanted base-line data against which control measures could be assessed in future.

The first comprehensive survey of ornamental alien plants was conducted in the Skukuza staff village in 1999. Thereafter, all the larger and most of the smaller camps and ranger stations were surveyed by 2003, with surveys continuing on an *ad hoc* basis in some of the more invaded tourist camps / villages.

In each of the camps, all staff gardens, the landscaped areas around the reception, shop and restaurant areas were searched. All alien plants encountered (including species typically found in disturbed areas and roadsides, as well as planted ornamentals) were recorded, and herbarium specimens collected for unknown species and photographed for later identification. Ideally camps should be resurveyed annually to monitor sites for re-growth, but the size of KNP and the numbers of camps / villages, meant surveys were more *ad hoc*. The plan is for surveys to continue in future.

Analysis of the plant species data

To estimate the potential influence of the urban/wild land interface, I carried out a nearest neighbour analysis to see how close parts of the park were from camps, and therefore from a potential source of invasive species (Nearest feature script, for Arcview GIS 3.2a).

To see how camp size and age affect the number of non-native species planted, I used a generalized linear model with a log-link function (because the response variable, species number, is a count) and the variance increasing with the square of the mean (as the variability in species richness at large camps is much larger than for small camps) (R Development Core Team 2004). The analysis was repeated with and without including data for Skukuza, as it has over twelve times the staff population of the next biggest camp. I also separated species on the basis of whether they were cultivated ornamentals or not, and compared the ratio of cultivated species to non-cultivated species at a camp using binomial errors.

To determine the relationship between the alien floras found in each of the camps, I used a measure of nestedness. I used the nestedness index d1 (Greve & Chown 2006), where a value of 0 is a perfectly nested species-presence-by-site matrix, and if each site has a completely different set of species, d1 tends from 0.5 to 1 as the size of the matrix increases. The level of nestedness was tested against 10,000 randomly generated matrices, where the randomizations kept the frequency or probability of either species richness per site or species occurrences constant.

Results and Discussion of the Plant Survey

Of the 257 alien plant species recorded (see appendix 2.1), at least 85 taxa are known to be invasive somewhere in the world (using a rapid assessment in a commonly used internet search engine). The most widespread and common species include *Alpinia zerumbet* (shell ginger), *Bryophyllum daigremontianum* (good luck plant), *Bryophyllum delagoense* (chandelier plant/mother of millions), *Callisia repens* (striped creeping inch plant), *Nephrolepis exaltata* (sword fern/Boston fern), *Sphagneticola trilobata* (Singapore daisy), *Syngonium podophyllum* (goose-foot plant/arrowhead-vine), *Tradescantia pallida* (purple wandering Jew/purpleheart), *Tradescantia spathacea* (boat plant/oyster plant). As is generally the case for invasive plants, species which are regarded to have been naturalized in KNP, tend to have been present for longer (13–14 years on average, Wilcoxon rank sum=8190, $p<0.001$), i.e. residence time is highly correlated with measurements of invasiveness (Wilson *et al.* 2007).

Although KNP is a large area, the median distance between camps or other infrastructure is only 9.1 km (range 35.9 km). This means that instead of having a large, uninterrupted natural area, foci for potential invasion are scattered fairly evenly across the landscape (Fig. 4.3). The camps thus form islands with sources of alien plant propagules in a sea of natural habitat. In particular, maps can be produced for any species recorded to show potential areas where naturalization may have occurred, and concentrate control efforts in these regions. For example, *Opuntia stricta* escaped from cultivation in Skukuza (Chapter 6), and is now widespread (Fig. 4.4).

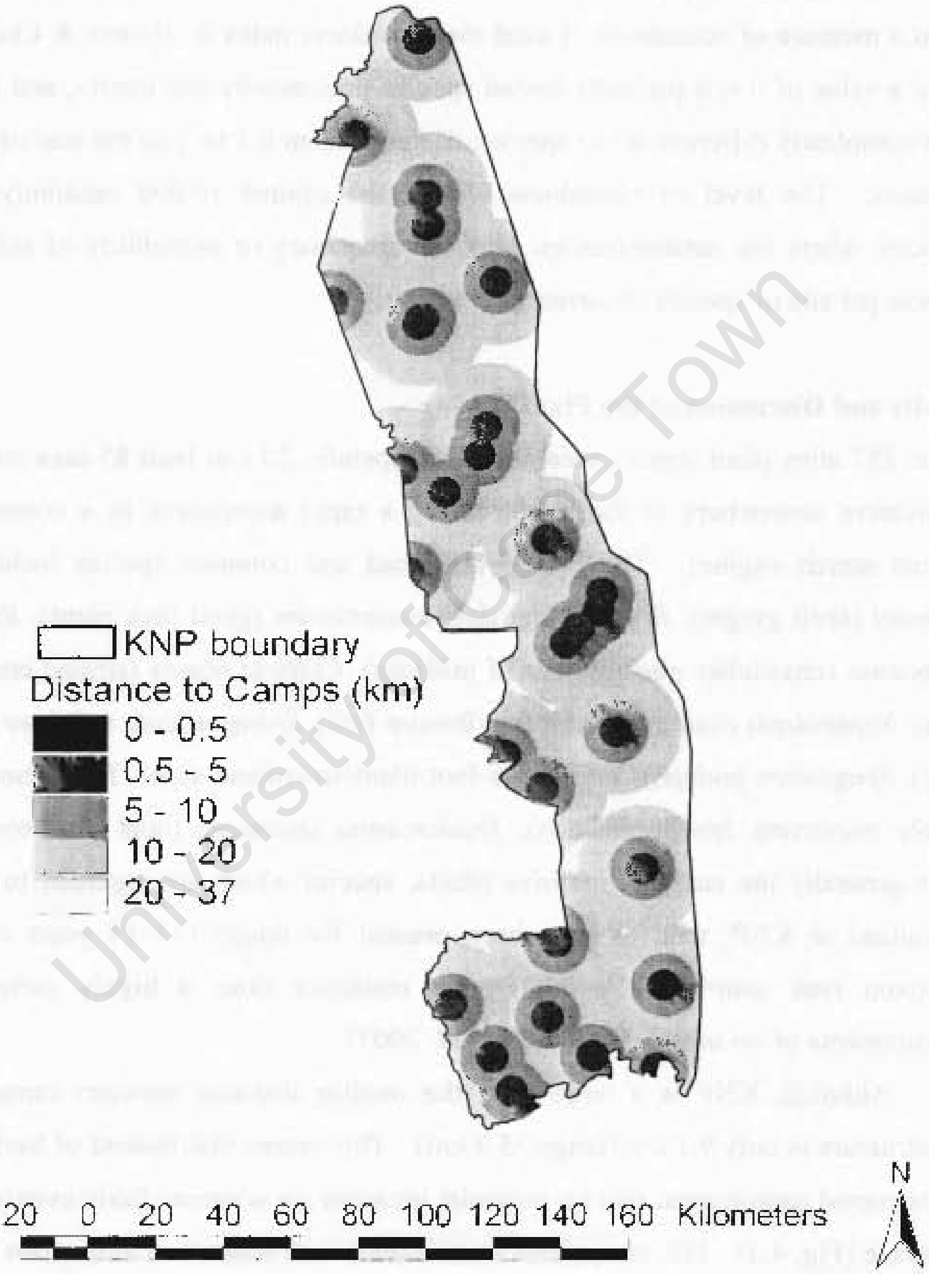

Figure 4.3: The distribution and distance between staff villages / tourist camps in Kruger National Park.

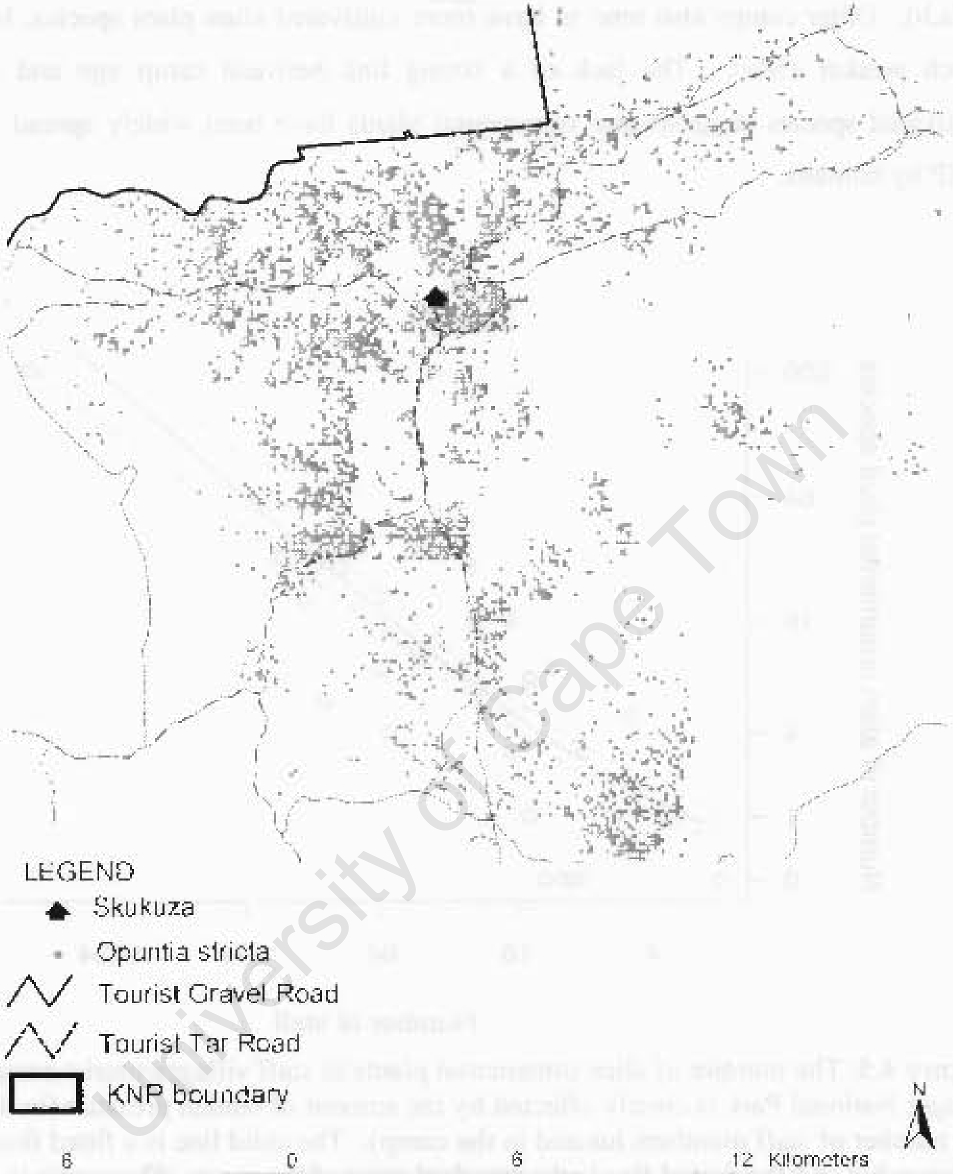

Figure 4.4: The distribution of *Opuntia stricta* in Kruger National Park. *Opuntia stricta* was first recorded in Skukuza staff village in 1953 where it was introduced as an ornamental species. It has since spread to an area of about 80 000 ha (Chapter 6). If *O. stricta* had been introduced to other camps, I expect that its distribution would have been substantially greater.

As has been shown for other "island" systems, for example, in the sub-Antarctic (Frenot *et al.* 2001) and the Czech Republic (Pyšek *et al.* 2002a), the level of human pressure (in this case, the number of staff housed in a camp) explains much of the diversity of alien plant species (Fig. 4.5). This is particularly noticeable for cultivated species (Table 4.2a,b). Older camps also tend to have more cultivated alien plant species, but this is a much weaker effect. The lack of a strong link between camp age and number of cultivated species suggests that ornamental plants have been widely spread around the KNP by humans.

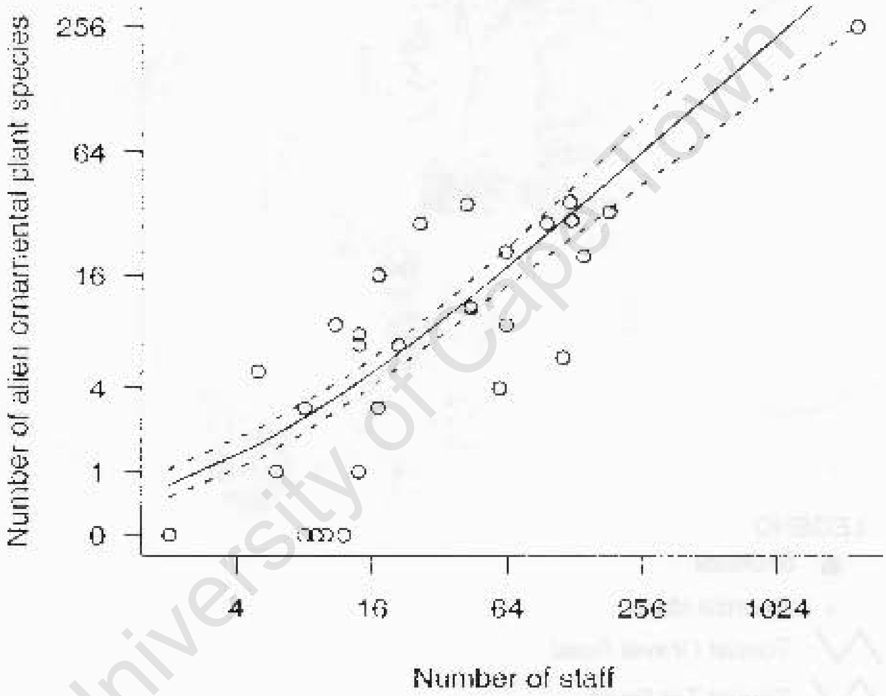

Figure 4.5: The number of alien ornamental plants in staff villages/tourist camps in Kruger National Park is clearly affected by the amount of human pressure (in this case the number of staff members housed in the camp). The solid line is a fitted line relationship and the dotted line is the standard error of the mean. The x axis is on a log scale, and the y axis is on a log (value + 1) scale to show the zero counts. The point to the far right is Skukuza, by far the largest camp in KNP. The inclusion of this Skukuza did not make a significant difference to the fit of the model ($F_{33,1}$=0.164, p=0.69).

Table 4.2: Factors affecting the number of non-native species. In a, b and c, errors are a log link function and variance increasing with the mean squared. In d, errors were Poisson distributed. The results were qualitatively similar if negative binomial errors were used.

(a) Cultivated species (Skukuza included)

	Estimate	Std. Error	t-value	p-value
Intercept	-3.19	0.935	-3.42	0.0017
log [Number of staff]	0.816	0.145	5.63	<0.001
log [Camp age]	0.664	0.277	2.39	0.0225

Dispersion parameter for quasi family taken to be 1.075
Null deviance. 75.6 on 35 degrees of freedom
Residual deviance: 17.6 on 33 degrees of freedom

(b) Cultivated species (Skukuza excluded)

	Estimate	Std. Error	t-value	p-value
Intercept	-3.49	0.995	-3.50	0.0014
log [Number of staff]	0.912	0.179	5.10	<0.001
log [Camp age]	0.668	0.285	2.34	0.0255

Dispersion parameter for quasi family taken to be 1.14
Null deviance: 47.4 on 34 degrees of freedom
Residual deviance: 18.3 on 32 degrees of freedom

(c) Non-cultivated species (Skukuza included)

	Estimate	Std. Error	t-value	p-value
Intercept	-4.96	2.49	-1.99	0.055
log [Number of staff]	0.642	0.386	1.66	0.106
log [Camp age]	0.521	0.739	0.706	0.485

Dispersion parameter for quasi family taken to be 7.64
Null deviance: 45.0 on 35 degrees of freedom
Residual deviance: 36.4 on 33 degrees of freedom

(d) Non-cultivated species (Skukuza excluded)

	Estimate	Std. Error	t-value	p-value
Intercept	-2.58273	1.66127	-1.555	0.12
log [Number of staff]	0.41842	0.29084	1.439	0.15
log [Camp age]	0.03577	0.48722	0.073	0.941

Dispersion parameter for poisson family taken to be 1
Null deviance: 37.8 on 34 degrees of freedom
Residual deviance: 35.0 on 32 degrees of freedom

The distribution of cultivated alien plant species between camps is heavily skewed whereas, with the exception of Skukuza, the distribution of non-cultivated alien plants species between camps is well described by a Poisson distribution (Table 4.2). Most of the non-cultivated species are in Skukuza (thirty as opposed a maximum of three at any other camp), and the number of non-cultivated species is not affected by camp age (Table 4.2c,d), and only marginally influenced by the number of staff ($p=0.04$ with Skukuza included, $p=0.09$ with Skukuza excluded). Despite this, the proportion of cultivated to non-cultivated non-natives at a site was not affected by camp age or number of staff if Skukuza was excluded ($p>0.1$ in all cases). The addition of Skukuza has a massive influence on the analysis (Cook's distance >60) and creates the spurious result that as the number of staff increases at a camp the proportion of non-cultivated species in the non-native species pool increases: in fact if Skukuza is excluded the opposite trend is observed.

I would argue that increased camp activity (either size or age) has lead to more ornamental species, while, with the notable exception of Skukuza, camp activity has had a much smaller effect on the number of non-cultivated species. Non-cultivated species were initially brought to and established in Skukuza, but then tend to be naturally dispersed, as opposed directly spread by humans between camps. This hypothesis is also supported by the nestedness of species.

I found that the distribution of alien plant species between camps was heavily nested (Appendix 2.2). For the matrix, with Skukuza included, d1 is 0.257 and if Skukuza is excluded d1 is 0.417. For all measures tested, the species-by-camp matrix for KNP was significantly more nested ($p<0.001$) than randomly generated matrices. For those species that were not cultivated, there is little evidence of nesting. Without Skukuza, d1 is 0.67 and is not significantly nested ($p=0.73$–0.93 depending on whether numbers per site or frequency of species are kept constant or as a set probability). With Skukuza, d1 is 0.24 ($p=0.68$-79 if numbers per site are kept constant or as a set probability, but $p<0.001$ if numbers per site can vary due to the large number of species found at Skukuza). When comparing values of d1 it should be noted that because only 9 camps had non-cultivated aliens, d1 is at most 0.875–0.89, for the nestedness of cultivated aliens, many potential matrices can have values of d1 approximating one.

The nestedness of cultivated species implies that the species present in camps with few species were usually a sub-set of those in camps with more species, with almost all species being found at Skukuza. Although several scenarios are consistent with this pattern, the most plausible explanation is that the ornamental species found in KNP were initially introduced to a few particular camps, and that these plants were then taken from these initial sources to the other camps. This level of nestedness, however, is inconsistent with the hypothesis that the ornamental species introduced to a site depends strongly on the environmental conditions at that site. In other words, preventing the introduction of new ornamental species to Skukuza would have been the best strategy for minimizing the number of alien ornamental species throughout the park. In contrast, of the species not cultivated 2 out of 32 were not found in Skukuza (cf. 2 out of 225 of the cultivated species, P from a Fisher's exact test is 0.077). The presence of non-cultivated species is more likely to be environmentally limited, and consequently those alien plants that do proliferate, are more likely to be invasive and may have reached some camps by natural dispersal.

I am currently collecting information on the number of ornamental species naturalized outside each camp, and this will further help to determine the different roles of residence time (Pyšek & Jarošík 2005) and human population size (Pyšek *et al.* 2002a) in structuring alien plant invasions in KNP. This will also enable the assessment of the value of early intervention in preventing naturalizations.

Lessons learnt

The problems faced by the invasion of alien plants intentionally introduced for horticulture in KNP are similar to those faced in many other areas around the world. The KNP situation is, however, somewhat unique in that staff villages, landscaped with alien plants, have created islands of abundant alien propagules that threaten native biodiversity throughout a large and otherwise naturally functioning national park. In these nodes, as in many other places in the world, humans have relied on imported alien organisms to create amenable living conditions. Results from this study show that the diversity of alien plants in such nodes is a function of the number of people that reside there. More people mean a greater range of tastes for "different" things, including alien plants, to "enhance" their surroundings. Until recently, the desire of humans to decorate their surroundings with alien plants was not perceived as inappropriate, even within one of the world's wildest national parks which has its own rich and unique flora. Only when the same plants that were used for ornamental purposes became invasive, either in the park or elsewhere in South Africa and the world did perceptions regarding the use of alien plants start changing. The example from KNP is insightful, as it shows the interplay between local conditions (the desire to use alien plants and a range of perceptions regarding the nature of the problem) and changing perspectives at a broader scale (increasing global awareness of problems associated with invasive plants), and ornamental plants in particular, and changing national policies and legislation. The KNP situation perhaps represents a simplified microcosm of the situation that prevails in other areas, which have a greater number of nodes, more humans, and less clear policies regarding the position of alien species.

In the KNP situation, education and increasing awareness of the issues among affected parties emerged as the most important factors contributing to increased support for the control initiatives. However, the most notable change in attitudes came when the programme received the support and leadership of senior KNP officials. The control initiative undertaken to remove ornamental alien plants in KNP is continuing, fortunately with increased support from most staff. To date most of the initial work has been done to remove the most obviously invasive species. However, awareness initiatives are ongoing and need to play a central part in the management programme. Currently the most important issue is the follow-up control of cleared areas, which needs to be maintained on a long-term basis. The importance of timely follow-up control is substantially increased as most plants are manually removed, due to the negative effects of herbicide drift on non-target species, resulting in many species propagating vigorously from small root or stem fragments left behind.

CHAPTER FIVE

PATTERNS OF ALIEN PLANT DISTRIBUTION IN A RIVER LANDSCAPE FOLLOWING AN EXTREME FLOOD[4]

Abstract

The availability of suitable patches and gaps in the landscape is a crucial determinant of invasibility for alien plants. The type and arrangement of patches in the landscape may both facilitate and obstruct alien plant invasions, depending on whether alien species perceive the patches as barriers. In February 2000 tropical weather systems caused an extreme flood with an estimated return interval of 90 to 200 years in the Sabie River, South Africa. The impact of the 2000 flood on the Sabie River landscape provides an array of patches that may provide suitable resources for the establishment of alien plants.

This study examines the distribution of alien plants in relation to patchiness of the Sabie River landscape. My hypothesis was that if certain patches in the river landscape do not represent environmental barriers to alien plant invasion, alien species will occur preferentially in these patch types. The Sabie River within Kruger National Park (KNP) was divided into six patch types (zones, channel types, elevations, geomorphic units, substrates and flood imprint types). I then examined the distribution of native and alien woody and herbaceous density and species richness in patches. The density and species richness of alien plants in the Sabie River in KNP is very low when compared to the density and species richness of native plants. Some patches (bedrock distributary and braid bar geomorphic units) contained higher density and richness of alien plants, indicating that these locations in the river landscape offer the resources necessary for alien plant establishment. Individual alien species are also associated with different parts of the river landscape. Failure of large numbers of alien plants to establish after the 2000 flood is most likely due to a combination of factors – the plant specific barriers imposed by landscape patchiness, the high abundance and richness of native vegetation leading to competition, and for some species certainly, the clearing by the management (Working for Water) programme.

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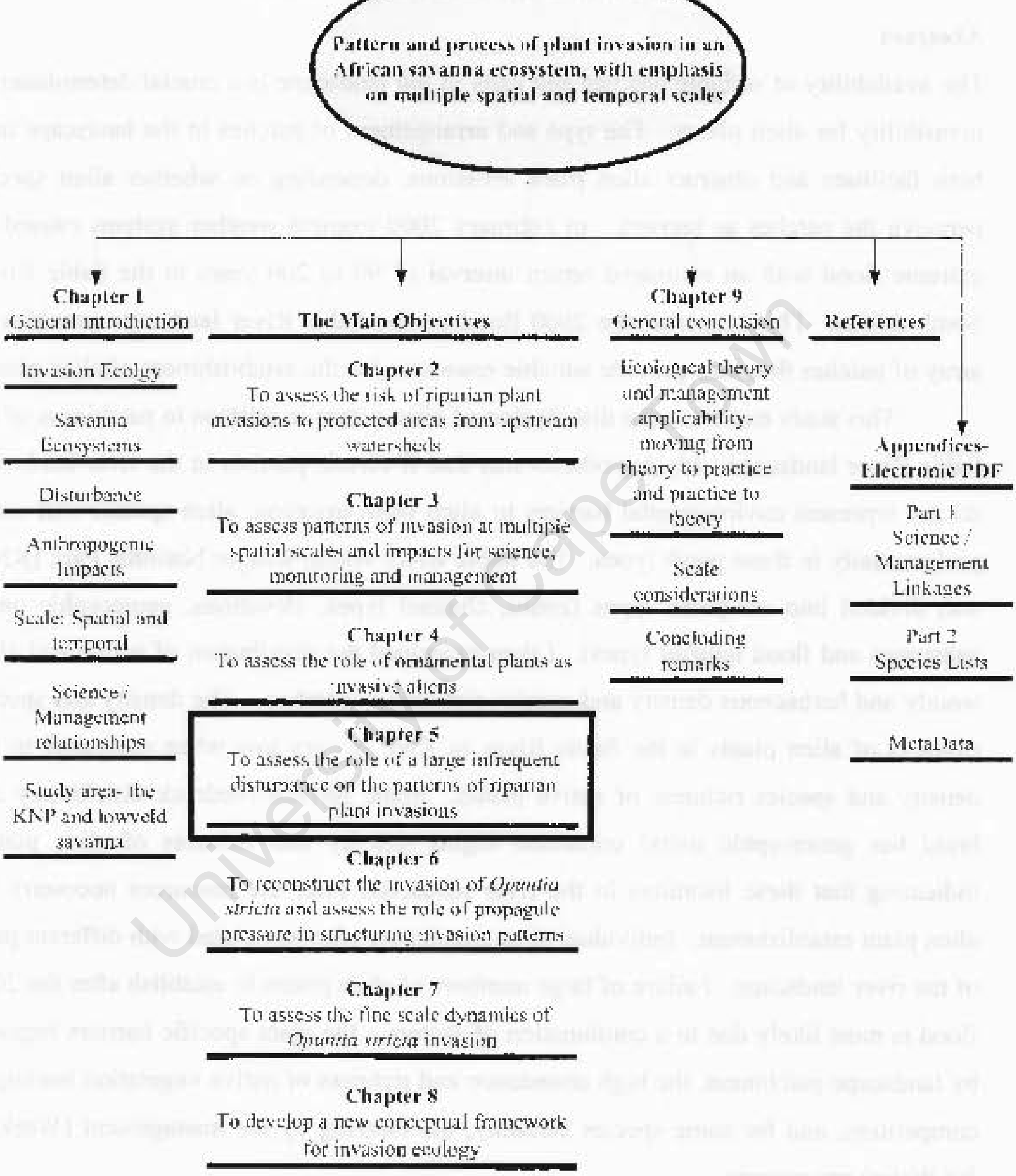
[4] Publication status: Foxcroft, L.C., Parsons, M. McLoughlin, C. & Richardson, D.M. 2007. Patterns of alien plant distribution in a river landscape following an extreme flood. *South African Journal of Botany*, In Press.


Pattern and process of plant invasion in an African savanna ecosystem, with emphasis on multiple spatial and temporal scales
Chapter 1
General introduction
Invasion Ecology
Savanna Ecosystems
Disturbance
Anthropogenic Impacts
Scale: Spatial and temporal
Science/ Management relationships
Study area- the KNP and lowveld savanna
The Main Objectives
Chapter 2
To assess the risk of riparian plant invasions to protected areas from upstream watersheds
Chapter 3
To assess patterns of invasion at multiple spatial scales and impacts for science, monitoring and management
Chapter 4
To assess the role of ornamental plants as invasive aliens
Chapter 5
To assess the role of a large infrequent disturbance on the patterns of riparian plant invasions
Chapter 6
To reconstruct the invasion of *Opuntia stricta* and assess the role of propagule pressure in structuring invasion patterns
Chapter 7
To assess the fine scale dynamics of *Opuntia stricta* invasion
Chapter 8
To develop a new conceptual framework for invasion ecology
Chapter 9
General conclusion
Ecological theory and management applicability, moving from theory to practice and practice to theory
Scale considerations
Concluding remarks
References
Appendices- Electronic PDF
Part 1 Science / Management Linkages
Part 2 Species Lists
MetaData

Introduction

The availability of suitable patches and gaps in the landscape is an important determinant of the susceptibility of riparian ecosystems to alien plant invasions (Richardson *et al.* 2007). Patches may occur as inherent variability caused by climate, topography and geology (White & Harrod 1997), or may be generated via the reorganization of landscapes by abiotic disturbances such as fires, floods, hurricanes, and anthropogenic land-surface alterations (Pickett & White 1985). Patches may also be created by biotic disturbances such as disease outbreaks and successional change (Knight 1987, Pacala & Crawley 1992). Thus, patches of early successional communities, open space, and resource-rich patches often owe their existence to disturbance events (Pickett 1998). Numerous studies have examined the response of invasive species to disturbance and disturbance-generated patches in the landscape (for example: Hobbs 1989, Hobbs & Heunneke 1992, Mack & D'Antonio 1998, Holmes *et al.* 2000, Berlow *et al.* 2001, Grace *et al.* 2001, Brooks & Pyke 2001, Cannas *et al.* 2002, Leishman *et al.* 2004). However, not all open spaces and patches in a landscape are invaded by alien species. Rather, to successfully invade and ultimately transform ecosystems, alien plant species must overcome a series of geographic, environmental, reproductive and dispersal barriers (Richardson *et al.* 2000), which are arrayed spatially within the landscape (Fig. 5.1). Although numerous studies have investigated the role of resource availability (e.g. Hobbs & Heunneke 1992), and the fluctuating availability of those resources (Davis *et al.* 2000), disturbance regimes (e.g. Hobbs 1989, Grace *et al.* 2001, Brooks & Pyke 2001), and empty niches (e.g. Cannas *et al.* 2002) in facilitating invasions, I know of only a few studies that have explicitly examined the role of landscape patches in the context of invasibility (With 2002, 2004). The type and arrangement of patches in the landscape may both facilitate and obstruct alien plant invasions, depending on whether an alien plant taxon perceives patches as a barrier, or as an area of suitable resource availability.

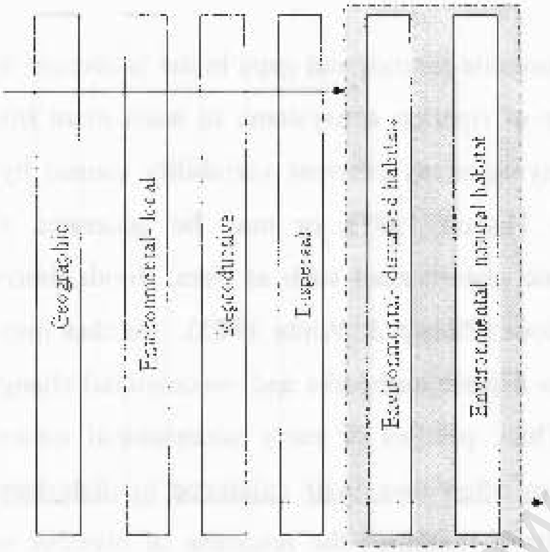


Figure. 5.1: Conceptual barriers in the invasion process (from Richardson *et al.* 2000). In the case of the Sabie River, alien plants will have overcome the first four barriers through various means, but need to overcome the local environmental barriers to become invasive. As disturbance is a natural feature of riparian systems, I see these barriers as being integrated. The reorganisation of the river landscape after a large flood event creates barriers to various alien plants, through the reorganisation of habitats, and the extent to which a particular alien plant perceives the patch as a barrier to, or a gap for, invasion.

Rivers are important conduits for alien plant invasions (Pyšek & Prach 1994, Foxcroft *et al.* 2007, Richardson *et al.* 2007), because rivers are continuous, highly connected components of the landscape. This connectivity facilitates the movement of native organisms between isolated areas in the landscape (van Wilgen *et al.* 2007), but also provides corridors for the transport of unwanted alien organisms (Chapter 2). Riparian areas are particularly prone to alien plant invasions because of their dynamic hydrology, the provision of favourable resource, moisture and nutrient conditions, and frequent disturbance by floods (Tickner *et al.* 2001). In South Africa's Kruger National Park (KNP) many invasive plant species have spread from areas outside the park to areas inside the park along river corridors (Foxcroft & Richardson 2003, Chapter 2). Given the multiple land uses and the abundance and diversity of invasive alien plant species in the watersheds drained by the major rivers of the KNP (Beater *et al.* 2007a,b, Chapter 2, Witkowski & Garner 2007), the incursion of alien species along river corridors is a major threat to riparian zones of KNP and, in turn, to the objectives of the park to maintain biodiversity (KNP 2005).

Disturbance is a fundamental driver of patchiness in river landscapes. The hydrological (flow-regime) and hydraulic actions of water are primary agents of disturbance, creating an irregular, dynamic and shifting mosaic of biotic and abiotic patches at multiple spatial and temporal scales within the river landscape (Tabacchi *et al.* 1998, Malard *et al.* 2000, Arscott *et al.* 2002, Dixon 2003). In the Sabie River, which flows through KNP, a hierarchy of geomorphological river system organization has been derived (van Niekerk *et al.* 1995). The catchment, zone, macro-reach, channel type, reach, geomorphic-unit and micro-site divisions of the hierarchy can be viewed as patches in the river landscape (Rogers & O'Keefe 2003). The type and arrangement of these patches subsequently influences the distribution of riparian vegetation assemblages because each level provides a characteristic physical environment (van Coller *et al.* 2000). However, these patches are not static in space and time and patches may be formed and re-formed by flow events of various magnitude and duration (Rountree *et al.* 2000, Rountree & Rogers 2004).

In February 2000, tropical weather systems caused an extreme flood with an estimated return interval of 90 to 200 years in the Sabie River (Smithers *et al.* 2001). Flow peaked at an estimated 3000 m^3 sec^{-1} where the river enters KNP and at 7000 m^3 sec^{-1} where the river exits the park 100 km downstream at the border with Mozambique (Heritage *et al.* 2001). These discharges compare with typical wet-season (November March) base flows of 15-20 m^3 sec^{-1} and dry season base flows of 3–5 m^3 sec^{-1}. The flood markedly altered the spatial pattern of channel-type, geomorphic-unit and micro-site patches in the river landscape by eroding and depositing sediment, and removing large amounts of riparian vegetation (Parsons *et al.* 2006). The flood also triggered substantial recruitment of riparian plants (Parsons *et al.* 2005), including alien species. As would be expected following disturbance events, the imprint left on the Sabie River landscape by the 2000 flood provides a range of patch types that potentially provide suitable resources for the establishment of alien plants. However, the type and arrangement of patches in the Sabie River landscape could also represent barriers to establishment. Although rivers are effective corridors of alien plant invasion and floods are effective dispersers of propagules, it is not known how alien plants overcome environmental barriers present in river landscapes after disturbance, in order to become established. Therefore, in developing an understanding of the role of barriers in the invasion process, this study examines the distribution of alien plants in relation to patchiness of the Sabie River landscape following the 2000 flood. It is known that the flood water volume was many orders of magnitude higher than average flows, and that the flood reset the river landscape to an early stage of the invasion process. There is also a substantial source of propagules in the upper catchment of the river and I assume that the opportunity for dispersal of propagules was even across the flooded landscape surface. My premise is that, assuming propagules have dispersed and are available (Fig. 5.1), if certain patches in the river landscape do not represent an environmental barrier to alien plant invasion, alien species will have preferences for these patch types. Conversely, if patches in the river landscape do represent an environmental barrier, alien species will not be present in high density and richness in these patch types.

Materials and Methods

Study area

The Sabie River rises in the Mpumalanga Highlands at an altitude of 2200 m and flows eastward for 210 km across the Lowveld and Lebombo geomorphological zones until its confluence with the Incomati River in Mozambique at an altitude of 150 m. It has a catchment area of 7096 km^2, almost half (48%) of which occurs inside KNP, where land is predominantly managed for conservation. Land uses in the portion of the catchment outside KNP comprise 20% cultivated lands, 7% degraded lands, 50% natural vegetation and 20% pine (*Pinus* sp.) and eucalypt (*Eucalyptus* sp.) forest plantations (Beater *et al.* 2007a, Chapter 2). Due to the high invasive species abundance and richness in the portion of watersheds outside KNP (Beater *et al.* 2007b), efforts have been made to assess risk of invasion down the rivers into KNP (Chapter 2). Management projects are currently underway in KNP to address the invasion of alien plant species by a number of vectors. The largest programme currently in operation aims at continuous follow-up or maintenance control operations against a suite of invasive riparian plant species by the national Working for Water programme (Foxcroft & Richardson 2003, appendix 1.2, Freitag-Ronaldson & Foxcroft 2003, appendix 1.3, Morris *et al.* 2007). This largely entails the use of mechanical and chemical methods to control woody shrubs, and uproot annual herbaceous weeds. All areas on both sides of the Sabie River are searched, where accessible, and all alien plants are removed. The most commonly controlled woody alien plants include *Chromolaena odorata*, *Lantana camara*, *Melia azedarach*, *Nicotiana glauca*, *Ricinus communis*, *Senna didymobotrya*, while the most widespread herbaceous alien plants include *Argemone* spp., *Datura* spp. and *Xanthium* spp. Ideally, the areas controlled should be added to this analysis in order to evaluate the influence that management has had on alien plant distribution. Unfortunately, although GIS data of the control areas are available, these readings were not sufficiently accurate to be compatible with the very precise nature of the data collected for the present study. Therefore, I am not certain whether the alien plants occur where they are because they were not cleared from those patches, or, because those patches allow higher rates of establishment due to the characteristics of the patch itself. However, the entire area should have been equally searched during control operations and should not bias my results.

This study focused on the distribution of alien plants within KNP, along the 110 km main-stem section of the Sabie River. The Sabie River has a geomorphologically complex, mixed bedrock and alluvial landscape, where one or more active channels flow within an incised macro-channel that ranges in width from 250–800 m and 8–15 m in depth (van Niekerk *et al.* 1995). Macro reach, channel type, geomorphic unit and micro-site are the nested levels of landscape organization relevant to the section of river within KNP (van Niekerk *et al.* 1995). Micro-sites are defined by their sediment character and elevation, in relation to the geomorphic unit in which they occur. Geomorphic units such as bedrock core bars, distributary channels, lateral bars, pools, riffles, mid-channel bars and benches occur together in specific combinations and proportions to characterise a channel type. Four dominant channel types have been identified in the Sabie River: braided (braiding within the confines of the macro channel), pool-rapid (pools separated by bedrock rapids), mixed anastomosing (multiple channels flowing through alluvium on a bedrock base) and bedrock anastomosing (multiple channels flowing through bedrock fissures) (van Niekerk *et al.* 1995). Macro-reaches, or zones, are characterized by broad changes in geology and discharge capacity in a downstream direction.

The Sabie River exhibits a seasonal, perennial flow regime but is subject to discharge extremes characteristic of semi-arid areas (Parsons *et al.* 2006). Inundation and disturbance of the river landscape by river flows is related to lateral and vertical topography of the template. The macro-channel is divided into two areas, namely the higher elevation macro-channel bank and the lower elevation macro-channel floor. The macro-channel floor can be divided into flow inundation areas, in which elevation is related to the frequency of inundation (Heritage *et al.* 1999). The active area is inundated annually for prolonged periods during both wet and dry seasons, or intermittently for short periods by small floods during the wet season (Parsons *et al.* 2006). The ephemeral area is only inundated during extreme floods.

Data collection and analysis

The Sabie River landscape was divided into six patch types based on physical and environmental characteristics (Table 5.1). Zones represent the broad change in geology and discharge capacity in a downstream direction. Channel types represent differences in macro channel width, channel gradient and geomorphic unit composition (van Niekerk *et al.* 1995). Elevation represents differential space-time inundation of the physical template by flows of different magnitudes. Geomorphic units represent differences in the bedform morphology of the channel, where different geomorphic units occur at different elevations and have different substrate character (Heritage & Moon 2000). Substrate represents the texture of the underlying sediment. Flood imprints represent the physical change in the river landscape due to the 2000 flood, and are calculated on the basis of whether an area of the river landscape changed state, or remained as the same state, following the 2000 flood (Parsons *et al.* 2005). Thus, each of the six patch types has characteristic environmental conditions that may pose an environmental barrier to the establishment of alien plants.

Table 5.1: Description of patch types in the Sabie River landscape.

Patch type	Description
Zone	Identified from maps
Upper	Granite geology, 3000 m^3s^{-1} flood discharge
Mid	Granite geology, intermediate discharge
Lower	Basalt geology, 7000 m^3s^{-1} flood discharge
Geomorphological channel type	Identified from aerial photographs (see Parsons *et al.* 2006)
Braided	Braiding within the confined channel
Pool rapid	Pools separated by bedrock rapids
Bedrock anastomosing	The connection of separate parts of a branching system to form a network; multiple channels flowing through bedrock
Mixed anastomosing	Multiple channels flowing through alluvium on a bedrock base
Elevation	Identified using a high resolution digital elevation model derived from LIDAR data
0–1m, 1–2m, up to >9m	Elevation is the vertical profile, from the level of the water, at one metre intervals
Geomorphic unit	Identified from aerial photographs
Bedrock core bar	Accumulation of finer consolidated sediments and sands on top of bedrock in bedrock anastomosing areas
Bedrock distributary	An individual active channel in a bedrock anastomosing system containing no consolidated and/or unconsolidated sediment
Bedrock pavement	Bedrock bed or base
Braid bar	Accumulation of unconsolidated sediment attached to the side of the channel, possibly associated with a rip-channel causing flow to diverge over a scale that approximates to the channel width
Lateral bar	Accumulation of unconsolidated sediment attached to the side of the channel, possibly associated with a rip-channel at the base of the macro-channel, forming in areas of reduced energy flow
Macro channel bank	The main/edge bank of the macro-channel which extends across the incised valley and contains the sedimentary deposits and riparian vegetation
Substrate	Measured in the field as the substrate in which each plant is rooted. Percent substrate composition in each plot was then calculated.
Bedrock	Bedrock bed / base / boulder
Fines	Silt, clay and organic particles, <0.06 mm
Sand	Coarse river sand, 0.06–2 mm
Sand and fines	Mixed sand and fine substrate
Bedrock and fines	Mixed bedrock and fine substrate
Bedrock and sand	Mixed bedrock and sand substrate
Flood imprint	Identified using a GIS (see Parsons *et al.* 2005 & 2006)
Vegetated to physical	Areas that were vegetated by reeds, shrubs, trees or herbaceous vegetation prior to the 2000 flood, but are now areas of physical rock, sand or water states following the flood.
Stayed vegetated	Areas that were vegetated by reeds, shrubs, trees or herbaceous vegetation prior to the 2000 flood, and remain as one of these vegetated states following the flood
Stayed physical	Areas that were a physical rock, sand or water state prior to the 2000 flood, and remain as one of these physical states following the flood
Vegetated or physical to debris	Areas vegetated by reeds, shrubs, trees or herbaceous vegetation, or that were a physical rock, sand or water state prior to the 2000 flood, but are now areas of woody debris following the flood

Twelve sampling sites were stratified across zones and channel types (Fig. 5.2). Woody riparian vegetation was sampled at each site between July and October 2004, in 30 x 5 m plots running contiguously along transects placed across the river between the tops of the macro-channel banks. Herbaceous riparian vegetation was sampled at each site between April and July 2005 in 5 x 5 m plots placed at 20m intervals along the centre of the woody vegetation transect. Real time differential GPS and a GIS were used to mark accurate plot boundaries. In each plot I identified and counted native and alien plants. Species nomenclature follows Germishuizen & Meyer (2003). The abundance of each species in each plot was converted to density (number of plants per ha), and species richness was calculated as the number of species in each plot. There are 548 plots in the woody vegetation data set and 156 plots in the herbaceous vegetation data set.

To determine the density and species richness of native and alien woody and herbaceous vegetation in the six patches, plots were assigned to each of the categories listed in Table 5.1. Each plot fell within a certain zone, geomorphological channel type and elevation. A geomorphic unit, substrate and flood imprint was derived for each plot in a GIS by considering the proportional area of the plot contributed by a dominant geomorphic unit, substrate or flood imprint type. If a plot was occupied by >70% of a certain geomorphic unit or substrate and >60% of a flood imprint type, then that geomorphic unit, substrate or flood imprint type was assigned to the plot. Plots not dominated by any certain geomorphic unit, substrate or flood imprint were deleted from the data set. In the geomorphic unit patch, 7 plots were deleted from the herbaceous data and 65 from the woody data, retaining 96 and 93% of total plant abundance respectively. In the substrate patch, 11 plots were deleted from the herbaceous data and 75 from the woody data, retaining 93 and 88% of total plant abundance. In the flood imprint patches, 24 plots were deleted from the herbaceous data and 167 from the woody data, retaining 81 and 82% of total abundance respectively.

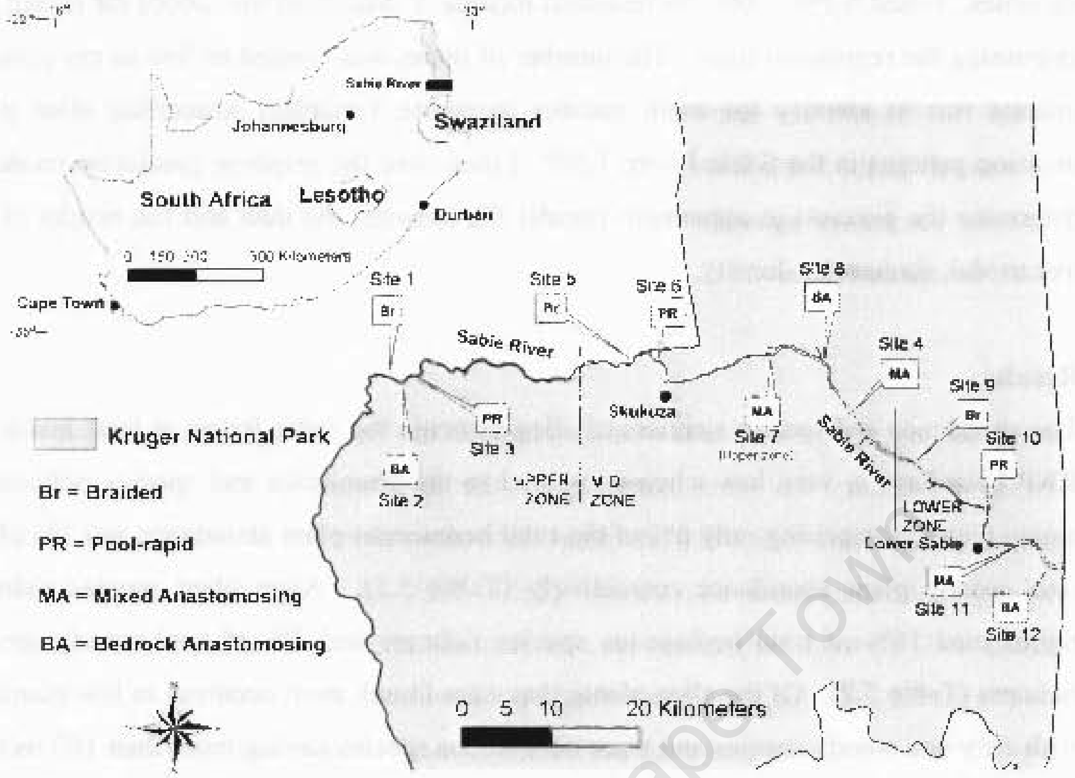


Figure 5.2: Location of sampling sites within zones and geomorphological channel types along the Sabie River. The insert places the study site in context with the rest of South Africa.

The plots belonging to each category within a patch type were used to calculate mean density and species richness of alien and native woody and herbaceous vegetation. One-way ANOVA was used to examine differences in density and species richness, using the categories within a patch (Table 5.1) as treatments. Sample sizes are unbalanced among treatments because of the complex morphology of the river channel, where different numbers of plots occurred in different zones, channel types, elevations, geomorphic units, substrates and flood imprints.

To examine the influence of the patches on individual alien species I used regression tree models. I only analysed 12 selected species for which there were more than 20 records across all 12 transects. Tree-based models provide an alternative to linear and additive logistic models for regression analysis (Breiman *et al.* 1984, Vayssieres *et al.* 2000). Regression tree models successively split data to form homogeneous subsets, resulting in a hierarchical tree of decision rules useful for exploring interactions between variables. I used S-Plus 2000 Professional Release 3 (MathSoft Inc. 2000) for fitting and examining the regression trees. The number of nodes was limited to five as my primary interest was to identify the main patches (response variables) structuring alien plant invasion patterns in the Sabie River, KNP. I then used the response prediction model to determine the percentage agreement (model fit) between the data and the results of the tree model, for species density.

Results

The abundance and species richness of alien plants in the Sabie River, at least inside the KNP boundary, is very low when compared to the abundance and species richness of native plants, comprising only 6% of the total herbaceous plant abundance and 3% of the total woody plant abundance respectively (Table 5.2). Alien plant species richness represented 16% of total herbaceous species richness and 7% of total woody species richness (Table 5.2). Of the alien plants that were found, most occurred in low numbers, with only one woody species and three herbaceous species having more than 100 records across all 12 transects (Table 5.3). Nine woody alien species were recorded during the survey, comprising only one naturalized species, but eight invasive species (Table 5.3). In contrast, 19 herbaceous alien species were recorded, with seven species considered invasive and the rest naturalized (Table 5.3).

Table 5.2: Summary of herbaceous and woody alien and native plant abundance and species richness in the Sabie River. Total sampling area for the herbaceous vegetation is 3 900 m^2 and for woody vegetation is 82 200 m^2.

	Abundance		Species richness	
	Number of individuals	**% of total**	**Number of species**	**% of total**
Herbaceous				
Alien	1463	6	19	16
Native	21377	94	99	84
Total	22840		118	
Woody				
Alien	306	3	9	7
Native	8547	97	127	93
Total	8853		136	

Table 5.3: Alien plant species recorded on the Sabie River.

Species	Authority	Abu	Status	Controlled
Herbaceous				
Acanthospermum hispidum	DC.	3	Naturalized	No
Argemone ochroleuca	L.	2	Invasive	Slash/uproot
Bidens biternata	(Lour.) Merr. & Sherff	4	Naturalized	No
Bidens pilosa	L.	1	Naturalized	No
Cardiospermum halicacabum	L.	38	Invasive	Uproot
Catharanthus roseus	(L.)G.Don	43	Invasive	Uproot
Chenopodium album	L.	2	Naturalized	No
Commelina benghalensis	L.	102	Naturalized	No
Crotalaria agatiflora	Schweinf.	1	Naturalized	No
Flaveria bidentis	(L.)Kuntze	8	Naturalized	No
Pennisetum setaceum	(Forssk.) Chiov.	67	Naturalized	No
Persicaria lapathifolia	(L.) Gray	241	Naturalized	No
Pistia stratiotes	L.	681	Invasive	Biocontrol
Pupalia lappacea	(L.) A.Juss.	32	Naturalized	No
Senna occidentalis	(L.) Link	15	Invasive	Cut-stump/herbicide
Tagetes minuta	L.	22	Invasive	No
Tridax procumbens	L.	78	Naturalized	No
Waltheria indica	L.	56	Naturalized	No
Xanthium strumarium	L.	67	Invasive	Slash/uproot
Woody				
Caesalpinia decapetala	(Roth) Alston	1	Invasive	Cut-stump/herbicide
Chromolaena odorata	(L.) R.M.King & H.Rob.	3	Invasive	Cut-stump/herbicide
Cocculus hirsutus	(L.) Diels	3	Naturalized	No
Lantana camara	L.	201	Invasive	Cut-stump/herbicide
Melia azedarach	L.	6	Invasive	Cut-stump/herbicide
Ricinus communis	L.	4	Invasive	Cut-stump/herbicide
Senna didymobotrya	(Fresen.) Irwin & Barneby	8	Invasive	Cut-stump/herbicide
Senna septemtrionalis	Willd.	7	Invasive	Cut-stump/herbicide
Sesbania punicea	(Cav.) Benth	73	Invasive	Biocontrol

Authority– following Germishuizen and Meyer (2003)

Abu Abundance

Status– Current status of alien plants in KNP (terms follow Pyšek *et al.* 2004).

In all six patches, there is an order of magnitude difference between native and alien plant density, for both herbaceous and woody vegetation (Fig. 5.3-5.8), indicating that native plants are numerically dominant in the post-flood river landscape. Similarly, in all patches, alien plant species richness is always markedly lower than native plant species richness. One anomaly was observed, where alien and native woody species abundance and richness is the same in the stayed physical flood imprint type. The stayed physical imprint type predominantly occurs at low areas of the channel (M. Parsons, unpublished data) and is therefore probably frequently disturbed.

Although the herbaceous alien plants showed some differences in density and species richness between patch types, there was only a significant difference in herbaceous density and species richness among geomorphic units (Fig. 5.7). Herbaceous alien plant density was almost an order of magnitude higher in the bedrock distributary and braid bar geomorphic units than in the other units, while species richness was highest in the braid bar geomorphic unit (Fig. 5.7).

There was a significant difference in woody alien density and species richness among zones (Fig. 5.3), channel types (Fig. 5.4), and geomorphic units (Fig. 5.7). There were no differences in woody alien plant density among elevations (Fig. 5.5) or in woody alien plant species richness among flood imprints (Fig. 5.6). Woody alien density and species richness is highest in the upper and mid zones (Fig. 3). Woody alien species are significantly lower in both density and richness in the pool rapid channel type, while the braided, mixed anastomosing and bedrock anastomosing channel types are have similar density and species richness (Fig. 5.4). Although not significantly different among elevations, woody alien plant density and species richness was highest in the braid bar geomorphic unit, with almost equal distribution of density and species richness across the other geomorphic units (Fig. 5.7). Woody alien species richness was highest below an elevation of 3 m, which is in contrast to native woody species richness which increases steadily up to an elevation of 7 m. Similarly, woody alien plant density was highest in the stayed physical flood imprint type, while the vegetated to physical and stayed vegetated flood imprint types had equal density, and the vegetated or physical to debris flood imprint type the lowest. Woody alien species richness was highest on sand substrates, and lowest on the bedrock and bedrock/fines substrates.

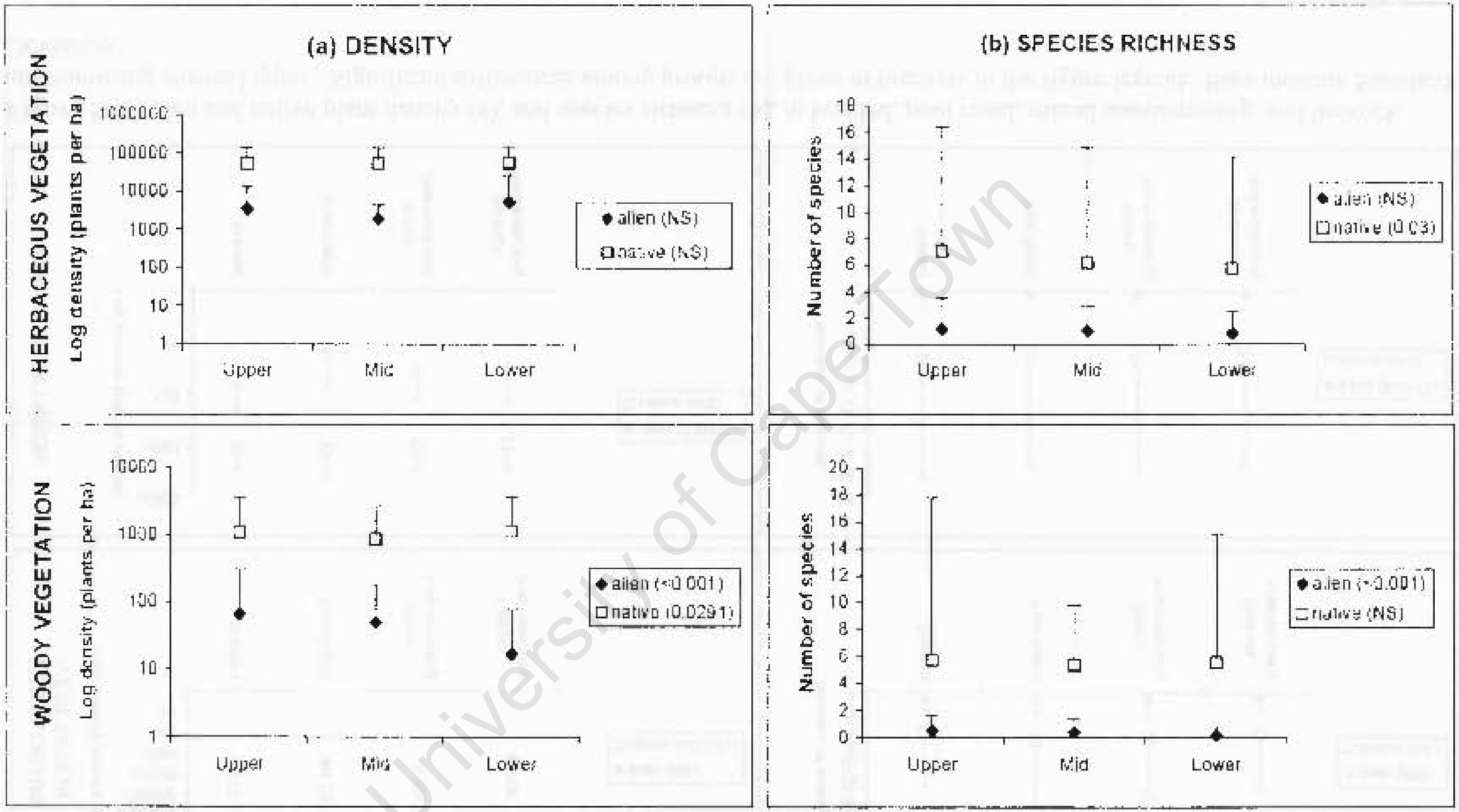


Figure 5.3: Alien and native plant density (a), and species richness (b), in upper, mid and lower zones. Significant differences among groups are given in brackets in the figure legend. Bars indicate Standard Deviation.

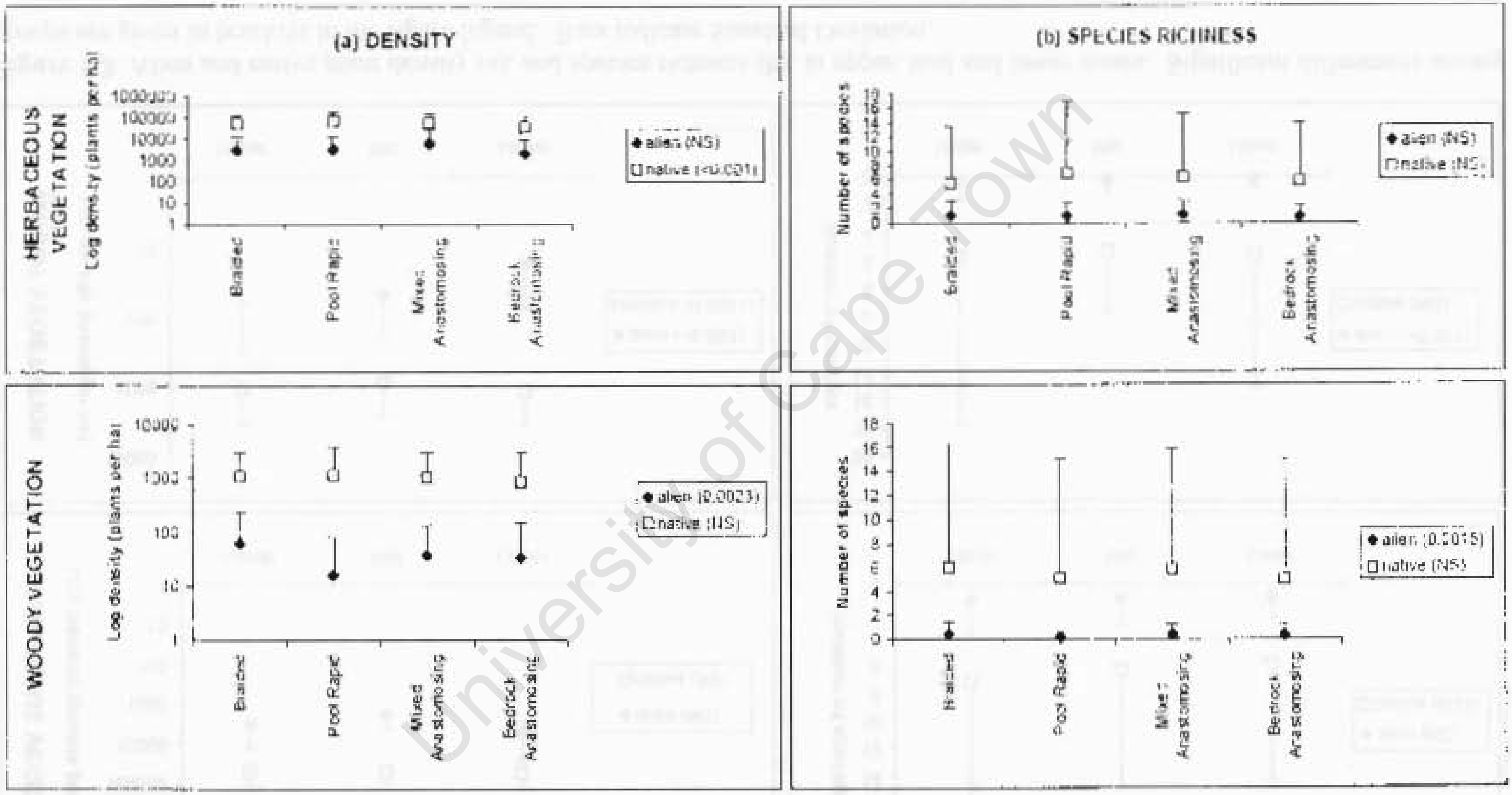


Figure 5.4: Alien and native plant density (a), and species richness (b), in braided, pool rapid, mixed anastomosing, and bedrock anastomosing channel types. Significant differences among groups are given in brackets in the figure legend. Bars indicate Standard Deviation.

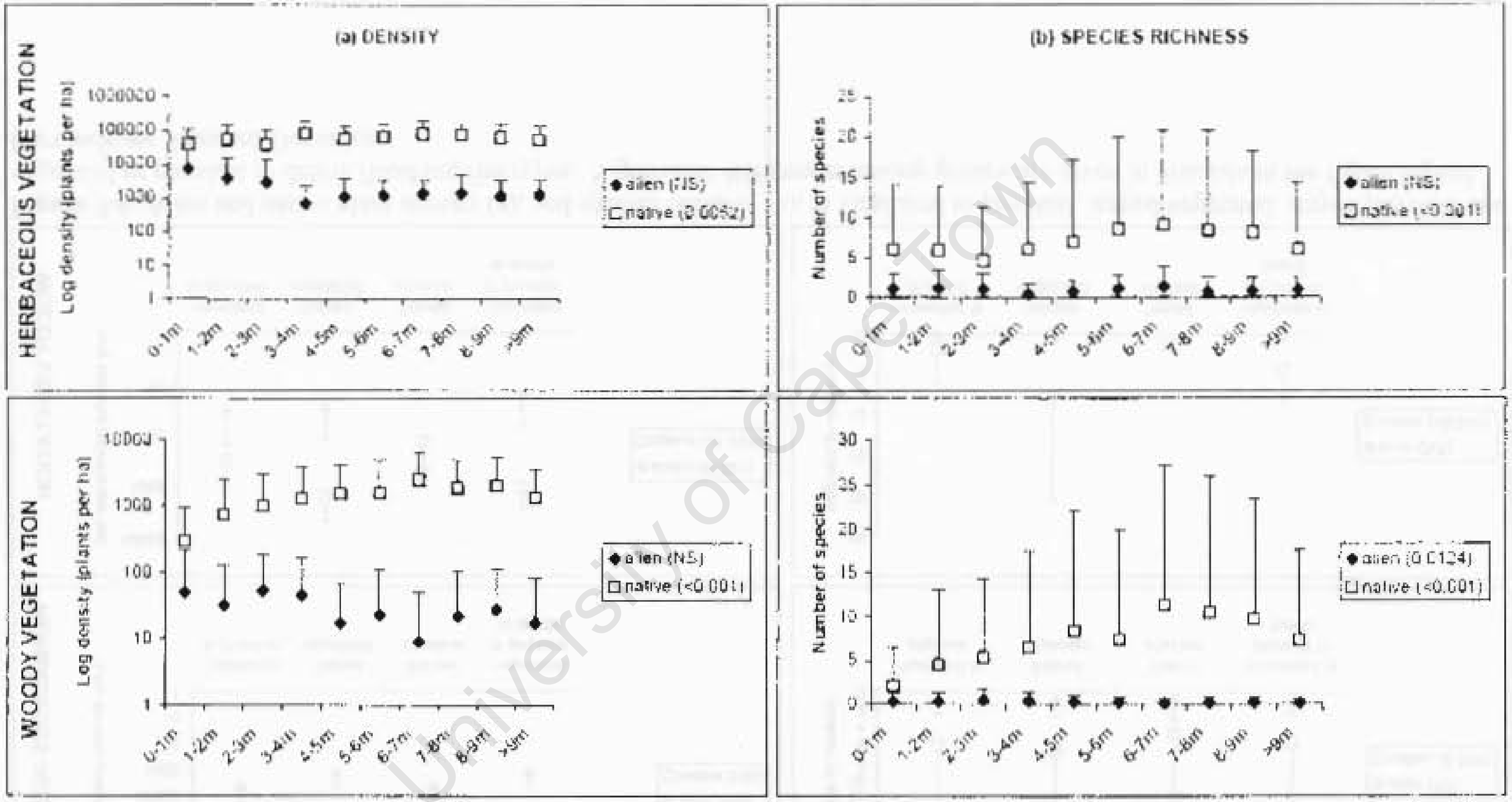


Figure 5.5: Alien and native plant density (a), and species richness (b), in 1–m elevation intervals. Significant differences among groups are given in brackets in the figure legend. Bars indicate Standard Deviation.

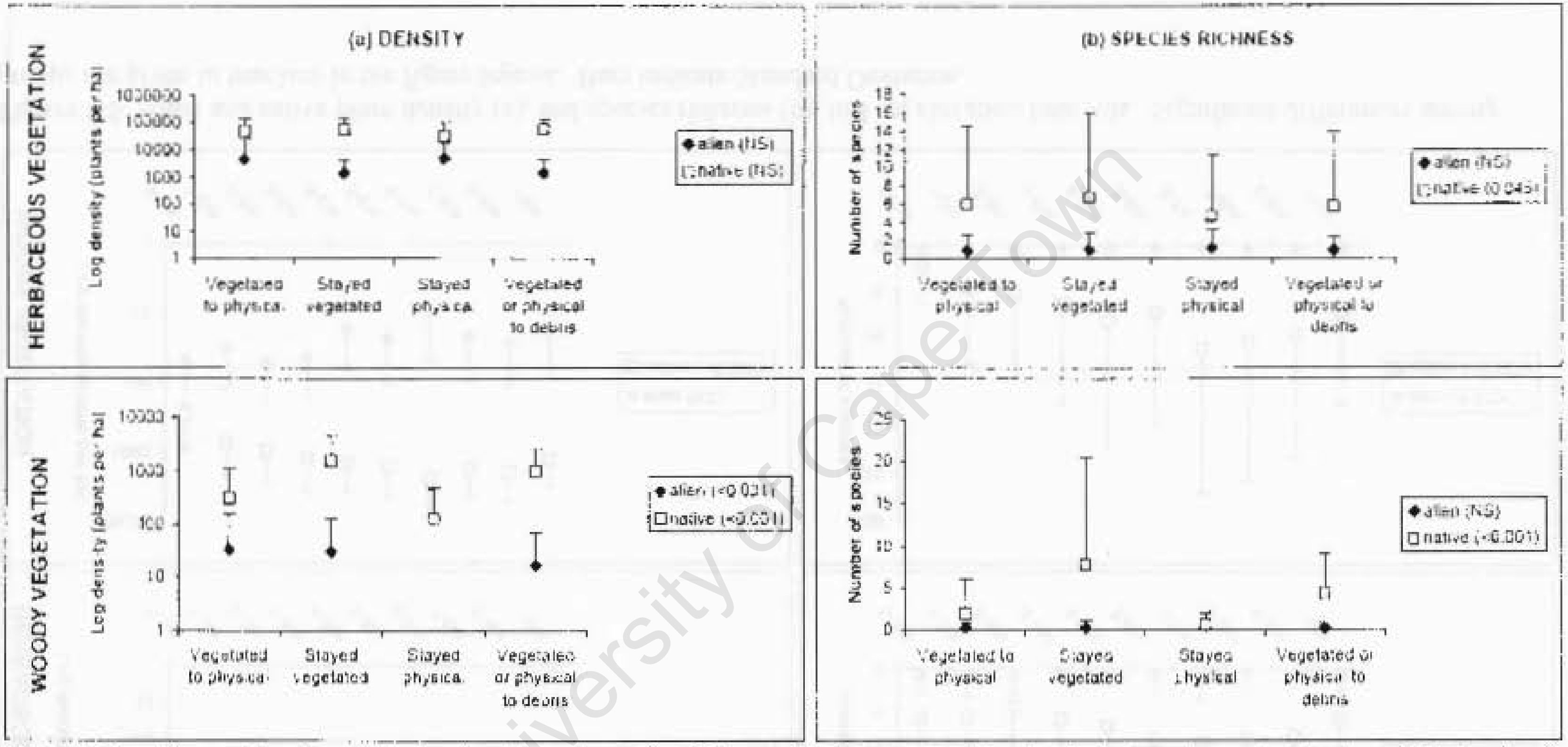


Figure 5.6: Alien and native plant density (a), and species richness (b), in vegetated to physical, stayed vegetated, stayed physical and vegetated or physical to debris flood imprint types. Significant differences among groups are given in brackets in the figure legend. Bars indicate Standard Deviation.

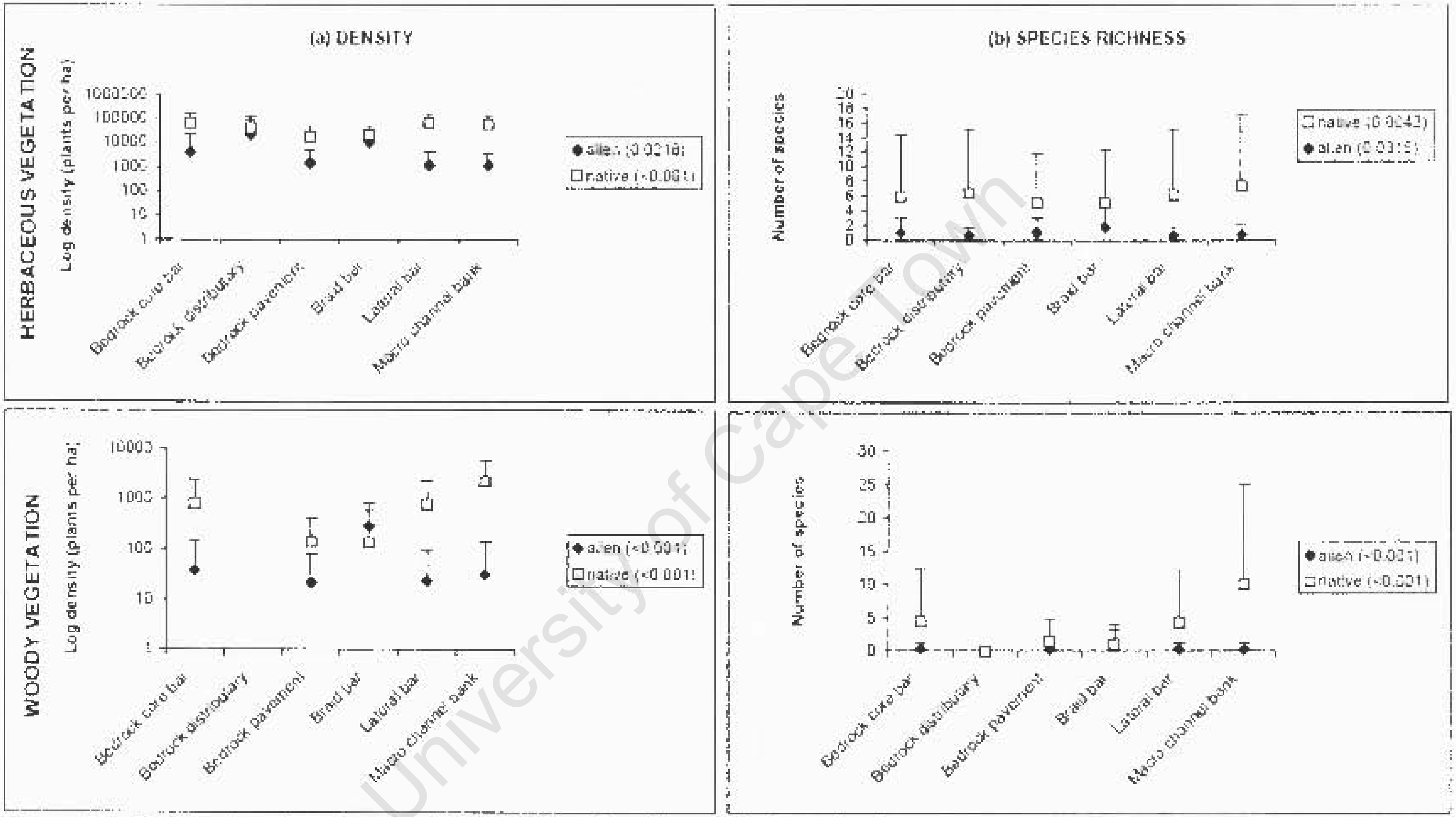


Figure 5.7: Alien and native plant density (a), and species richness (b), in bedrock core bar, bedrock distributary, bedrock pavement, braid bar lateral bar, and macro-channel bank geomorphic units. Significant differences among groups are given in brackets in the figure legend. The bedrock distributary geomorphic unit does not contain any woody vegetation. Bars indicate Standard Deviation.

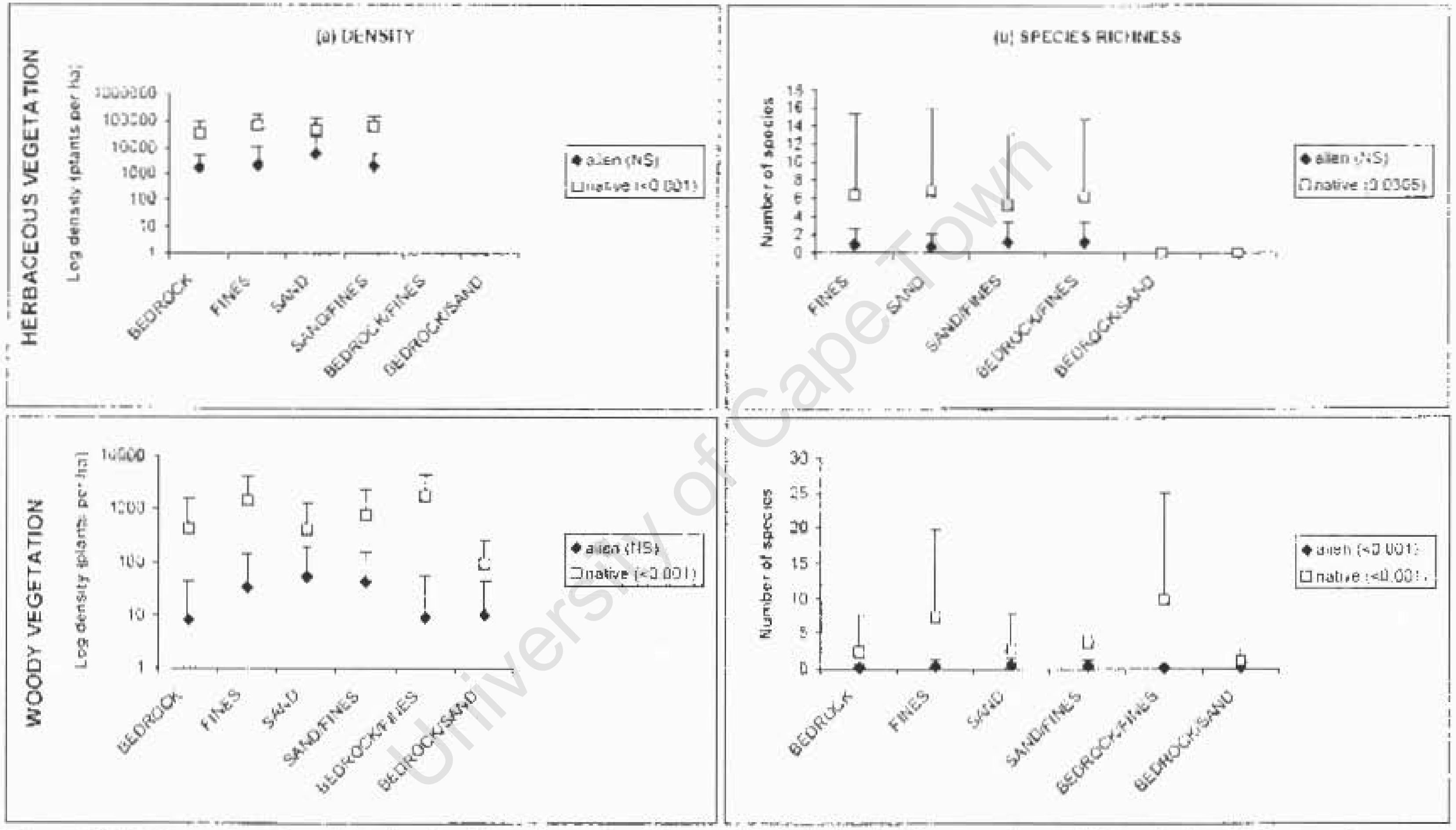


Figure 5.8: Alien and native plant density (a), and species richness (b), in bedrock, fines, sand, sand/fines, bedrock/fines, and bedrock/sand substrates. Significant differences among groups are given in brackets in the figure legend. Bars indicate Standard Deviation.

Two woody species (*Lantana camara* and *Seshania punicea*) and 10 herbaceous species (Table 5.4) were analysed using regression tree analysis (Fig. 5.9., *S. punicea*, for an example), to determine the main patch type (variable) influencing the pattern of that species (Table 5.4). The percentage agreement between the data and the fitted model varied from 78% to 95% (Table 5.4). *Lantana camara* appears to have responded primarily to the flood imprint type, with the highest abundance being recorded in vegetated to physical, stayed vegetated or vegetated or physical to debris flood imprint types. The lowest density of *L. camara* was found in the stayed physical flood imprint type, as well as between 0–2 m elevation and >4 m elevation. *Seshania punicea* responded mainly to geomorphic units, and was found in high density in braid bars, below an elevation of 1 m. *Cardiospermum halicacabum* responded in a similar manner to *L. camara*, being found in high density in the same disturbance patch types. The response of *C. roseus* to elevation was slightly unclear, but it appears that the highest abundances were found between an elevation of 1–7 m. *Commelina benghalensis* responded mainly to substrate, with highest abundances on rock, sand and fine substrates, and not on the combined substrates. *Pennisetum setaceum* responded solely to geomorphic units being found in abundance only on braid bars and in low abundance in all other units. *Persicaria lapathifolia* responded similarly, but was found on braid bars, lateral bars and bedrock core bars in high abundance. *Tagetes minuta* was found in high abundance on sandy substrates, in the bedrock anastomosing and pool rapid channel types. *Tridax procumbens* was found in highest abundance between an elevation of 1–3 m, and in low abundance in all other elevations. *Waltheria indica* also responded primarily to elevation, and while not entirely clear, appears to be found in high abundance in the mid elevation ranges. Although *Xanthium strumarium* responded to flood imprint type, this response is unclear as high densities of *X. strumarium* were found in the stayed physical, vegetated to physical, vegetated or physical to debris flood imprint types. However, *X. strumarium* is also found in the upper zone, at low elevation in high abundance. Thus, individual woody and herbaceous alien plant species are associated with different patch types in the Sabie River landscape.

Table 5.4: Response of selected alien plants to patch type, as suggested by the regression tree analysis (see Fig. 5.9 for an example). The main response variable is the variable (patch type) that is responsible for the first split in regression tree. The % agreement was determined using the response prediction model to determine the percentage agreement (model fit) between my data and the results of the tree model.

Species	**Number of records**	**Main response variable (patch type)**	**Response**		**% agreement Abundance (plants/ha)**	**Management type**
			High abundance	**Low abundance**		
Woody						
Lantana camara	201	Flood imprint	Vegetated to physical, stayed vegetated, vegetated or physical to debris.	All flood imprint types except for those indicated in the high abundance column, and, elevation between 0–2 m, >4 m.	78	Cut stump treatment
Sesbania punicea	73	Geomorphic unit	Braid bar, and, at an elevation of <1 m.	All geomorphic units except for braid bar, and, at elevations of >1 m.	94	Biological control
Herbaceous						
Cardiospermum halicacabum	38	Flood imprint	Vegetated to physical, stayed vegetated, vegetated or physical to debris.	All flood imprint types except for those indicated in the high abundance column, and, elevation between 0–2 m, >4 m, and, on all channel types except for braided bar and macro-channel bank/ bedrock core bar.	85	Uprooting
Catharanthus roseus	43	Elevation	At elevations between 1–3 m, 4–5 m, 6–7 m, and, on braided channel types.	At elevations of 0–1 m, 3–4 m, 5–6 m and >7 m.	92	Uprooting
Commelina benghalensis	102	Substrate	On rock, sand and fine substrates, and, on flood imprint types of vegetated or physical to debris, vegetated to physical, or stayed vegetated.	On all combinations of substrates, except for those indicated in the high abundance column.	78	None

Pennisetum setaceum	67	Geomorphic unit	Braid bar units.	All other geomorphic units.	95	
Persicaria lapathifolia	241	Geomorphic unit	Braid bar, lateral bar, bedrock core bar.	All other geomorphic units.	78	None
Pupalia lappacea	32	Elevation	Elevation of 3–4 m, 5–6 m, >8 m, and, fine substrate, and, in the mid zone.	Elevation of 0–3 m, 4–5 m, 6–8 m.	92	None
Tagetes minuta	22	Substrate	Sand substrate, and, flood imprint types of vegetated to physical, stayed vegetated or stayed physical, and, in bedrock anastomosing and pool rapid channel types.	Elevation of 0–5 m, >6 m.	95	Uprooting/ slashing
Tridax procumbens	78	Elevation	Elevation of 1–3 m, and, patch types of vegetated to physical, stayed vegetated and vegetated or physical to debris, and, substrate of sand or sand/fines.	Elevation of 0–1 m, >3 m.	81	None
Waltheria indica	56	Elevation	Elevation of 4–5 m, 6–8 m, >9 m, and, in the lower zone, and, in bedrock anastomosing and mixed anastomosing channel types.	Elevation of 0–4 m, 5–6 m, 8–9 m.	87	None
Xanthium strumarium	67	Flood imprint	Flood imprint types of stayed physical, vegetated to physical, vegetated or physical to debris, and, in the upper zone, and, at elevations of 1–2 m.	On all other flood imprint types and combinations thereof.	93	Uprooting/ slashing

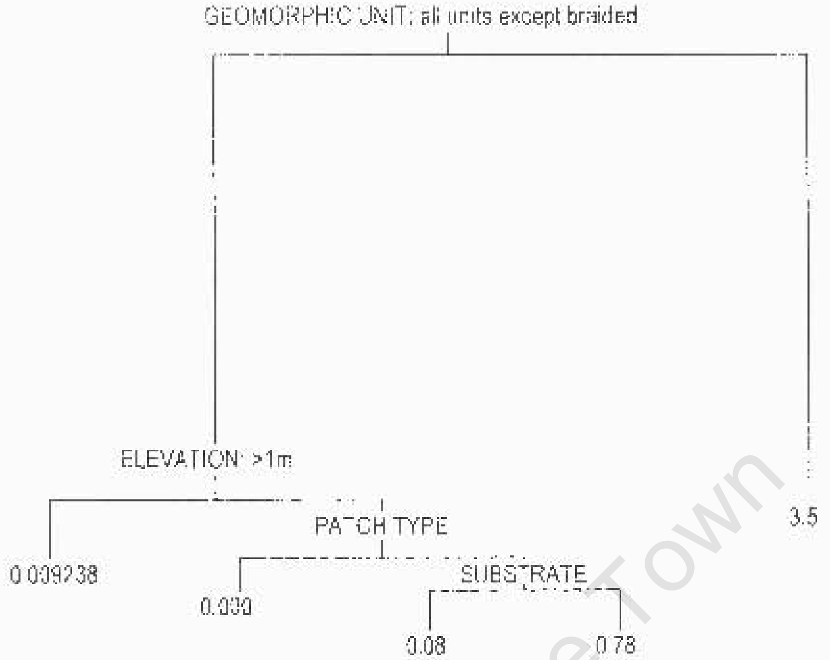


Figure 5.9: Regression tree of *Sesbania punicea* abundance along the Sabie River. Rules indicated on top of each splitting branch apply to the left branch. Values at terminal nodes indicate the predicted density (plants/ha). The variable at the top of the tree represents the most important variable by which the data is successively split to form the homogenous groups at the terminal nodes.

Discussion

My hypothesis of patches acting as barriers in the river landscape is supported. Some patches contained higher density and richness of alien plants, indicating that these locations in the river landscape offer the resources necessary for alien plant establishment. Density and species richness of herbaceous alien plants appear to be strongly associated with geomorphic units in the Sabie River. This was supported by a number of species which indicated geomorphic units to be the main driver of distribution. In particular, the braid bar geomorphic unit appears to be particularly important. Braid bars are characteristically eroded and reformed during major floods (Heritage & Moon 2000), through accumulation of unconsolidated sediment. It is most likely that alien plant propagules are deposited in the sediments of the newly formed (thus disturbed) bars, and are able to colonize these areas quickly. The response of alien plants to flood imprints are however not very clear, as there was no preference to either the staved physical, vegetated to physical, vegetated or physical to debris flood imprint types. It does appear though that some alien plant species were more frequently found in patches of woody debris, matching the response found by Pettit & Naiman (2006) who report higher abundance and richness of seedlings taken from soil under debris piles in comparison to the surrounding area. This is not surprising, as the debris piles would provide protection to seedlings and increased surface detritus and nutrients from the accumulated decomposing material (Pettit & Naiman 2005).

To gain further insight into the roles of patches in the landscape as barriers to alien plant invasion, the similarities and contrasts of both the trends in alien plant density and richness, as well as trends of the individual species, should be compared. Although trends in alien plant density and richness broadly indicate preferences of herbaceous and woody life forms for certain patches, individual alien species are more clearly associated with different patches. This indicates that patches act as barriers to the invasion of individual species in the river landscape. However, the variation and standard deviations for density and species richness across all the patches indicates a high degree of variability in the system. This may indicate the inherent variability of plant distribution in the river landscape. The higher species richness and density of alien plants at lower elevations (0-3 m), although only significant for herbaceous species, is probably an indication of the higher frequency of disturbance by subsequent flows at lower elevations in the river channel. However, when viewed at the species level, except for *Sesbania punicea* which has higher abundances below 1 m, the response of individual species to elevation is not very clear. This possibly means that *S. punicea* invasion is facilitated by the conditions provided at low elevations in the channel, perhaps more frequent inundation or disturbance. However, it is also interesting to note that native species richness is also lowest in the disturbed conditions at lower elevations. Clearly, patchiness or gaps in the system provide for increased invasion ability (With 2002). However, no work has assessed the response of individual species to a range of potential barriers present in a particular system. The specific traits of each alien species will influence the degree to which it is associated with different patch types, and thus the degree to which certain patches then act as barriers to invasion. This will most likely be a product of the dispersal mode and propagule production, defence mechanisms, resource demands, competitiveness, seed banking strategies and seed size of each species. Thus, individual species invasions are associated with different parts of the river landscape following a large flood.

Two additional factors may be important barriers for the establishment of alien species in the Sabie River landscape. These are the management programme (clearing by Working for Water teams) and the richness and density of native vegetation in the landscape. Alien plants currently represent a small percentage of the total plant abundance and species richness in the Sabie River within KNP, and half of the species I recorded are controlled either mechanically/chemically or biologically (Table 5.3). The fact that less than six percent of the total plant abundance comprises alien species may indicate the effectiveness of the clearing programme. The low abundance of alien plants is thus either a limitation of the study or an indication of the barriers to species establishment in the system. However, the low abundance of alien plants might be an important strength of the study as well, as this represents the situation as is currently experienced in an area that is receiving ongoing management, and perhaps, the current population of alien plants might then represent preferential areas for growth and which supply sufficient resources to allow rapid re-colonisation. It also appears that the high native species abundance and richness might be playing an important role in maintaining invasions at low level. Parsons *et al.* (2005) reported that 75% of woody plant abundance in the post-flood landscape was contributed by plants that established after the flood and 25% by residual plants that survived the flood. The presence of relatively high abundances of both newly established and residual native plants in the Sabie River landscape may exert competitive influences on alien plants. Although there is a vast literature that both supports and contradicts the competitive role of native vegetation viewpoint (for example, Kennedy *et al.* 2002, Stohlgren *et al.* 2003), there is clearly a substantial difference in abundance between alien and native vegetation along the Sabie River. This warrants further investigation, probably at multiple spatial scales, before the effect of native species richness on alien plants is better understood.

Overall, alien plants represented a small proportion of the vegetation in the Sabie River landscape after the 2000 flood. Given the propagule pressure from outside the park, this is perhaps unusual. The slight trend of decreasing density and richness between the upper, mid and lower zones of the Sabie River indicates the importance of propagule pressure in the watershed to the west of KNP, agreeing with other studies that have highlighted this area as a major source of invasion for the lower reaches (Beater *et al.* 2007b, Chapter 2, Witkowski & Garner 2007). The failure of many alien plant species to establish after the 2000 flood is likely due to a combination of factors – the plant specific barriers imposed by the structure and pattern of patches in the landscape, the high abundance and richness of native vegetation leading to competition, and for some species certainly, the clearing operations.

If management was only concerned with one species, it is likely that the barriers and promoters of invasion could be determined, and priority areas mapped accordingly. However, where multiple species are concerned and the removal of one species may result in replacement by another alien species, a more holistic approach is needed. For example, overall, the braid bar is an important patch for most species. However, it does not appear to be at all important for *L. camara*, which remains a high priority species in the KNP. The most important consideration for managers controlling alien plants then might be to determine which areas of the landscape patch mosaic are most likely to be invaded by 1) a suite of invasive plants, the combined effect of which might be particularly harmful, and 2) aggressive species which might occur over a wider area, and then determine what indigenous species are likely to be impacted in these highly invaded areas.

I have taken a new approach to elucidate patterns of alien plant invasion by considering the river landscape as patches that may act as barriers to the establishment of alien plants after a large flood disturbance. I have shown that different densities, species richness and individual alien plant species occur in different patches in the Sabie River landscape following a large flood. Management strategies of largely natural systems such as KNP should be based on an understanding of alien species distributions and preferences for patches in the river landscape. Managing for plant invasions at places in the landscape that alien plants do not have a preference for, and without consideration of the ways that patches may act as barriers to invasion, can be wasteful of resources and may allow invasions to progress rather than be inhibited.

CHAPTER SIX

RECONSTRUCTING FIFTY YEARS OF *OPUNTIA STRICTA* INVASION: ENVIRONMENTAL DETERMINANTS AND PROPAGULE PRESSURE[5]

Abstract

Many factors influence the spread dynamics and distribution of invasive alien organisms. Despite progress in unravelling the determinants of invasiveness and invasibility, robust, spatially-explicit predictive models for explaining real-world invasion dynamics remain illusive. Reconstructing invasion episodes is a useful way of determining the roles of different factors in mediating spread and proliferation. In many cases, however, human-aided dispersal and other anthropogenic factors blur the roles of natural controlling factors. I describe the reconstruction of an isolated invasion event from a known source: the 50-year invasion history of *Opuntia stricta* in Kruger National Park. My aim was to explore the relative roles of environment and propagule supply in shaping the invasion pattern. Environmental variables (landscape heterogeneity and distance from water sources) were moderately useful for explaining the presence/absence of *O. stricta* in 1-ha cells across the 660 km^2 (53% of cells correctly classified). Adding fire frequency increased the accuracy of the model (68%). However, when I considered the role of propagule pressure (measured as the distance of sites from the known primary invasion focus and putative secondary invasion foci), model accuracy was greatly improved (77%). No environmental variables or propagule pressure correctly explained spatial variation in abundance (expressed as cladode density in 1-ha cells). I discuss implications of the importance of propagule supply for modelling and managing invasions.

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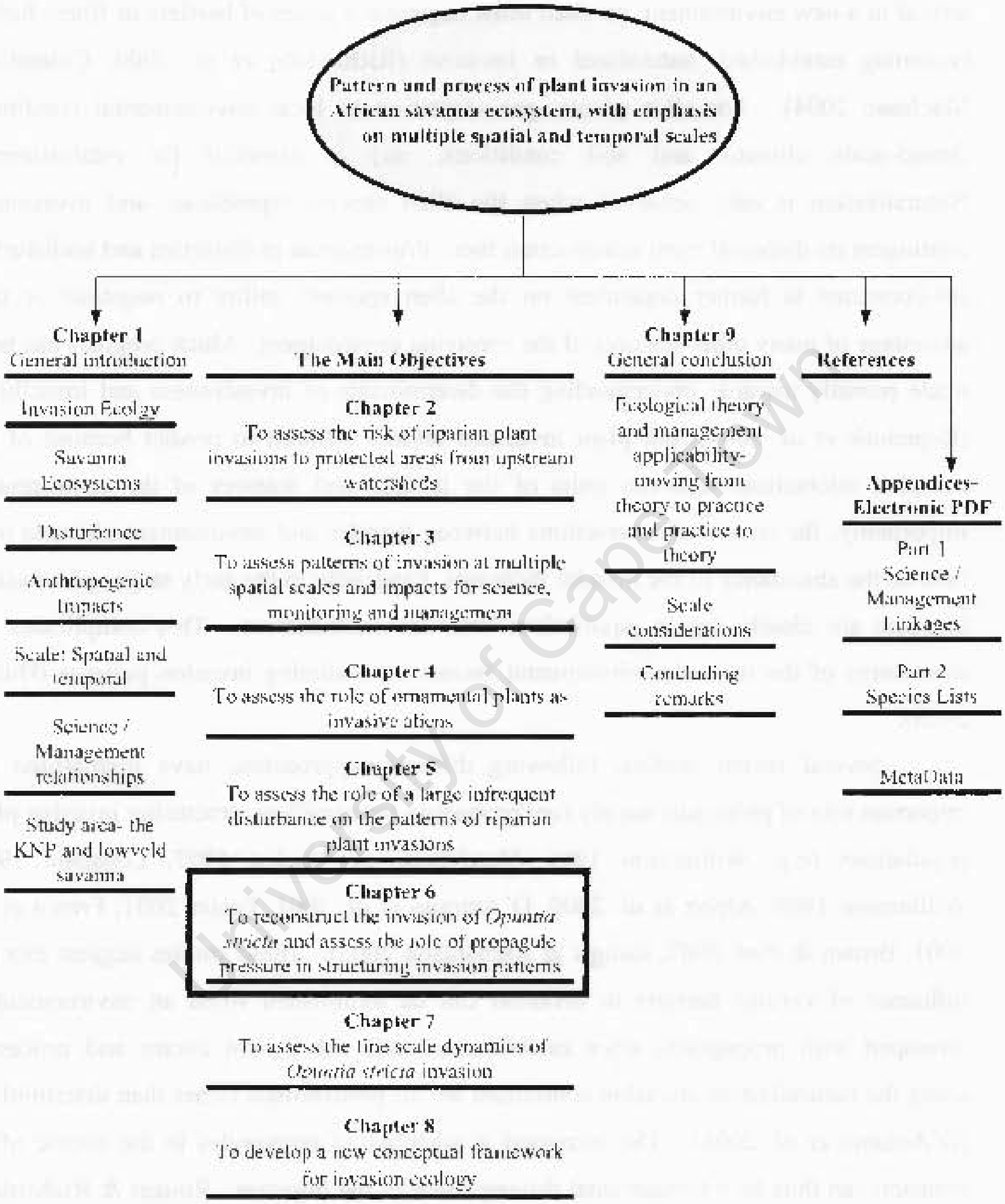
[5] Publication status: Foxcroft, L.C., Rouget, M., Richardson, D.M. & MacFadyen, S. 2004. Reconstructing 50 years of *Opuntia stricta* invasion in the Kruger National Park, South Africa: environmental determinants and propagule pressure. *Diversity and Distributions* 10: 427–437.


Pattern and process of plant invasion in an African savanna ecosystem, with emphasis on multiple spatial and temporal scales
Chapter 1
General introduction
Invasion Ecolgy
Savanna Ecosystems
Disturbance
Anthropogenic Impacts
Scale: Spatial and temporal
Science / Management relationships
Study area- the KNP and lowveld savanna
The Main Objectives
Chapter 2
To assess the risk of riparian plant invasions to protected areas from upstream watersheds
Chapter 3
To assess patterns of invasion at multiple spatial scales and impacts for science, monitoring and management
Chapter 4
To assess the role of ornamental plants as invasive aliens
Chapter 5
To assess the role of a large infrequent disturbance on the patterns of riparian plant invasions
Chapter 6
To reconstruct the invasion of *Opuntia stricta* and assess the role of propagule pressure in structuring invasion patterns
Chapter 7
To assess the fine scale dynamics of *Opuntia stricta* invasion
Chapter 8
To develop a new conceptual framework for invasion ecology
Chapter 9
General conclusion
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Introduction

Many biotic and abiotic factors affect the performance of an introduced organism. Upon arrival in a new environment, an alien must negotiate a series of barriers or filters before becoming established, naturalized or invasive (Richardson *et al.* 2000, Colautti & MacIsaac 2004). For alien plants, pre-adaptation to local environmental conditions (broad-scale climatic and soil conditions, etc) is essential for establishment. Naturalization is only achieved when the alien species reproduces, and invasion is contingent on dispersal from introduction foci. Proliferation in disturbed and undisturbed environments is further dependent on the alien species' ability to negotiate or take advantage of many other features of the receiving environment. Much progress has been made recently towards understanding the determinants of invasiveness and invasibility (Rejmánek *et al.* 2004), but plant invasions remain difficult to predict because of the complex interactions between traits of the invader and features of the environment. Importantly, the nature of interactions between invader and environment changes over time as the abundance of the invader increases. Especially in the early stages of invasion, invaders are clearly not in equilibrium with the environment. This complicates the assessment of the role of environmental factors in mediating invasion patterns (Hulme 2003).

Several recent studies, following different approaches, have highlighted the important role of propagule supply (or "propagule pressure") in structuring invasive plant populations (e.g. Williamson 1996, Hutchinson & Vankat 1997, Lonsdale 1999, Williamson 1999, Alpert *et al.* 2000, D'Antonio *et al.* 2001, Foster 2001, Frenot *et al.* 2001, Brown & Peet 2003, Rouget & Richardson 2003). These studies suggest that the influence of various barriers to invasion can be diminished when an environment is swamped with propagules, since establishment and subsequent events and processes along the naturalization-invasion continuum are all probabilistic rather than deterministic (D'Antonio *et al.* 2001). The increased availability of propagules in the course of an invasion can thus be a fundamental driving force in the invasion. Rouget & Richardson (2003) showed for three invasive tree species that models incorporating propagule pressure were markedly superior to those invoking only environmental parameters in explaining distribution patterns and abundance of invaders at a regional scale. These results suggest that accurate reconstructions of invasion events, and attempts to model ongoing and future invasions, must incorporate propagule pressure. Further examples detailing the explicit roles of propagule pressure in invasions are required to help in developing robust theories and models for building propagule pressure into quantitative invasion ecology. This paper presents insights in this regard from a study of the invasion dynamics of *Opuntia stricta*.

Opuntia stricta (Cactaceae) is widespread as an invader over large parts of South Africa (Henderson 2001) is the most widespread invasive alien plant in South Africa's Kruger National Park (Foxcroft & Richardson 2003). Its invasion of KNP since the early 1950s represents a discrete invasion event with a defined single source (see below). A study employing Principal Components Analysis revealed a poor correlation between *O. stricta* distribution and environmental variables, suggesting that the species can grow and invade a wide range of habitats in the region (Foxcroft 2003). The acquisition of 14,504 additional distribution records and additional GIS layers of environmental information provided the opportunity to gain further insights on invasion processes at the regional scale over 50 years. In particular, given the observed poor correlation between *O. stricta* distribution and environmental factors, this offered an opportunity to explore the extent to which propagule pressure could be acting as a driving force in this invasion.

The aims of the study were to: 1) reconstruct the invasion history of *O. stricta* over 50 years to elucidate invasion rates and patterns of spread; and 2) explore the role of propagule pressure in structuring the invading population.

Methods

Study area

The study was located in the southern region of KNP around Skukuza village, extending 40 km east-west and 40 km north-south (24.85-25.2 degrees S, 31.45-31.8 degrees E) (Fig. 6.1). The topography is moderately undulating to flat, intersected by numerous dry streambeds, which flow mainly as storm water conduits draining into the Sabie River. A few granite hills occur, protruding from archaic granites and gneiss. The landscape has developed mainly as a result of the accumulation of clay and mineral elements in the low-lying areas (Gertenbach 1983).

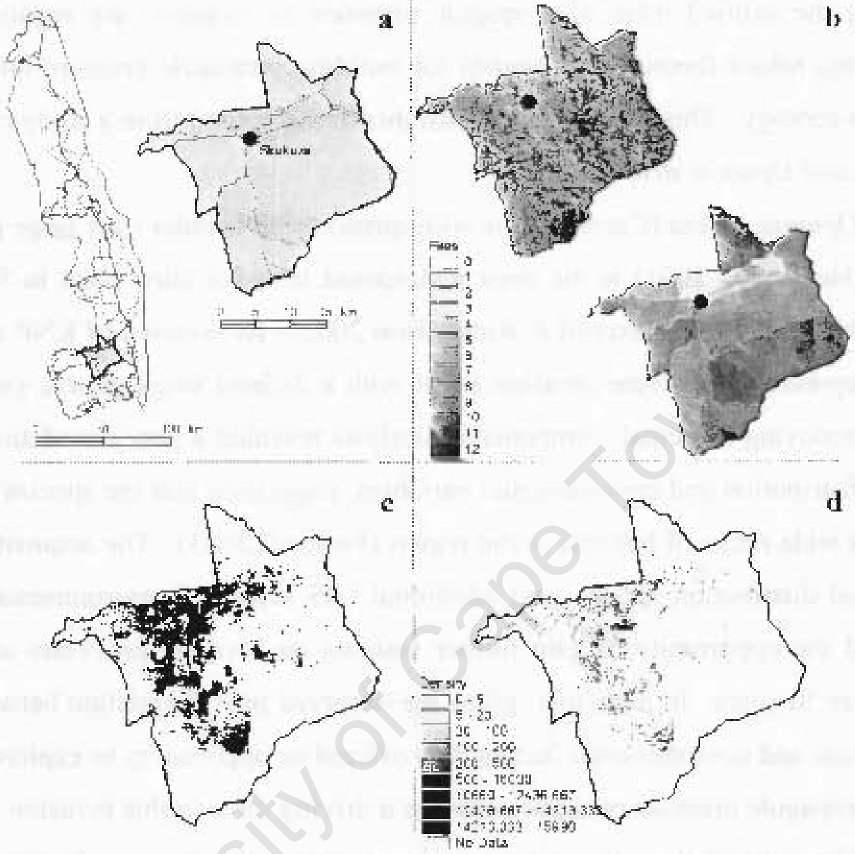

Figure 6.1: (a) Study area in relation to Kruger National Park, (b) Landscape heterogeneity as indicated by satellite imagery grouped into 20 classes (top); number of fires between 1950 and 2003 (bottom), (c) Mapped distribution of *O. stricta* (19,849 points), (d) Cladode density of *O. stricta* in 1-ha cells.

Study species

The platyopuntoid cactus *Opuntia stricta* (Haw.) Haw. var. *dillenii* (Ker Gawl.) L. D. Benson (Cactaceae; sour prickly pear) is a perennial succulent shrub native to North and Central America. Fleshy fruits are borne on the modified succulent stems called cladodes. It is well established as an invasive alien species in Australia (Johnson 1982), Spain (Vilà & Gimeno 2001, Gimeno & Vilà 2002, Vilà *et al.* 2003), and South Africa (Henderson 2001, Nel *et al.* 2004). The species (*O. stricta*) was first recorded in the KNP in 1953 when it was grown as an ornamental plant in Skukuza village (Lotter & Hoffmann 1998). *Opuntia stricta* soon naturalized and by about 1980 was spreading rapidly around Skukuza. The species has invaded nine *Opuntia* management units (units developed for the integrated control of *O. stricta*, as described by Lotter & Hoffmann 1998) covering some 66,000 ha, making it the most widespread invasive alien plant in KNP (Foxcroft & Richardson 2003, appendix 1.2) (Fig. 6.2). In KNP the ripe fleshy fruits are mainly eaten by baboons (*Papio ursinus*) and elephants (*Loxodonta africana*): these species are presumably the dominant dispersal agents of *O. stricta*, but no work has been done on the dispersal ecology of the species in the region. Birds eat the fruit and disperse seeds of *O. stricta* in other parts of its adventive range (e.g. in Catalonia, Spain: Gimeno & Vilà 2002), but no birds are known to feed on *O. stricta* in the KNP. Little is known about the biology and ecology of *O. stricta* in its natural habitat (Reinhardt *et al.* 1999). The germination of other *Opuntia* species increases with age of the seeds, indicating some inherent primary dormancy which probably allows seed banks to accumulate in the soil (Mandujano *et al.* 1997). Dodd (1940) found seeds of *Opuntia* species to be viable after 15 years. Under one set of trials in controlled conditions, 64% of *O. stricta* seeds germinated, and 90,6% of the seedlings survived for longer than 12 months (Lotter 1997). Although *O. stricta* is a prolific seed producer, in common with many other *Opuntia* species, vegetative propagation is also achieved through ramets (i.e. fragments containing one or several cladodes) (Mandujano *et al.* 2001).

Figure 6.2: A dense stand of *Opuntia stricta* in 1997, near Skukuza in Kruger National Park. The picture shows a healthy stand, with only minor damage caused by the introduced biological control agent *Cactoblastis cactorum* (Photograph: J.H. Hoffmann).

Attempts to control *O. stricta* have been conducted in KNP since 1985, with the implementation of an herbicidal control programme (Foxcroft & Hoffmann 2003). Herbicides have been unsuccessful because populations are replenished from soil-stored seeds, many small plants are overlooked in spraying operations, and insufficient follow-up work was carried out. Biological control using the phycitid moth *Cactoblastis cactorum* commenced in 1988 and has made some contribution to slowing the spread, mainly by stunting growth and extending the time that plants take to reach sexual maturity (Hoffmann *et al.* 1998a,b). The release of the cochineal bug (*Dactylopius opuntiae*) in 1997 considerably improved the biological control of *O. stricta* (Foxcroft & Hoffmann 2003). The species is, however, still expanding its range in KNP and in many other parts of South Africa. Detailed information on the invasion dynamics of this species in KNP could assist in planning more effective intervention strategies.

Mapping Opuntia stricta distribution and abundance

The distribution of *Opuntia stricta* in the study area was mapped between November 2000 and November 2003 using Geographic Positioning System (GPS; Garmin 12XL) units with an accuracy of about 7 to 15 m. Mapping was done as part of the systematic release of *D. opuntiae* for biological control of *O. stricta*. Mapping involved a team of 10 persons moving through the field in a straight line, approximately 10 m apart, mapping individual plants and clumps. Current remote-sensing techniques are not appropriate for mapping this species in the study area, as most *O. stricta* individuals and stands occur in densely wooded savanna (Fig. 6.1) or are hidden in a dense herbaceous under storey. Plants were individually mapped, except when they comprised more than about 150 cladodes, or when plants occurred in dense patches. In such situations, the number of cladodes was estimated by regression analysis using length, breadth, and height dimensions of the patch (as described in Hoffmann *et al.* 1998a).

Environmental data

Detailed environmental data were available as Geographic Information System (GIS) layers from the Savanna Ecological Research Unit at KNP. Data layers selected for inclusion in the study are described in Table 6.1. Classification of a Landsat7 ETM+ image (obtained from the USGS/EROS Data Centre), and processed to the Level 1G (radiometrically and geometrically corrected) was used to derive a classification of landscape heterogeneity. The unsupervised classification of bands 4 (near-IR), 5 (Short Wavelength Infrared (SWIR), and 3 (Red) displayed as red, green and blue respectively of a Landsat7 ETM+ image, iteratively classified pixels into 20 spectrally distinct classes. Classes were determined by spectral distinctions that are inherent in the Landsat7 image, through the Iterative Self-Organizing Data Analysis Technique (ISODATA) clustering method (Tou & Gonzalez 1974). The assumption is made that the spatial patterns of these classes relate to "hypothetical" habitats within the study area. This provided the best available indication of landscape heterogeneity (see Fig. 6.1b: top). Landscape heterogeneity is understood as the degree of variability across the landscape and is regarded as the highest level of biodiversity (Pickett *et al.* 2003, Rogers 2003).

Table 6.1: Environmental variables (including fire) used to characterise presence/absence and abundance (cladode density) of *Opuntia stricta* in Kruger National Park.

Code	Meaning
Soil variables	
Soil Form	Major soil forms classified into 15 types (Institute for Soil, Climate and Water, 1997)
Soil Texture	Soil texture based on the proportion of sand, loam and clay (10 categories) (Institute for Soil, Climate and Water, 1997)
Venter Soil	A classification of soil types as described by Venter (1990)
Climatic variables	
Rainfall	Average annual rainfall (mm)
Habitat variables	
Venter Land Type	56 "land types" as described by Venter (1990) on the basis of soil and vegetation patterns and which are combined with landform characteristics
Distance From Water	Distance from major water sources (rivers, artificial and natural boreholes)
Landscape heterogeneity	Classification of a Landsat7 ETM - image was used to derive a classification of landscape heterogeneity
Management	
Fire	Number of fires since 1955

Selection of the appropriate spatial scale

Although distribution data for *O. stricta* were available as point records, I decided to work at the scale of 100 m x 100 m (1-ha) cells. One-ha cells reduced the influence of under sampling *O. stricta*, especially in densely wooded, inaccessible areas. Working at this resolution also enabled me to compute presence/absence and abundance at the same spatial scale. Since I was mainly interested in density with reference to propagule pressure (the role of dense stands as foci for further invasion), I computed cladode density in terms of the total number of cladodes per 1-ha cell. One-hectare cells were also suitable for relating distribution and abundance data to environmental variables which were collected/collated at varying scales of resolution but which were all suitable for interrogation at the scale of 1-ha cells.

Definition of invasion foci and reconstructing the invasion chronology

The need to quantify the role of propagule pressure necessitated the identification of patches of *O. stricta* that functioned as the most important sources of propagules (referred to as foci). I assumed that propagule pressure would be related to the distance from such foci. Based on propagule pressure, I would expect most high-density patches to occur near foci, and very few invaded cells far away from the foci. As a first step in assessing the role of propagule pressure in structuring invasive populations I defined two levels of foci. The primary focus of invasion is the known origin of the invasive population in the Skukuza village (hereafter the "primary focus"). Putative secondary invasion foci ("secondary foci") were defined as the top 5% of 1-ha invaded cells ranked by cladode density (there were 260 cells with > 500 cladodes ha; see Fig. 6.3d). This selection was supported by a rapid decline in the frequency distribution of cladode density in 1-ha cells.

Preliminary analyses indicated that cladode density per 1-ha cells was indeed negatively correlated with the distance from foci. To ensure that the selected foci provided more important sources of propagules than a random selection of other invaded cells, I analysed the spatial pattern of cladode density per 1-ha cell in relation to the distance from a randomly-selected set of invaded cells. The correlation obtained was much weaker than with distance from selected foci. I was thus confident that I had correctly identified the most important sources of propagule supply and that distance from foci was a good indicator of propagule pressure.

The density of *O. stricta* cladodes in 1-ha cells was also the best available proxy for aging stands, so density was used in reconstructing the invasion chronology. In the reconstruction of the invasion chronosequence I ranked cells by cladode density and divided the invaded cells into six categories (<200; 201-500; 501-1000; 1001-2900; 2901-5000; and >5000 cladodes per ha) based on natural breaks in the frequency distribution of cladode density over the entire study area. The spatial distribution of categories was mapped to indicate the likely pattern of expansion of the population. The areal extent of each category was estimated using the GIS software Arcview.

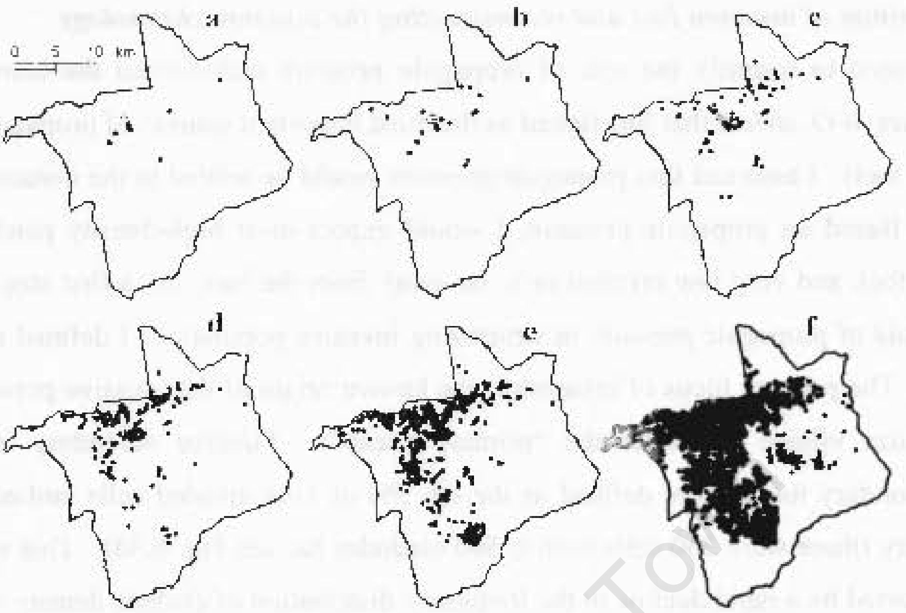

Figure 6.3: Snapshots of the reconstructed distribution patterns at different stages of invasion of *Opuntia stricta*. [shows the known source of the invasive *O. stricta* in the Skukuza village. (a) ≥ 5000 cladodes (13 cells), (b) ≥ 2900 (26), (c) > 1000 (103), (d) > 500 (260), (e) > 200 (725), (f) ≥ 1 (5180).

Statistical analyses

Tree-based models provide an alternative to linear and additive logistic models for classification and regression analysis (Breinam *et al.* 1984, Vayssieres *et al.* 2000). Tree models successively split the data to form homogeneous subsets, resulting in a hierarchical tree of decision rules useful for prediction or classification. This approach is particularly useful for exploring interactions between variables (e.g., between environmental variables and propagule pressure). I used S-Plus 2000 Professional Release 3 (MathSoft Inc. 2000) for fitting and examining classification and regression trees. The number of nodes was limited to 10 as my primary interest was to identify the main factors structuring the invasion patterns. A training set consisting of 75% of the full data set was used to develop the models. To fit the model I used cells where *O. stricta* was present and a random set of 1-ha cells selected across the entire study area where *O. stricta* was absent. The number of absence cells was proportionate to the size of the study area relative to the area invaded.

To explore the role of environmental factors and propagule pressure in determining invasion patterns of *O. stricta*, I ran classification trees for species distribution and regression trees for species abundance (expressed as number of cladodes per ha). For each model I used a combination of environmental variables only, environmental variables plus fire, propagule pressure alone (as measured by distance from primary and secondary foci), and then both environmental variables and propagule pressure. This was done to determine whether by adding a range of variables, the predictive ability of the models was improved, and to tease out the most significant of the variables.

The predicted distributions were generated using model results in Arcview (version 3.2). For presence/absence, model accuracy was determined by the percentage of correctly classified cells, and the Kappa statistic (Cohen 1960). For abundance, cladode density was reclassified into four classes (absent; <5; 6-100; >100) and the model accuracy was determined by the percentage of cells classified in the correct density category.

Results

Distribution patterns

By the end of 2003, the total range of *O. stricta* in the study area covers about 40,000 ha, although only 5180 1-ha cells were mapped as invaded. The species has spread 18,5 km from the known source in Skukuza village (Fig. 6.2c).

The reconstructed chronosequence for *O. stricta* invasion in the study area indicates initial expansion largely within 8 km of Skukuza, with outliers at up to 14 km (Fig. 6.3 a&b). Later stages of invasion involve coalescence of satellite foci and colonization of additional areas up to 18 km from the source (Fig. 6.3 c-f). To determine likely dates associated with different stages in the sequence (a-f in Fig. 6.3) I plotted the areal extent of each stage on the curve of invaded area against time based on estimates of total *O. stricta* extent in the study area collated by Foxcroft & Hoffmann (2003). This approach puts approximate dates to the phases shown in Fig. 6.3 (a-f) in the twenty-year period between 1980 and 2000 (Fig. 6.4).

Figure 6.3d shows the distribution of putative foci, representing 5% of the invaded cells and were estimated to be at least 10 years old (Fig. 6.4).

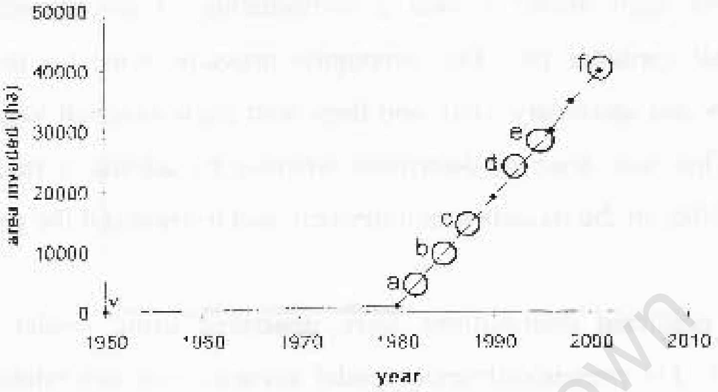

Figure 6.4: Areal extent of each stage of the invasion on the curve of area against time based on estimates of total *O. stricta* extent in the study area. Invasion stages refer to the reconstructed distribution pattern illustrated in Fig. 6.3 (a) ≥ 5000 cladodes, (b) ≥ 2900, (c) ≥ 1000, (d) ≥ 500, (e) ≥ 200, (f) ≥ 1. v Indicates the source of the invasion at Skukuza.

Determinants of presence/absence of Opuntia stricta

Only three environmental variables (habitat classes defined from satellite imagery, distance from water source, and soil form) clearly explain *O. stricta* presence/absence (Fig. 6.5a&b). Seven out of 20 habitat classes were positively associated with *O. stricta* presence. Adding the number of fires over the last 48 years substantially improved my ability to explain the distribution of *O. stricta* (Fig 6.5b). *Opuntia stricta* was much less likely to occur in areas burnt more than five times (Fig. 6.5b), and at sites more than about 1 km from water sources. Model accuracy ranges from 53% (habitat classes and distance from water sources; Fig 6.5a) to 67% (habitat classes, fire and soil form; Fig 6.5b) (Table 6.2).

Propagule pressure, approximated by distance from primary and secondary foci, was a much better predictor of *O. stricta* distribution than any set of environmental variables. These two variables correctly classified 77% of cells *O. stricta* presence/absence (Table 6.2). *Opuntia stricta* is highly likely to occur at sites within 7.9 km from the primary focus and 1.4 km from secondary foci (Fig. 6.6).

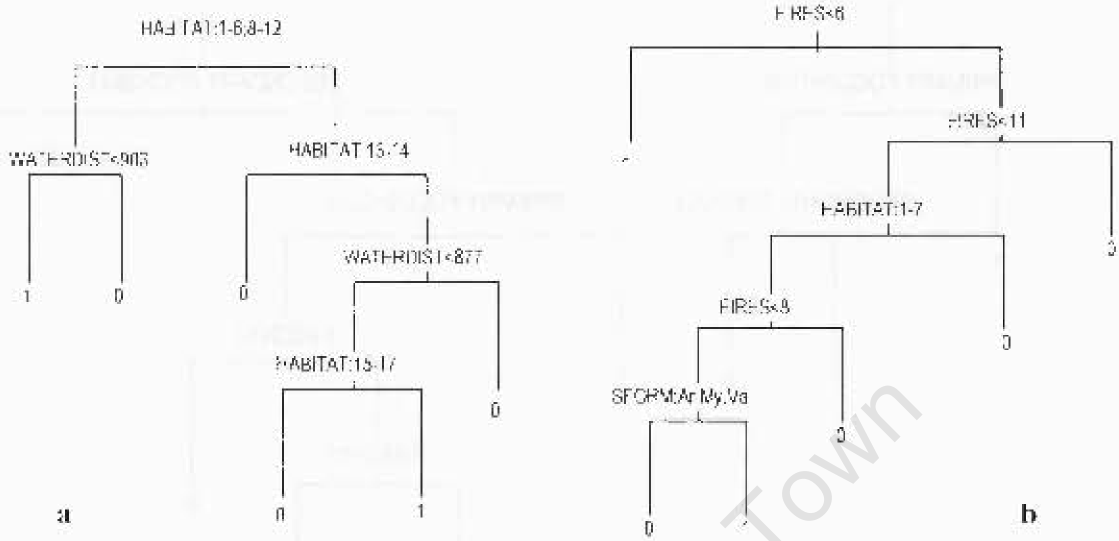

Figure 6.5: Classification tree of distribution (presence/absence) of *Opuntia stricta* based on environmental factors only (panel a) and environmental factors plus fire (panel b). Rules indicated on top of each splitting branches apply to the left branch. Values at the terminal nodes indicate predicted presence (1) or absence (0).

Table 6.2: Model accuracy of classification trees (used for predicting presence/absence) and regression trees (used for predicting cladodes density). The percentage of correctly classified cells is indicated for presence, absence and density. Models were derived using 75% of the full dataset.

Analysis	% Presence	% Absence	% Total	Kappa
Presence / Absence				
Environmental variables exc. Fire	68.21	49.21	52.67	0.098
Environmental variables inc. fire	60.33	69.41	67.76	0.215
Propagule pressure only	78.50	76.17	76.59	0.41
Environmental variables and propagule pressure	89.45	65.15	69.58	0.348
Cladode density	<5 <100 <500 Total			
Propagule pressure only	0.1 85.3 0.33 44	62.4	51.5	-

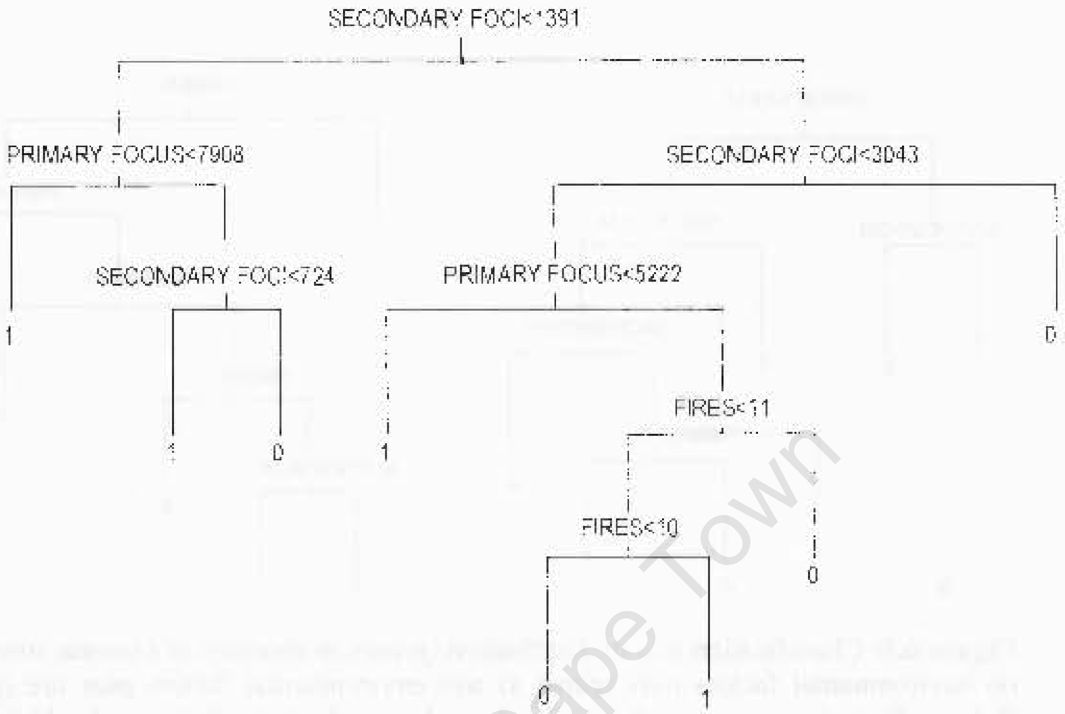

Figure 6.6: Classification tree of distribution (presence/absence) of *Opuntia stricta* based on propagule pressure. Primary focus represents the distance (in m) from the original introduction (in Skukuza village), secondary foci represent the distances from invaded cells with >500 cladodes (see Fig. 6.3d). Rules indicated on top of each splitting branches apply to the left branch. Values at the terminal nodes indicate predicted presence (1) or absence (0).

Determinants of abundance (cladode density) of Opuntia stricta

No environmental variables explained abundance patterns for *O. sricta* (only 14% of cells classified in the correct categories). However, propagule pressure as measured by distance from foci was a reasonable predictor of abundance pattern (Fig. 6.7). About 52% of cells were correctly classified. Cells within 170 m of secondary foci and 1.9 km of primary focus have 212 cladodes on average whereas cells further than 1.4 km from secondary foci have 3 cladodes on average (Fig. 6.7). However, no density category, especially high-density, could be correctly identified based on propagule pressure or environmental variables. The addition of environmental factors did not improve the accuracy of regression tree model based on propagule pressure only, as no environmental factors were able to explain the occurrence of dense stands far from any foci.

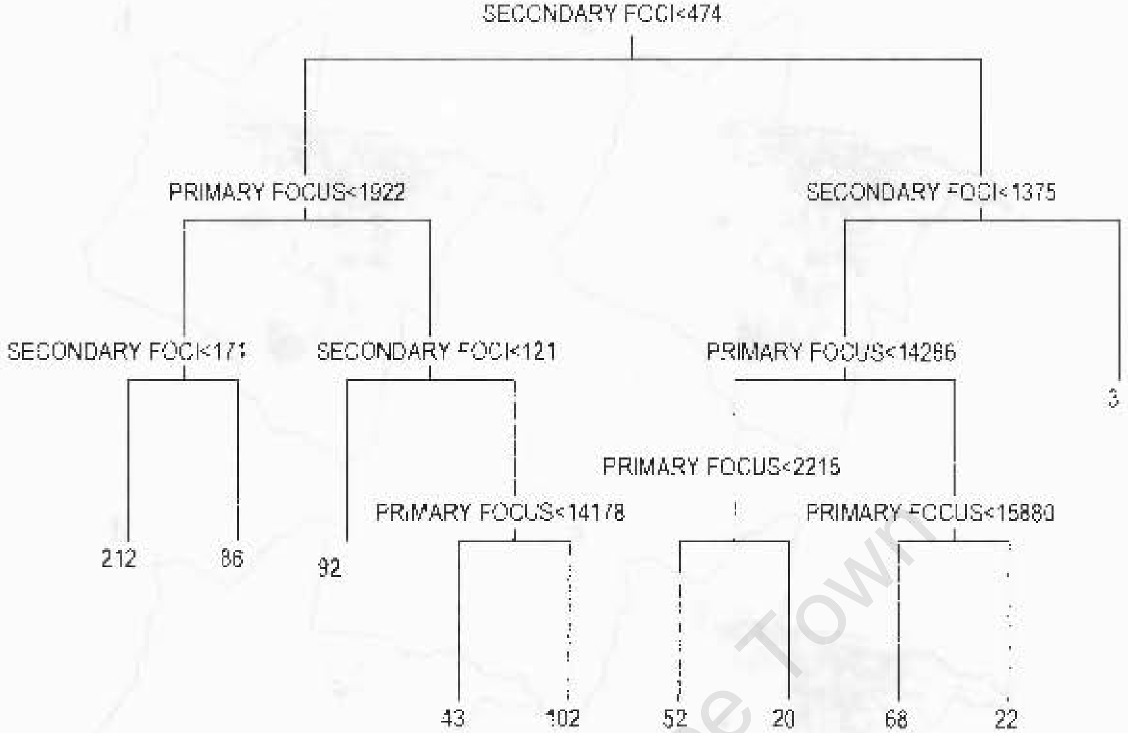

Figure 6.7: Regression tree of abundance (cladode density) of *Opuntia stricta* based on propagule pressure. Primary foci represent the distance (in m) from the original introduction (in Skukuza village), secondary foci represent the distances from invaded cells with >500 cladodes (see Fig. 6.3d). Rules indicated on top of each splitting branches apply to the left branch. Values at the terminal nodes indicate the predicted number of cladodes per 1 ha cell.

Spatial predictions of distribution and abundance of Opuntia stricta

Based on outputs from the classification and regression trees, about 25% of the study area (ranging from 21.8% to 28.5% for different models) is suitable for invasion by *O. stricta* (Fig. 6.8). Using environmental variables only, suitable sites were identified throughout the study area (Fig. 6.8a), whereas the addition of fire or propagule pressure provided spatial predictions similar to the current range of *O. stricta* (Fig. 6.8b&c). High-density invaded stands were predicted only near primary and secondary foci (Fig. 6.8d).

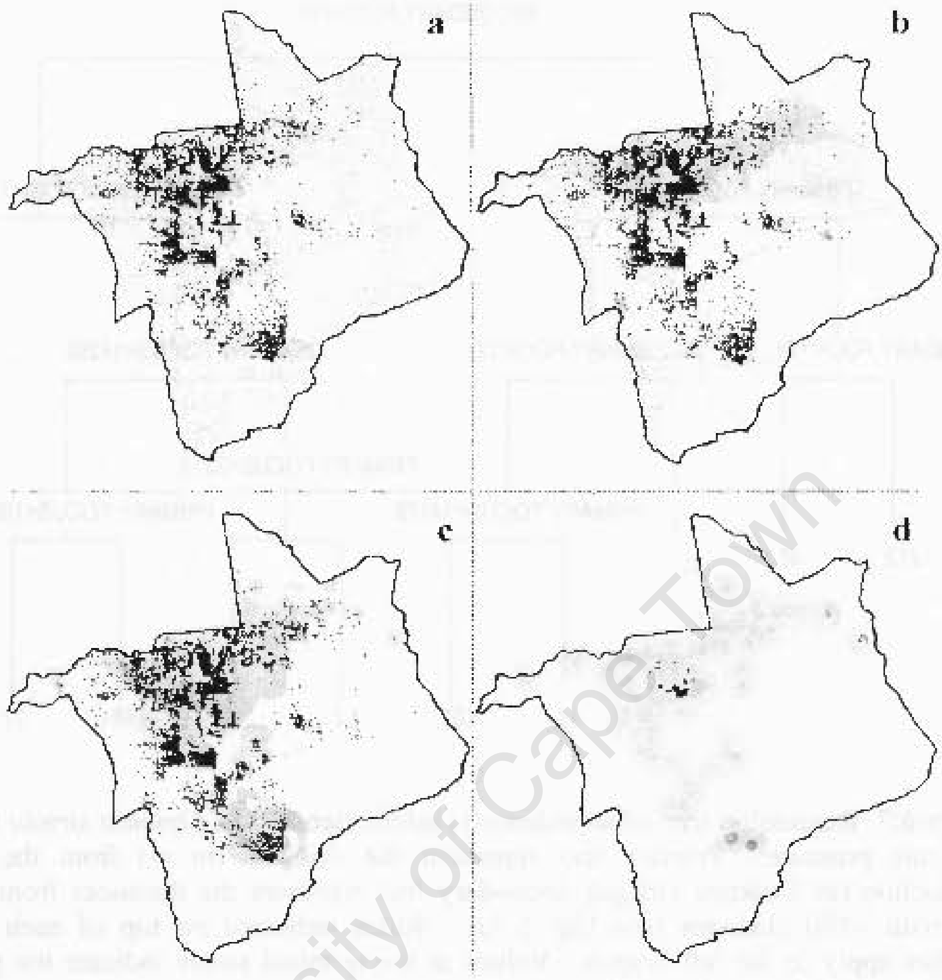

Figure 6.8: Spatial predictions of distribution and abundance of *Opuntia stricta*, based on outputs from the classification and regression trees. (a) Predicted distribution using environmental variables only, (b) predicted distribution using environmental variables plus fire, (c) predicted distribution using propagule pressure only, (d) predicted cladode density using propagule pressure. Black dots represent *O. stricta* distribution data, and grey represents predicted distribution.

Discussion

The distribution of invading *Opuntia stricta* in Kruger National Park was weakly correlated with the selected set of environmental variables at the study scale (see Table 6.2), but the correlation was improved when fire frequency was added. The lack of good correlations between distribution and environmental features was not unexpected. A previous study in the same area, using only about a quarter of the distribution points and a

Principal Components Analysis (Foxcroft 2003), arrived at a similar conclusion. Also, at the scale of the whole of South Africa, a bioclimatic analysis for *O. stricta* based on presence in quarter-degree cells showed that almost half of the area of South Africa, Lesotho and Swaziland is potentially suitable for this species (Rouget *et al.* 2004). In KNP, *O. stricta* grows in a very wide range of micro-sites, including small rock crevices, forks of trees, and even on a corrugated iron sheet (L.C. Foxcroft, pers. obs), attesting to the ability of the species to grow in a very wide range of sites. It is thus not surprising that a large part of the study area, and probably KNP, was shown to be potentially invasible for *O. stricta*.

Propagule pressure added considerable explanatory power to the distribution models (environmental variables plus propagule pressure yielded an accuracy of 77%). Propagule pressure was not, however, a very good predictor of species abundance (44% of density classes correctly classified, Table 6.2). When considering the observed contribution of propagule pressure on presence/absence, the following assumptions should be considered. Firstly, I assumed that the effects of propagule pressure (the spatial mass effect) are adequately measured by the distance to known and putative foci. I selected a set of dense cells as putative foci based on the frequency distribution of cladode density in cells. Clearly, the selected cut off is arbitrary, and some cells or clusters other than those selected may well have functioned as foci. Furthermore, the approach clearly assumes that all important foci have been accurately mapped and that no clumps of plants that acted as foci at any stage during the invasion (50 years) disappeared before the mapping in 2002-2003. Despite the history of control efforts directed at *O. stricta*, I am reasonably confident that these potential problems have not markedly affected the dataset. To my knowledge, no substantial clumps of *O. stricta* have disappeared. Had any clumps been substantially reduced through herbicidal control, they would have quickly regenerated due to the lack of follow-up measures. Biological control, although certainly assisting in management efforts, did not provide the levels of control required to result in a large-scale decrease in plant density. Considering these caveats, the role of propagule pressure quantified in this paper should be seen as indicative rather than absolute. I am confident that my approach is sufficiently robust to capture meaningful contributions of propagule pressure towards population expansion.

I made no attempt to explain the spatial position of the selected foci in the landscape. Their location is presumably determined by dispersal events generated through movements of the two main dispersal agents, elephants and baboons, both of which are highly mobile species. Unfortunately, no data are available to model dispersal dynamics.

The fact that adding fire frequency during the invasion history as a variable added substantially to the explanatory power of the model, suggests that fire frequency could potential be manipulated as part of an integrated control programme. Although fire ecology has received considerable attention in KNP, including its role as driver of ecosystem variability (van Wilgen *et al.* 2003), no work has been done on the fire ecology of *O. stricta*. The important role of fire in the model suggests that *O. stricta* is extremely fire sensitive. It is debatable whether fire frequency in management units could be manipulated specifically to reduce *O. stricta* occurrence (van Wilgen *et al.* 2004).

This study has demonstrated that propagule pressure is an important and quantifiable driver of alien plant invasions, in a manner similar to that of Hutchinson & Vankat (1997) and Rouget & Richardson (2003). What are the implications of these findings for modelling and managing plant invasions? Firstly, the results underscore the major importance of isolated foci in population growth (Moody & Mack 1988). For example, in the reconstructed invasion chronology, the isolated focus at 15 km from the primary source at a very early stage of the invasion (Fig 6.3a, top right point) and the cluster of foci 5 km north of the primary focus at a later stage of the invasion (Fig 6.3d) have clearly been hugely important in producing the noticeable west-east and north-south arms of the invasion pattern that remained evident in 2003 (Fig 6.3f). It is likely that no amount of data on seed dispersal dynamics of *O. stricta* would ensure accurate prediction of this pattern. Only with the benefit of hindsight can the weight of such events be appreciated. Regarding management implications, the results support the already widely stated notion that isolated foci are the most cost-effective targets for management intervention (Moody & Mack 1988, Higgins & Richardson 1999).

It is difficult to extend the findings from this study to predict invasion dynamics in other parts of southern Africa, or elsewhere. For example, nowhere else do elephants (apparently the main seed disperser in KNP) move freely over such large areas. Other parts of the world where *O. stricta* is invasive differ in so many respects from KNP that it is unlikely that results from this study would be directly transferable, or that insights from such studies will be much use for understanding invasion dynamics in KNP. For example, the well-studied invasions in Catalonia, Spain, take place in planted pine forests, abandoned olive groves and vineyards characterized by high levels of a range of anthropogenic disturbances (Gimeno & Vilà 2002, Vilà *et al.* 2003). Seed dispersal in Catalonia was by birds (thrushes and starlings) and wild boars. Whereas perch sites for birds in the invaded sites define regeneration micro-sites in Spain (Vilà & Gimeno 2001), dispersal by baboons and elephants is much less likely to result in predictably clumped regeneration micro-sites.

Management of invasive species such as *O. stricta* whose dynamics are so clearly driven by propagule pressure, and where biotic and abiotic drivers are much less important is probably much more challenging than for species where distribution and abundance follow patterns that can be predicted by such factors.

CHAPTER SEVEN

WHAT HELPS *OPUNTIA STRICTA* INVADE KRUGER NATIONAL PARK: BABOONS OR ELEPHANTS?[6]

Abstract

Is *Opuntia stricta* more frequent, and its patches larger, under trees suitable for baboon roosting? If so, does it mean that baboons are major dispersal agents and that plants established under these trees are important foci of *Opuntia stricta* spread? I surveyed an area invaded by *Opuntia stricta* in the Skukuza region of KNP. The survey included plots under potential baboon roosting trees, plots under trees unlikely to support baboons, and paired randomly located open sites. The null hypothesis – tree-*Opuntia* spatial independence – can be rejected for *Acacia nilotica*, but not for *Spirostachys africana*. *Opuntia* plants are positively associated with *Acacia* trees suitable for baboon roosting. However, there is no significant difference between frequency of *Opuntia* under *Acacia* trees suitable and unsuitable for baboon roosting. It appears that all *Acacia* trees can serve as nurse trees for *Opuntia*. Compared to plots under *Acacia* trees, frequencies of old and robust *Opuntia* plants are significantly higher in open areas and under dead trees. While baboons may be responsible for long distance *Opuntia* dispersal (over kilometres), their role is not detectable at a local scale. On the other hand, elephants seem to contribute substantially to the local vegetative propagation of this species. *Opuntia* establishment and growth are more influenced by micro-habitat than previously thought.

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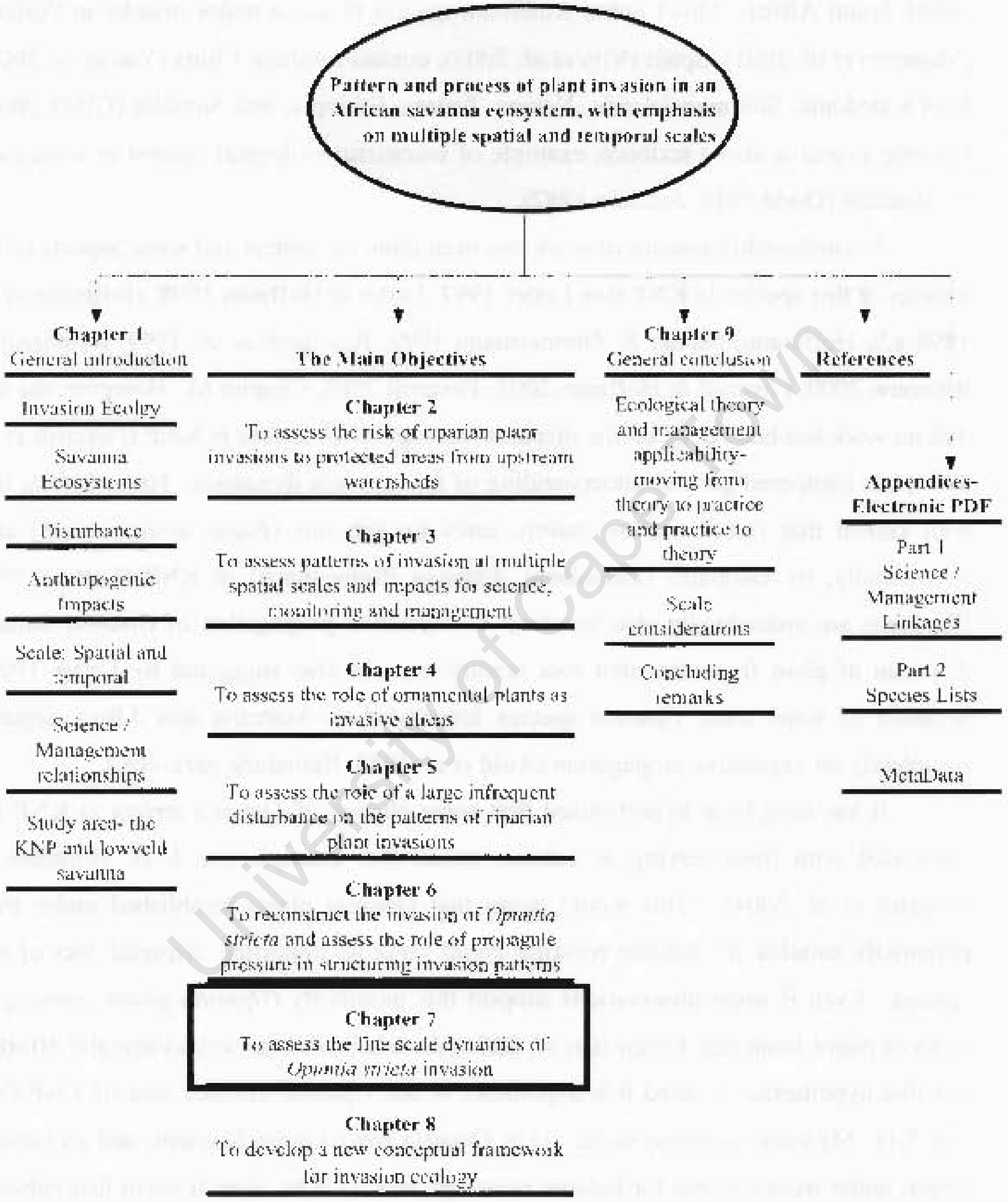
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Introduction

Opuntia stricta (Haw.) Haw. var. *dillenii* (Ker Gawl.) L. D. Benson (sour prickly pear) is one of the most important plant invaders in Kruger National Park (KNP; Foxcroft *et al.* 2004), South Africa. This Central American species is also a major invader in Portugal (Monteiro *et al.* 2005), Spain (Vilá *et al.* 2003), coastal southern China (Yan *et al.* 2001), New Caledonia, Solomon Islands, Yemen, Eritrea, Ethiopia, and Somalia (GISD 2005). *Opuntia stricta* is also a textbook example of successful biological control in some parts of Australia (Dodd 1940, Johnson 1982).

A considerable amount of work has been done on control and some aspects of the biology of this species in KNP (see Lotter 1997, Lotter & Hoffman 1998, Hoffmann *et al.* 1998 a,b, Hoffmann, Moran & Zimmermann 1999, Reinhardt *et al.* 1999, Reinhardt & Rossouw 2000, Foxcroft & Hoffman 2003, Foxcroft 2003, Chapter 6). However, the fact that no work has been done on the dispersal ecology of *O. stricta* in KNP (Foxcroft *et al.* 2004) has hampered general understanding of the invasion dynamics. Nevertheless, it is well known that ripe fruits are mainly eaten by baboons (*Papio ursinus* Kerr.) and, occasionally, by elephants (*Loxodonta Africana* Blumenbach) in KNP (Lotter 1999). Elephants are undoubtedly also involved in vegetative propagation of *Opuntia* through dispersal of plant fragments that root readily (as was also suggested by Lotter 1996). Invasion of some other *Opuntia* species introduced to Australia and Africa depends completely on vegetative propagation (Auld *et al.* 1983, Rejmánek pers. obs.).

It has long been hypothesized that some clumps of *Opuntia stricta* in KNP are associated with trees serving as baboon roosts (for example see J. H. Hofmann in Foxcroft *et al.* 2004). This would mean that *Opuntia* plants established under trees potentially suitable for baboon roosting could serve as important dispersal foci of this species. Even if some observations support this possibility (*Opuntia* plants growing in forks of major branches; Foxcroft *et al.* 2004) there has not been any systematic effort to test this hypothesis. I tested this hypothesis in one *Opuntia* infested area of KNP (See Fig. 7.1). My main questions were: 1) is *Opuntia stricta* more frequent, and its patches larger, under trees suitable for baboon roosting? and, 2) if so, does it mean that baboons are major dispersal agents and that plants established under these trees are important foci of *Opuntia* spread?

Materials and Methods

Study area

My study was located in the southern region of KNP near Skukuza camp (centre of plot being 25°00'537 S and 31°58'480 E). The area is classified as the 'Skukuza land type' by Venter (1990). The Skukuza land type is associated with the Sabie River valley and adjoining low-lying areas. The area is generally characterised by a complex soil pattern, although generally shallow and of the Glenrosa soil form. There is generally a dense shrub layer with sparse grass cover, and frequently dense stands of *Spirostachys africana* on the foot-slopes.

Sampling

Field work was conducted at the end of the dry season between 27 September and 2 October 2005.

Only two tree species, *Acacia nilotica* (L.)Willd. Ex Delie subsp. *kraussiana* (Benth.) Brenan and *Spirostachys africana* Sond., contributed to more than 90% of tree individuals in the area invaded with *Opuntia stricta*. In the study area of approximately 340 x 380 m, sixty trees of *Acacia* and sixty trees of *Spirostachys* were found to be morphologically suitable for baboon roosting (strong branches- with a minimum diameter of 5 cm, <20°). Under each tree, a circular plot, with the radius corresponding to the extent of branches that could potentially support baboons (0.5 to 2.5 m) was searched for *Opuntia* plants. *Opuntia* patches were only recorded when their centres were situated within the defined radius. The size of the *Opuntia* patch was quantified by two perpendicular measurements of their diameters. The area of individual patches was estimated as $\pi((d_1 + d_2)/4)^2$, where d_1 and d_2 are the two perpendicular diameters, with d_1 on the longest axis. For each tree-centred plot, one reference circular plot, of the same radius was located in a random direction 5 m away from the tree, and analyzed in the same way for *Opuntia* presence/abundance. If more than one patch of *Opuntia* was present their areas were combined. If the randomly located plot was situated under a canopy of another tree, a new random direction was chosen. Shrub cover in each plot was visually estimated and the diameter at breast height (dbh) of trees measured as well.

Opuntia plants were classified into three robustness categories: 1 – 'young', relatively small plants consisting of less than 10 cladodes; 2 – medium size plants; 3

obviously older plants, consisting of more than 30 cladodes, >50 cm tall, or parts of large (>10 cm diameter) basal stems visible. As frequencies of *Opuntia* in the *Spirostachys* dominated area were relatively low (see Results), the data on *Opuntia* plant robustness were analyzed only for *Acacia* plots and corresponding open plots. In addition, 19 *Opuntia* populations under dead *Acacia* trees were also evaluated for plant robustness in the same area.

To separate the effect of microhabitats created by the trees themselves, 60 plots under *Acacia* trees obviously unsuitable for baboon roosting (thin, very dense branches) were analyzed in the same manner, including paired reference plots. In this analysis, half of the *Acacia* crown radius was consistently used as a radius for sampled pairs of plots.

Data analyses

The data on frequency (presence/absence) of *Opuntia* plants in analyzed plots were summarized into two by two contingency tables and the null hypothesis of tree-*Opuntia* spatial independence was tested using the chi-square test. Strength of interspecific association was measured as Q (Pielou 1977). The coefficient Q is equal to −1 when at least one of the two species is never present with the other one (complete negative association), and is equal to +1 when at least one of the two species is always present with the other one (complete positive association). Robustness of *Opuntia* plants (three categories) in three habitats (*Acacia*, open, dead *Acacia*) was analyzed as a three by three contingency table. To compare mean areas of *Opuntia* patches under trees and in reference open areas, the paired t-test was used to analyze the pairs where *Opuntia* was present in both the tree and corresponding open plot. The paired t-test was also used to test differences in shrub cover under *Acacia* trees and in corresponding open plots. The relationship between *Opuntia* presence and shrub cover was tested using logistic regression. For all statistical analyses I used StatView 5.0.1 (SAS Instruments Inc. 1998).

Results

The null hypothesis, tree-*Opuntia* independence, can be rejected for *Acacia nilotica* ($p < 0.002$; see Table 7.1 for a summary of frequency data). It can not be rejected for *Spirostachys africana*. Here however, even if the overall frequency of *Opuntia* is very low (only 20 presences were recorded in 120 plots), there is a tendency for *Opuntia* to be present under *Spirostachys* trees rather than in open areas. There is also a tendency for *Opuntia* patches to be larger under *Acacia* trees compared to open areas (4.71 m^2 vs. 3.11 m^2). However, the difference is not significant (paired t-test, $t = 1.86$, $df = 21$, $p = 0.076$).

Table 7.1: Two by two contingency tables summarizing frequency (presence/absence) of *Opuntia* plants under trees suitable for baboon roosting.

		Acacia nilotica		*Spirostachys africana*	
		Present	Absent	Present	Absent
Opuntia stricta	Present	41	24	13	7
	Absent	19	36	47	53
		$X^2 = 9.7$, $p = 0.0018$, $Q = -0.53$ → positive association		$X^2 = 2.16$, $p = 0.14$ → not significant	

The overall heterogeneity of the frequency data on *Opuntia* plant robustness, summarized in a three by three contingency table (Table 7.2), is highly significant ($X^2 = 48.3$, $p = 0.0001$; Table 7.2). Obviously, the source of the contingency table heterogeneity is the low frequency of the large plants (third category) under *Acacia* trees. There is no significant difference in frequencies in open areas and under dead trees; both habitats exhibit a high frequency of old and robust *Opuntia* plants. Therefore, even if the frequency (presence) of *Opuntia* under *Acacia* trees is higher than in open areas and mean *Opuntia* patch size also seems to be larger under *Acacia* trees, *Opuntia* plants are, on average, more robust and, presumably, older in open areas and under dead trees.

Table 7.2: Three by three contingency table summarizing frequencies of the three *Opuntia* robustness categories (small, medium, large) in the three habitats. Numbers in parenthesis are expected frequencies.

		Habitat		
		Acacia nilotica	Open areas	Dead *A. nilotica*
Opuntia robustness	1	18 (8.6)	2 (8.6)	0 (2.7)
	2	25 (15.1)	9 (15.1)	1 (4.8)
	3	17 (36.3)	49 (36.3)	18 (11.5)

Frequency data on presence/absence of *Opuntia* under *Acacia* trees **not** suitable for baboon roosting and in the paired open plots (Table 7.3) again shows that the null hypothesis, *Acacia-Opuntia* independence, can be rejected ($p = 0.001$). The overall frequency of *Opuntia* plants in this analysis is somewhat lower. However, this can be easily explained: because the trees not suitable for baboon roosting were in general smaller, with mean dbh = 13.9 (vs. 21.2 cm), the mean radius of searched plots was also smaller (0.99 m vs. 1.66 m).

Table 7.3: Two by two contingency table summarizing frequency (presence/absence) of *Opuntia* plants under *Acacia* trees **not** suitable for baboon roosting.

		Acacia nilotica	
		Present	Absent
Opuntia stricta	Present	37	19
	Absent	23	41
		$X^2 = 10.85$, $p = 0.0010$, $Q = +0.55$ → positive association	

Discussion

The first important conclusion from this study is that even if populations of *Acacia nilotica* subsp. *kraussiana* and *Spirostachys africana* are mixed to some extent, patches dominated by *Spirostachys* are much less infested by *Opuntia* than neighbouring patches dominated by *Acacia* (Fig. 7.1). Even if *Spirostachys* trees seem to be morphologically more suitable for baboon roosting than *Acacia* trees (crown radii significantly larger, no spines, and more horizontal branches) and baboon faeces are often found under them, significantly fewer *Opuntia* patches are under *Spirostachys*. The reason for this difference may be more intensive grazing under *Spirostachys* trees (substantially more heaps of pellets are found here and grass grazed completely to the ground: Foxcroft & Rejmánek pers. obs.) and associated soil erosion (denudated tree roots and other recent erosion phenomena; Foxcroft & Rejmánek pers. obs.).

Figure 7.1: *Opuntia stricta* invasion in Kruger National Park. The *Opuntia stricta* / *Acacia nilotica* association is visible in the background, while no plants are visible at the base of the *Spirostachys africana* tree (front, right). (Photograph: L.C. Foxcroft).

The second conclusion is that there is higher frequency (presence) of *Opuntia* plants/patches under *Acacia* trees suitable for baboon roosting compared to corresponding open areas. This could be explained either as a result of baboon seed defecation from their roosts, or as a habitat modification of by *Acacia* trees. Obviously, these two factors are not mutually exclusive. However, if there is any beneficial *Acacia* habitat effect (e.g., shading and/or nitrogen addition), this would have to be important only in initial stages of *Opuntia* plant establishment because plants in open areas and under dead trees are, on average, significantly more robust.

The analysis of *Opuntia* abundance under *Acacia* trees unsuitable for baboon roosting sheds some light on this intriguing question. As there is virtually no difference between results presented in Tables 7.1 and 7.3, it may be concluded with a high degree of certainty that establishment of *Opuntia* plants, either from seeds or from elephant dispersed cladodes, is significantly facilitated by the micro-environment created by *Acacia* trees. A study on an *Acacia schaffneri* – *Opuntia strepcantha* association in southern Chihuahuan desert (Yeaton & Romero Manzanares 1986) hypothesized that either *O. strepcantha* (an erect platyopuntia, as is *O. stricta*) utilized the increase in available nitrogen or shade preferences explained their habitat preferences. As *Opuntia* plants in open areas are significantly more robust, it does not seem to be increased soil nitrogen content but protection of young plants from direct solar radiation that facilitates their establishment. Similar results were reported for the native cactus *Neobuxbaumia tetetzo* in the Tehuacan Valley, Mexico (Valiente-Banuet & Ezcurra 1991). It seems that while Cactaceae are a xerophytic family *par excellence*, propagules of some species in this family need shade of nurse plants for their successful establishment (Arriaga *et al.* 1993, de Viana *et al.* 2001). In addition, there is one more factor potentially involved in the *Opuntia* establishment process in KNP. The mean cover of shrubs is significantly higher under *Acacia* trees (29.1%) compared with open areas (16.6%; paired t-test, $t = 4.9$, $n = 120$, $p < 0.001$). Therefore, not only *Acacia* shade, but also shrub shade may contribute to survival of young *Opuntia* plants. Moreover, shrubs may also protect *Opuntia* seedlings against grazing. Nevertheless, logistic regression did not reveal any dependence of *Opuntia* presence on shrub cover under *Acacia* trees ($p = 0.70$). Similarly, there was no relationship between the total area of *Opuntia* patches and shrub cover under *Acacia* trees ($p = 0.51$). The higher cover of shrubs under *Acacia* trees may indicate that habitats under them are also more suitable for establishment of other perennial plants than *Opuntia*.

As I only found a very few seedlings in the course of this research (<10), I believe that propagules primarily involved in the spread of *Opuntia* at this level of infestation and at this spatial scale are in more than 90% of cases individual *Opuntia* cladodes or fragments consisting of a several cladodes. These are dispersed short distances, presumably up to 10 m, by elephants walking through *Opuntia* stands. Most of the dispersed cladodes readily root and give rise to new plants. I found that out of the 50 randomly collected cladodes, 31 had formed roots and most likely will survive. Further, cladodes that had not formed roots appeared as thought they had mostly been deposited recently.

Seed dispersal by birds can not be excluded. However, dispersal of *O. stricta* by birds seems to be negligible in Spain (Gimeno & Vilà 2002). While some other *Opuntia* species in South Africa are dispersed by crows (Dean & Milton 2000), there is not any indication that that *O. stricta* is dispersed by birds in KNP. Further, there is no other evidence of utilization by any other animals. My overall impression is that baboons may contribute to long-distance dispersal of *Opuntia*, but satisfactory evidence is still not available. On the other hand, once *Opuntia* plants grow to the stage of several cladodes, I am certain that elephants are the key dispersers, through the action of breaking off and dispersing *Opuntia* fragments. This then promotes coalescence of individual patches and overall *Opuntia*-homogenization of the habitat suitable to establishment of this species, i.e., with sparse tree cover and exposed to intermediate disturbance (moderate grazing, and only light soil erosion).

This, of course, is a very unfortunate situation because landscapes with these characteristics are common, if not prevailing, in KNP and elephants are an integral part of the system. Detection and eradication of new isolated foci should have a highest priority (Rejmánek & Pitcairn 2002). Attempts to control *Opuntia stricta* biologically with two herbivorous insects *Cactoblastis cactorum* (Bergroth) (Lepidoptera, Phycitidae) and *Dactylopius opuntiae* (Cockerel) (Homoptera, Dactylopiidae) had not been successful in KNP. Fortunately, the new biotype of *D. opuntiae* ('*stricta*') was imported to South Africa, tested and released in KNP in 1997. This biotype has become abundant in the vicinity of the release sites and has caused considerable local suppression of *O. stricta* (Hoffmann *et al.* 1999). A massive *Dactylopius* rearing operation is currently under way in the KNP. As mechanical and/or herbicidal control of all *Opuntia* species is very difficult, biological control, if successful, is the only possible solution in this situation.

CHAPTER EIGHT

BEYOND FILLING THE GAPS: ADVANCING THE SCIENCE OF PLANT INVASION ECOLOGY USING A NEW CONCEPTUAL FRAMEWORK[7]

Abstract

The ecological and economic impacts of biological invasions are increasing. The ability to predict and manage invasions however is lagging. Although advances have been made in understanding the mechanisms underlying invasions, these are mostly case specific, with little generality. The understanding of and research on invasions is also in danger of becoming increasingly fragmented and frequently disassociated from the rest of ecology. Conceptual frameworks and models have been successfully used in developing new understanding of ecological phenomena such as ecological boundaries and spatial heterogeneity.

I describe a framework and model template that contextualises the key components and linkages in the plant invasion process. This new framework is inclusive in order to generalise across invasive species, systems and scales, and to provide a structure for synthesizing research in invasion ecology.

I use an example from Kruger National Park, South Africa, to further suggest how this framework can guide management response to plant invasions. The suggested framework provides a structure to facilitate syntheses across scales and situations that might promote generalization. It is general enough to provide a common understanding, while at the same time, providing the mechanisms that can be specified to answer questions about particular invasions. I suggest that application of the framework will lead to better integration and understanding of alien plant invasions.

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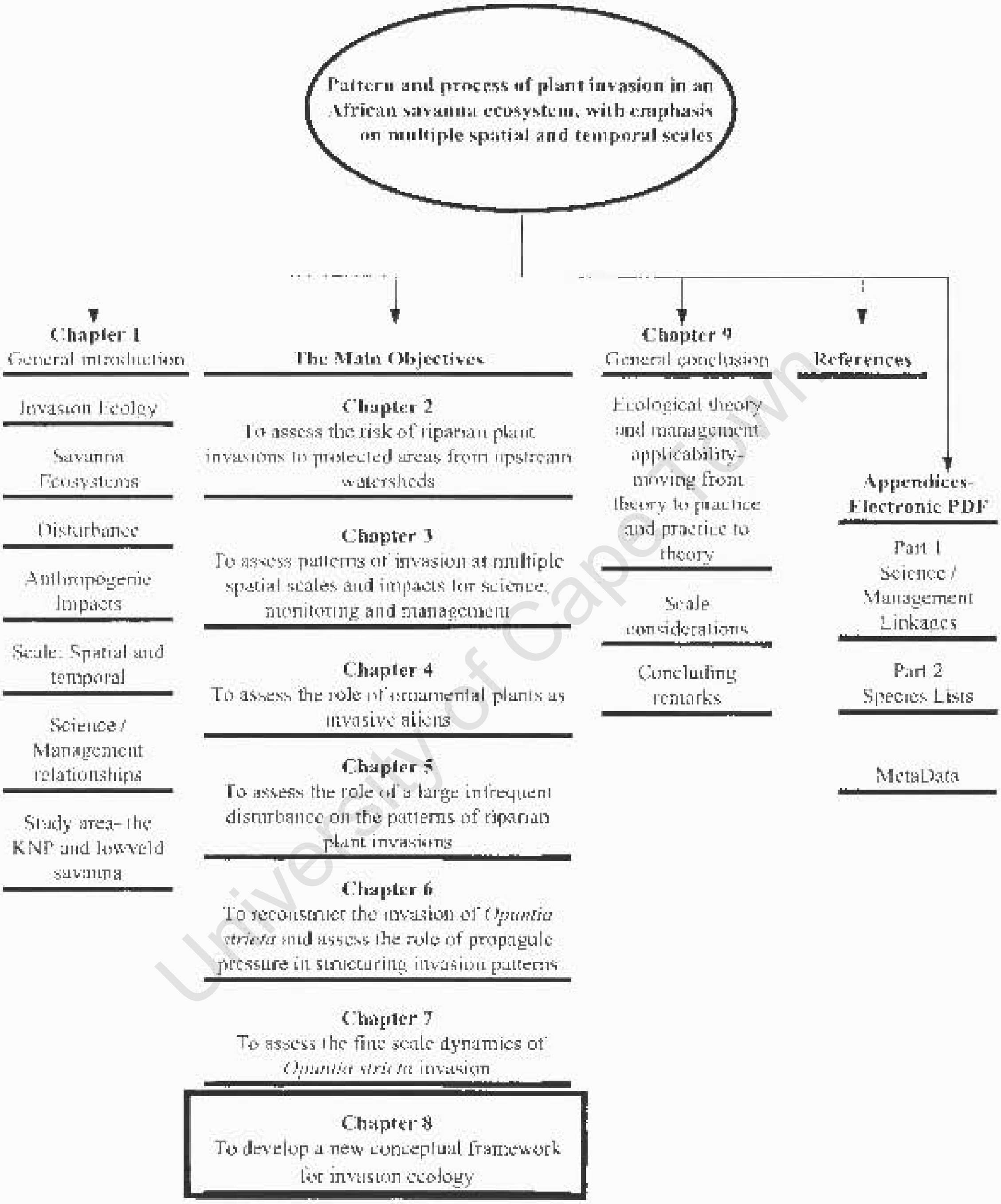
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Introduction

Biological invasions are increasingly widespread phenomena, threatening the integrity and functioning of ecosystems (Wilcove *et al.* 1998). The SCOPE (Scientific Committee on Problems of the Environment) programme of the 1980s focused on biological invasions (Drake *et al.* 1989), and sought to identify the attributes that allow organisms to invade and the features that make some environments more invasible than others. This programme made progress in specific cases (Rejmanek *et al.* 2005). However, attempts to link the characteristics of invaders and the receiving environment in models to provide a general understanding of the invasion process have been largely unsuccessful (e.g. Vermeij 1996). This has led to the suggestion that it is unrealistic to expect general rules to emerge for predicting potential invaders and susceptible environments (e.g. Crawley 1987, Gilpin 1990, Lodge 1993, Vermeij 1996). It is argued that the complexity of interactions between the potential invader and the receiving environment precludes general predictability (Roy 1990, DeFarrari & Naiman 1994, Burke & Grime 1995, Pyšek & Pyšek 1995, Thompson *et al.* 1995). Existing theoretical models of invasion cannot handle such complexity and have not been of much heuristic value (Crawley 1987, Gilpin 1990, Lodge 1993). In addition to this, it has been argued that disassociation of invasion ecology from the rest of ecology, in particular succession ecology, has contributed to the lack of developing reliable generalizations (Davis *et al.* 2001, 2005).

Attempts to synthesize current knowledge have focused on developing common understanding of terminology and concepts. For example, it is suggested that due to the possible anthropocentric association of "invasion" and the notion this invokes, the field of invasion ecology has had a proliferation of terminology and concepts (Richardson *et al.* 2000). These are frequently confused and misused. The "barriers or naturalization – transformation model" suggested by Richardson *et al.* (2000) helps order the confusion and clarify terms. It is probably the most widely cited and most useful current conceptual understanding of the invasion process. The key advancements provided by the barriers model are 1) defining the various terminologies more precisely and, consequently, leading to a much needed common understanding, 2) providing insight into the controls on successful establishment of an alien species, and 3) clearly articulating the net effects of invasions, which result in usefully differentiated states of the system. I cast the barriers model into a flow diagram format (Fig. 8.1) which clearly indicates the barriers associated with each phase or term, and therefore the resulting state. How species respond to each of the successive barriers will determine their degree of invasion success, as well as the terminology that should be associated with a specific invasion. While this and other work (e.g. Heger 2001, Colauti & MacIsaac 2004, Pyšek *et al.* 2004) has provided a more neutral and shared understanding of the concepts and terms, a new framework for the invasion process may provide additional mechanistic insights.

I describe in detail three conceptual tools to expose the mechanisms of invasions and to integrate across species, systems and scales. These tools include 1) a framework to articulate and organize the causal factors, 2) a model template to suggest general relationships among causal factors in the framework, and 3) working models to apply the framework to specific cases. I suggest a novel framework aimed at understanding the invasion process. The framework complements the barriers model of Richardson *et al.* (2000) and incorporates mechanisms driving 1) the invasion capabilities of a species, 2) the invasibility of a particular system and 3) the influence of the spatial and temporal context of the system. This framework is purposefully comprehensive and inclusive of systems, plant species and scales. The comprehensiveness of the framework is suggested by the fact that it addresses the various site specific conditions, species characteristics, and biotic interactions that are identified by the general theory of succession as important to species invasion, establishment, persistence and demise (Pickett & Cadenasso 2004). The framework I propose places these processes of community assembly and change into the context of invasive species. I begin my detailed exploration of this new framework by reviewing the nature and role of frameworks. I also discuss the value of conceptual frameworks for organizing and synthesizing a body of literature as well as for identifying the gaps in knowledge to suggest important research areas.

I then present the specifics of the framework for invasions and describe its components. I illustrate how to operationalise the framework, using the example of the invasion of *Opuntia stricta* in Kruger National Park. This example will be carried through additional sections of the paper. I also suggest how the framework can not only organise and guide research but also guide management decisions and interventions.

Future dialogue between science and management can refine the framework as greater understanding is achieved.

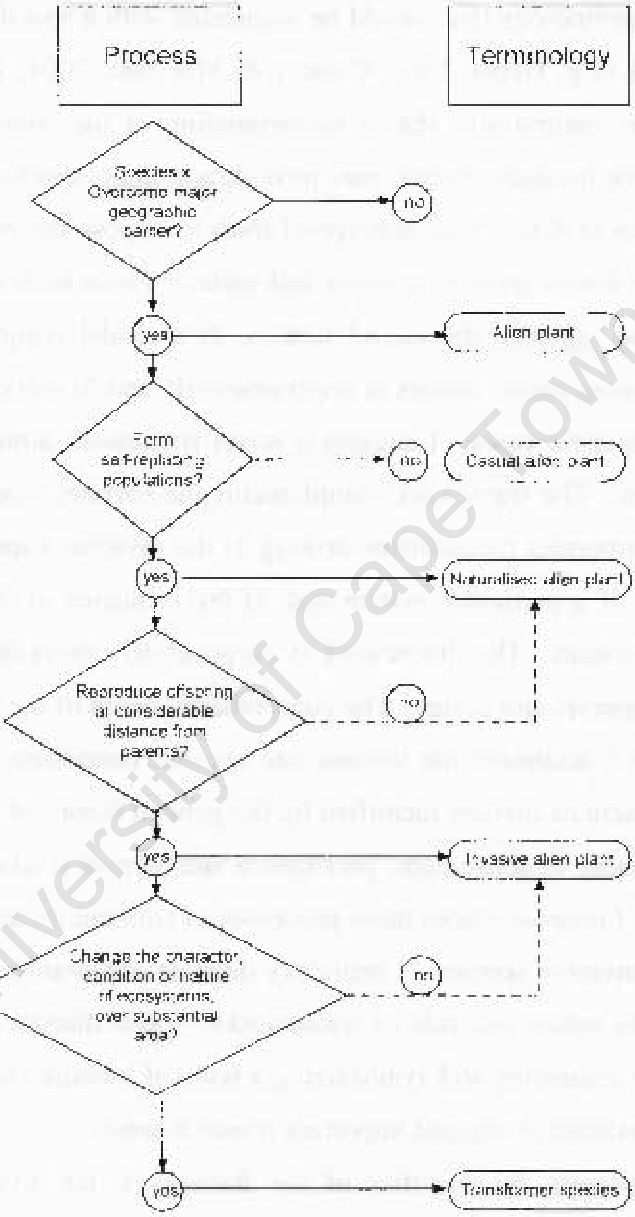


Figure 8.1: A flow diagram of processes and associated terminology used in invasion ecology. The left hand column shows the switch points in overcoming sequential barriers to invasion. The barriers are geographic, reproduction, wide dispersal, and environmental alteration. The right hand column shows the terminology that is applied to species that successfully pass each kind of barrier. Abstracted from descriptions in Richardson *et al.* (2000).

A new conceptual framework for plant invasion ecology

Value of conceptual frameworks

Conceptual frameworks are powerful tools to organise and evaluate conceptual advancement in an area of study (Pickett *et al.* 1994). The strength of the framework approach lies on the basis of providing a common understanding. The insights gained from specifying how the general components identified by a framework apply in detailed situations can then test the general understanding of the processes, by comparing across regions and management agendas. Understanding of ecological systems has been advanced by many conceptual frameworks (Pickett *et al.* 1999), with notable examples being the ecological boundary (Cadenasso *et al.* 2003) and succession frameworks (Pickett *et al.* 1987, Pickett & Cadenasso 2004).

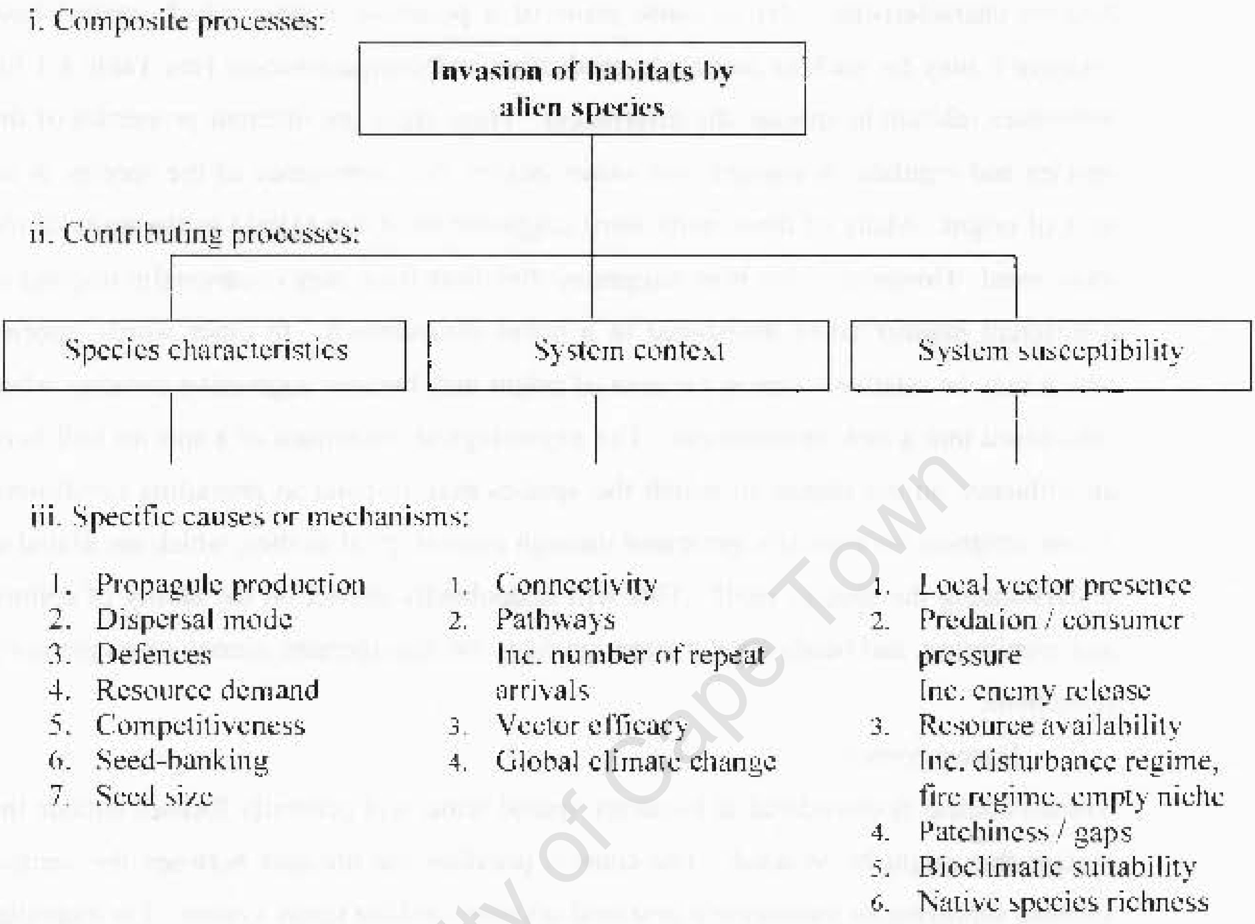
There is a trade-off between specificity and comprehensiveness within a framework, but both can be accommodated by a hierarchical structure (Cadenasso *et al.* 2003). Frameworks are hierarchical, in that the high level processes are decomposed into lower level, more specific mechanisms. For example, case specific investigations will necessarily call for detailed causes and mechanisms, while constructing generalizations will call for more broadly comprehensive mechanisms. The higher levels of a framework are more abstract and therefore more generalisable. Therefore, frameworks identify core concepts and processes that must be operationalised for different systems and scales through specification (Cadenasso *et al.* 2003).

Novel framework for the invasion process

The goal of this framework is to understand the invasion of habitats by alien plant species (Fig. 8.2). At the middle hierarchical level, the invasion process is divided into the three contributing components, 1) species characteristics, 2) system context, and 3) system susceptibility. Of course, Drake *et al.* (1989) already identified two important aspects of the invasion process, namely, attributes that allow organisms to invade, and features of the receiving environment that make some environments more invasible. However, the relationship between these components was not specific, and lacked the broader spatial context. In addition, the bipartite framework of Drake *et al.* (1989) can be interpreted as an "either-or" approach to the topic, suggesting competing alternative hypotheses rather than a unified approach. Furthermore, narrow attention to the receiving site may cause geographic or landscape spatial contexts to be neglected. Therefore, for the sake of comprehensiveness, and for providing the richest base for generating models and hypotheses, I partition the spectrum of causes of invasion success into the three processes of species characteristics, system context, and system susceptibility. In essence, the framework identifies internal features of the receiving site, features and processes that act outside the site, and the nature of the potential invaders to be the broadest topics of concern in invasion (Fig. 8.3). This tripartite categorization prevents misinterpretation of the Drake *et al.* (1989) scheme to suggest that internal features act independently of external features, or that site features versus species characteristics are alternative hypotheses. These limitations are addressed in the framework I propose.

The three components are considered to be a logically complete enumeration of the general causes and constraints on invasion. Hence, I expect them to be stable, while the lower level details are intended to be added to and change as research expands. These three component processes of invasion, discussed in more detail later, represent the coarsest level controls to the invasion process.

On the lowest hierarchical level, the elements of these three components are specified for a particular situation. The possible detailed variables would be drawn from other relevant theories, both general to ecology (e.g. succession theory) and other specific research areas (e.g. population ecology). The influence of these variables may be positive or negative, depending on the specific scenario. These details will vary and demonstrate shifts in relative importance among regions or times. Further, not all of the aspects of the three key components need be present, although a successful invader will most likely rely on a combination of several of the factors. In order to explain the use and functionality of the framework, I describe the component variables below (Table 8.1). This compilation is by no means a complete list and the references are shown for illustrative purposes. Rejmanek *et al.* 2005 provide a more comprehensive review of the mechanisms invoked in invasion ecology currently. However, the mechanisms of Rejmanek *et al.* (2005) can be allocated to the three general categories of process I identify.



Numbers are cross-referenced to the literature cited in Table 1

Figure 8.2: A framework for invasion ecology. The highest level of the hierarchy identifies the general processes of interest. The second level down identifies the three broad kinds of contributing processes that can affect the success or failure of invasion in any particular case. Each of the three mid-level processes is disaggregated into its component causes or mechanisms on the lowest level of the hierarchy. The mechanisms are numbered to correspond to the supporting literature for each, listed in Table 8.1. The numbering does not imply a ranking of importance among components.

Species characteristics

Species characteristics refer to those traits of a potential invader which control how invasive it may be, such as propagule production and competitiveness (see Table 8.1 for references relating to species characteristics). These traits are inherent properties of the species and regulate, in concert with other factors, the prominence of the species in its area of origin. Many of these traits were suggested by Baker (1965) as the traits of the ideal weed. However, it has been suggested that these traits may occasionally respond in a different manner when introduced to a novel environment. In other words, species which may be relatively rare in the area of origin may become aggressive invaders when introduced into a new environment. The physiological limitations of a species will have an influence on the degree to which the species may respond to prevailing conditions. These variables are typically generated through autecological studies, which are aimed at understanding the species itself. This will undoubtedly impact on the ability of control and monitoring, and needs careful attention from the management agency when planning operations.

System context

System context is considered at a coarser spatial scale, and generally focuses outside the system that might be invaded. The context provides the linkages between the various systems supplying or transporting potential invaders and the target system. For example, ballast water transfers (Carlton 1985) are pathways of invasion which provide the connection between a source environment, the inherent traits of the invader and features of the receiving environment. If the context of the receiving environment did not include ballast water transfer, invasion would be impeded. Even when ballast water transport exists, the details of how it functions becomes an additional factor of context. For example, the increased speed of ships allowed more potential invaders riding in ballast water to survive the shorter voyages. The context changed based on the nature of the voyage, which is external to the receiving system and different from the species characteristics per se. Clearly, the two interact.

The system context differs from vector science (see Carlton & Ruiz 2005) in that vector science focuses on one aspect of system context, namely, human-mediated movement of living organisms. Vector science therefore includes, amongst others, cause, route, vector and vector strength. While these components describe the particular pathway, the system context provides a broader understanding of how the species characteristics and the susceptibility of the system relate to one another.

Connectivity is a key aspect of system context. It is both structural and functional. Structural connectivity refers to the arrangement of habitats on the landscape adjacent to each other, while functional connectivity refers to the interaction between the habitats that may promote or impede transfer between patches. For example the connectivity between riparian and upland habitats may be due to structural differences in the vegetation, or due to functional factors such as the differential activity of dispersal agents between the two (Cadenasso *et al.* 2003). Pathways explain how a species is transferred to a new habitat (e.g. ballast water) and also includes the number of repeat arrivals at the destination. The number of repeat arrivals indicates the probability of the invasive species reaching whatever site or conditions that are required for establishment in the system, such as open patches and sufficient resources. The higher the number of attempts, the higher the likelihood of success of landing in the site or resource level appropriate for successful establishment. Linked to this is the introduction of ornamental plants which subsequently become invasive. Ornamentals plants will usually be introduced, cultivated and dispersed in large numbers, increasing the likelihood of becoming invasive. Vector efficacy refers to the ability of the available vectors to successfully disperse or aid the dispersal of the species. Global climate change is suggested as a driver which will either promote or impede species becoming invasive.

The contextual component of global climate change affects the hospitability or existence of pathways between source areas and potentially invasible sites. For example, a pathway may open up due to a shift in vegetation patterns, or due to the release from a previous limiting factor, such as minimum temperature or moisture regimes along the migratory pathway.

System susceptibility

System susceptibility refers to those aspects of the receiving environment that either promote or impede the invasion process, such as resource availability, local vector presence and predator or consumer presence. This is therefore a measurable feature within the system or time of interest, and can be assessed by the investigator (Fig. 8.3).

Unlike variables of system context, those of system susceptibility are spatially and temporally localized within the potentially invasible system as defined by researchers or managers.

The susceptibility of the system may be the result of a number of factors. The presence of potential vectors once a species has established in an area may rapidly promote invasion success. Predator or consumer pressure may minimise the chances of invasion if generalist predators or consumers within the site can utilise the new species. However, the absence of generalists may invoke the hypothesis that plants that are released from natural enemies, in accord with the 'enemy release' hypothesis (Keane & Crawley 2002), allow for increased invasion potential. Resource availability determines the extent to which the species requirements are met within the site, and may be influenced by various other factors such as disturbance and fire. Patchiness or open gaps, especially of anthropogenic origin, are often associated with increased invasions (Alpert *et al.* 2000, With 2002, 2004; Table 8.1). Where stable communities are altered, these gaps are frequently colonised by non-native species. Bioclimatic suitability refers to broad similarities in the features of the receiving environment to those of the area of origin. For example, matching the climatic needs for a species occurring in Mediterranean type ecosystems in one area may provide insight into the potential of the species to invade other Mediterranean type ecosystems elsewhere (see Brundu *et al.* 2004 for an example). Native species richness has frequently been suggested as a useful predictor of invasion potential in a site (see references in Table 8.1). However, studies report contradictory conclusions (Kennedy *et al.* 2002, Stohlgren *et al.* 2003), due to the specific nature of the cases and the lack of consideration of other interacting variables. Geographic or landscape variables of the sort I include under the category of system context are potentially important contributors to the ability to generalize about the effects of species richness of the receiving site.

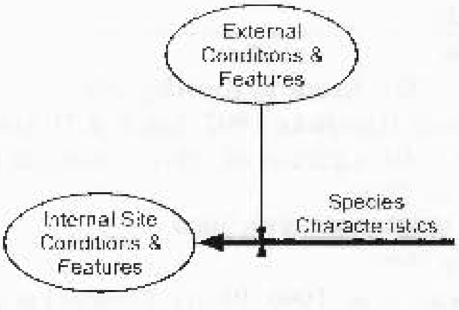


Figure 8.3: Conceptualizing invasion as determined by conditions external to the potentially invasible site, conditions internal to that site, and characteristics of the potentially invasive species. What is external versus internal, in time and space, depends on the boundaries set by the research model or the management goals. Given a model of the system that defines convenient, jurisdictional, or natural boundaries, this list of general kinds of influences on invasion is logically complete. A framework elaborating these three features would therefore be comprehensive.

Table 8.1: References illustrating work in particular areas of invasion biology. The references are organized by the three components of the invasion framework: species characteristics, system context and system susceptibility. The numbers in front of each reference refer to the numbered mechanisms in Figure 8.2. This compilation is by no means a conclusive list. Rather the references are shown for illustrative purposes.

No	Reference
	Species characteristics
1	Rejmánek 1996, Rejmánek & Richardson 1996, D'Antonio *et al.* 2001, Foster 2001. Holmes 2002, Buckley *et al.* 2003, Levine *et al.* 2003, Colautti & MacIsaac 2004
2	Heywood 1989, Higgins *et al.* 1996, Rejmánek 1996, Higgins & Richardson 1998, Vilà & D'Antonio 1998, Callaway & Aschehoug 2000, Campbell & Gibson 2000, Pakeman 2001, Nathan *et al.* 2002, van der Wall 2002
3	Hutchenson 1998, Sieman & Rogers 2003
4	Alpert *et al.* 2000, Leishman *et al.* 2004
5	Bakker & Wilson 2000, Corbin & D'Antonio 2004, Reinhardt *et al.* 2004, Vilà & Weiner 2004
6	Holmes 2002, Christian & Stanton 2004
7	Rejmánek & Richardson 1996, Buckley *et al.* 2003
	System context
1	Reichard & White 2001, Gelbard & Belnap 2003, Foxcroft *et al.* 2004, With 2004
2	Reichard & White 2001, McKinney 2002
3	Foxcroft *et al.* 2004

4	Dukes & Mooney 1999, Stohlgren *et al.* 1999, Stachwicz *et al.* 2002, Kritikos *et al.* 2003, Weltzin *et al.* 2003
	System susceptibility
1	Foxcroft *et al.* 2004
2	Prier-Richard *et al.* 2001, Keane & Krawley 2002
3	Hobbs 1989, Hobbs & Heunneke 1992, Mack & D'Antonio 1998, Holmes *et al.* 2000, Berlow *et al.* 2001, Grace *et al.* 2001, Brooks & Pyke 2002, Cannas *et al.* 2002, Leishman *et al.* 2004
4	Alpert *et al.* 2000, With 2002, With 2004
5	Hobbs & Huenneke 1992
6	Huston 1994, Crawley *et al.* 1996, Planty-Tabacchi *et al.* 1996, Kennedy *et al.* 2002, Stohlgren *et al.* 2003, Cleland *et al.* 2004

Operationalising the framework- a species specific example

The overriding goal of the framework is to understand the invasion of habitats by alien species. I apply this framework to a specific case in an attempt to understand the invasion of Kruger National Park (KNP) by *Opuntia stricta*. KNP is one of the world's premier conservation parks and invasions are a key management concern (Freitag-Ronaldson & Foxcroft 2003). For this application of the framework, the general goal can be restated into a more focused question: "What controls the invasion of KNP by *O. stricta*?

Opuntia stricta is regarded as one of the most serious invasive plant species in the KNP, covering an area of about 80 000 ha (Chapter 2). This species has been relatively well studied (Hoffmann *et al.* 1998a,b, Lotter & Hoffmann 1998, Foxcroft & Hoffmann 2000, Foxcroft 2003, Chapter 2) and some studies invoked factors such as lack of consumers or predation pressure (Foxcroft 2003), propagule production (Chapter 2) and vector efficacy (Lotter & Hoffmann 1998, Foxcroft *et al.* 2004) as the mechanisms underlying its invasion. The framework, however, indicates the potential for interrelatedness among these factors which invoke all three framework components. The potentially invasible sites exist as a variety of distinct areas or habitats within KNP. The relevant species characteristics are the production of highly viable seeds as well as an ability to propagate vegetatively. The most important feature of system susceptibility is the relatively dry and open nature of the KNP sites, which are amenable to *O. stricta* establishment and growth, while the system context is governed by the efficacy of the baboons and elephants as dispersal vectors between habitats in KNP. These three components of the framework combined have led to the successful invasion of *O. stricta*. Any study attempting to explain the distribution and spread of *O. stricta* without the combined interaction of all three components will most likely fail to unravel the invasion dynamics. In other words, understanding how the invasion process takes place requires not only understanding the two factors identified by Drake *et al.* (1989), i.e., species characteristics and the nature of the receiving site, but also spatially external, contextual variables.

The framework further helps to discriminate the net effects of invasions, or the outcomes of the various mechanisms of invasion, from the mechanisms themselves. One such complex effect is propagule pressure, which is gaining interest as a mechanism of explaining invasion patterns (McKinney 2002, Rouget & Richardson 2003a,b, Pauchard & Alaback 2004, Lockwood *et al.* 2005). However, propagule pressure is an interaction of distance to source, amount of propagules produced, connectivity (spatial arrangements of patches and vectors) and time since arrival. In essence, propagule pressure aggregates features of species characteristics, system geographic context, and the within site demographic dynamics. In a similar manner, "lag-phases", which are commonly referred to in invasion ecology literature (see Binggeli 2000, Pysek *et al.* 2004), are an aggregate outcome rather than a mechanism of invasion. The time taken to observe the rapid spread phase is an interaction between the characteristics of the species, the susceptibility of the system and the system context. In addition, the issue of detectability may play a role in the phenomenon of lag phases.

A model for invasion ecology

A broad and inclusive framework, such as the one I am proposing, can be operationalised by using a model template which elucidates the general kinds of relationship among framework components. This is done in an abstract manner and can later be applied to a particular situation by specifying the components of the model for that case. I use the basic "flow chain" approach (Shachak & Jones 1995) to progress from the inclusive framework to a model template for invasion ecology (Fig. 8.4). The components identified in the framework (Fig. 8.2) are placed into action in describing the change between State 1 and State 2. The state changes may be described for the specific case by the investigator, and thus are abstracted in the model template to represent any existing (State 1), altered (State 2), or desired state (State 2). For example, the change in state may be described as the change from an un-invaded state to a completely transformed state, or from an un-invaded to lightly invaded state, depending on the investigation. In the framework the agent of change is the alien and potentially invasive species. The degree and manner in which the potential invader will change the state from State 1 to State 2, is controlled by the interactions between species characteristics and system context. The combined outcome of these interactions is then controlled by the system susceptibility. In other words, both the species characteristics and system context will act upon the potentially invasive species to determine its invasion potential. However, this is then modulated by the systems susceptibility, to determine the degree to which change will be affected between State 1 and State 2.

Unfortunately there are few cases where it is possible to return from State 2 to State 1, and if there is, it is controlled largely by management in the early stages. On some time scales it may appear that an invaded state returns to the previous, uninvaded state without the intervention of management (Simberloff & Gibbons 2004). However, over a long time scale this may be considered an un-successful invader (naturalised alien species), because the species was unable to sustain itself (Fig. 8.1).

Returning to my example of *O. stricta* in KNP, I used the model template and specify the components for this case. In a study attempting to determine the causes of invasion of *O. stricta* in KNP, I concluded in Chapter 6 that the invasion was largely a function of propagule pressure. However, as I have shown earlier, propagule pressure is an aggregate function of distance to source, amount of seeds produced, connectivity of both the source and new environment and habitats across the new environment and, time since arrival. Through the use of the model the interrelatedness of the model components can clearly be seen.

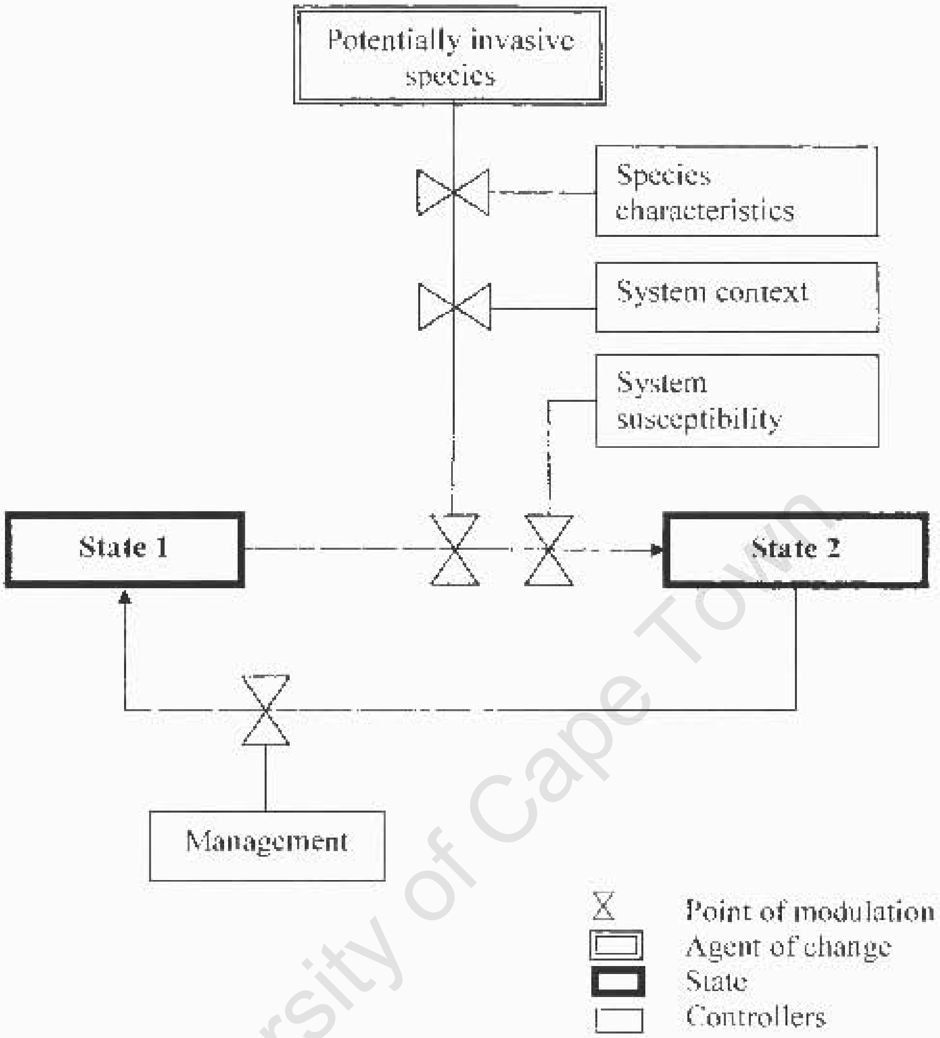


Figure 8.4: An invasion ecology model template. This general model form suggests how the causes identified in the invasion framework (Fig. 8.2) can interact with one another in any situation where invasion is to be analyzed. The model identifies two states of the system or of a system at two time periods (State 1 and State 2). Whether a potentially invasive species actually can shift the system from State 1 to State 2 is determined by the three kinds of controllers, which correspond to the mid-level processes in the invasion framework. In addition to the mechanisms identified in the framework, the model recognizes that management can be brought to bear on an altered system (State 2) in an attempt to revert it to State 1. Specific models aimed at particular systems or conditions would specify how the general model components shown here can be parameterized for that specific case. This general model format follows the strategy of ecological flow chains as presented by Jones *et al.* (1994).

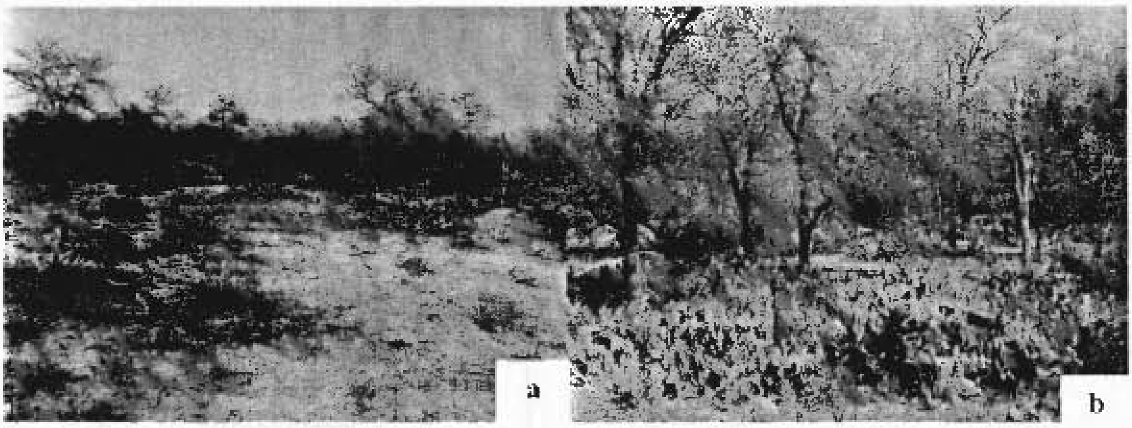


Figure 8.5 (a) An un- or pre-invaded state, characterised as the Sabie/Crocodile thorn thickets, (b) An invaded site with scattered individuals and impenetrable thickets of *Opuntia stricta*. (Photographs: L.C. Foxcroft). The state change observed in KNP is from an un-invaded to invaded state, with the agent of change being *O. stricta*. The change in character of the area invaded is from the Sabie/Crocodile thorn thickets (as described by Gertenbach 1983), which is dominated by an *Acacia nigrescens / Combretum apiculatum* association (State 1; Fig. 8.5a), to a patchwork of scattered individuals or impenetrable thickets of *O. stricta*, several hectares in extent (State 2; Fig. 8.5b).

The inherent characteristics of *O. stricta* that promote its invasion success include the production of large quantities of highly viable seeds (Lotter *et al.* 1999, Reinhardt *et al.* 1999) and an ability to reproduce vegetatively (Anthony 1954). The fleshy fruits are attractive to baboons and elephants and thus easily dispersed (Lotter & Hoffmann 1998). The plant is also well protected by spiny thorns and has a bitter taste that discourages browsing.

The system context includes the intentional pathway, through which the plant was introduced into KNP as an ornamental plant by humans (Lotter & Hoffmann 1998). Further, the vectors are highly effective as they are mobile and can move vast distances, starting new invasion foci (Chapter 6 and 7). The combination of these characteristics are then controlled by the susceptibility of the system, which is climatically suitable to *O. stricta*, has no consumer pressure such as browsing and is freed of at least eight associated natural enemy species (Foxcroft 2003).

Relevance of the invasion ecology framework and model to management

The invasion of a plant into an area elicits a number of management responses. These may range from no action due to a lack of awareness, knowledge or resources, to a comprehensive control operation. However, an approach focusing on the methods, chemicals and tools for species removal is the most frequent response (Moody & Mack 1998). Only more recently have efforts been made to provide a more holistic and sustainable approach to invasive species management (see Wittenberg & Cock 2001, KNP 2005), which includes integrated pest management or biological control.

By applying the model template, I am thus able to contextualise the various responses, evaluating each component and providing insight into a holistic management approach specified for a particular problem (Fig. 8.6). I expand on the model in more detail below.

The potentially invasive species – characteristics and context

Much may be done to enhance the capacity to predict invasions and thus enact preventative measures. Although the success of a preventative programme may not be as visible as that of a removal programme, the results are undeniably beneficial. This may be achieved by comparative studies on the potentially invasive species' broad bioclimatic suitability (Rouget *et al.* 2004), or through combining an understanding of the species' inherent characteristics, and the system context in which the species is likely to be found. For example, Nel *et al.* (2004) describe the objective development of a list of invasive alien plants in South Africa, using available quantitative data and expert knowledge on current patterns of distribution and abundance, life-history traits, and (for emerging invaders) characteristics of potential habitat.

Although short of breeding or genetic engineering, little may be done to directly impact the traits of an invader, the management options to control the species may be enhanced by developing an understanding of the species. Minimising the efficacy of the traits of the invader that make it more invasive is largely the work of biological control agents. For example, minimising either seed production or competitiveness alone may be sufficient to manage the invader.

Anthropogenic pathways are probably one of the most visible but difficult to manage, especially considering the increase in international trade and travel. The intentional introduction of horticultural plants for example, is widely known to have been the origin of many serious invasions. Further, 'slash and burn' or clear felling, creates fragmented landscapes and anthropogenic disturbance which may greatly facilitate invasion. However these invasion pathways may be ameliorated through careful habitat manipulation and compatible land use and corridors to neighbouring areas. This is an especially important component when considering the invasion of protected areas, which are rapidly becoming fragments in an array of different, often incompatible (high intensity crop production) land uses (Freitag-Ronaldson & Foxcroft 2003, appendix 1.3).

The management response to invasion will almost always be directly related to the temporal and spatial extent of the invasion. In other words, the degree of change between State 1 and State 2 will determine whether a species will be detected at an early stage, and may be amenable to rapid response techniques. More frequently however, invasions are only detected at an advanced stage and control actions often only initiated once the chances for easily reversing the negative impacts are substantially reduced. The success of the control response will determine the degree to which the system may be reverted back to the original or a desired state. However, where the invasion results in a more permanent impact, control of the invasive species alone will not be sufficient to undo the damage and re-engineering of some sort will be required. I discuss this further in the next section.

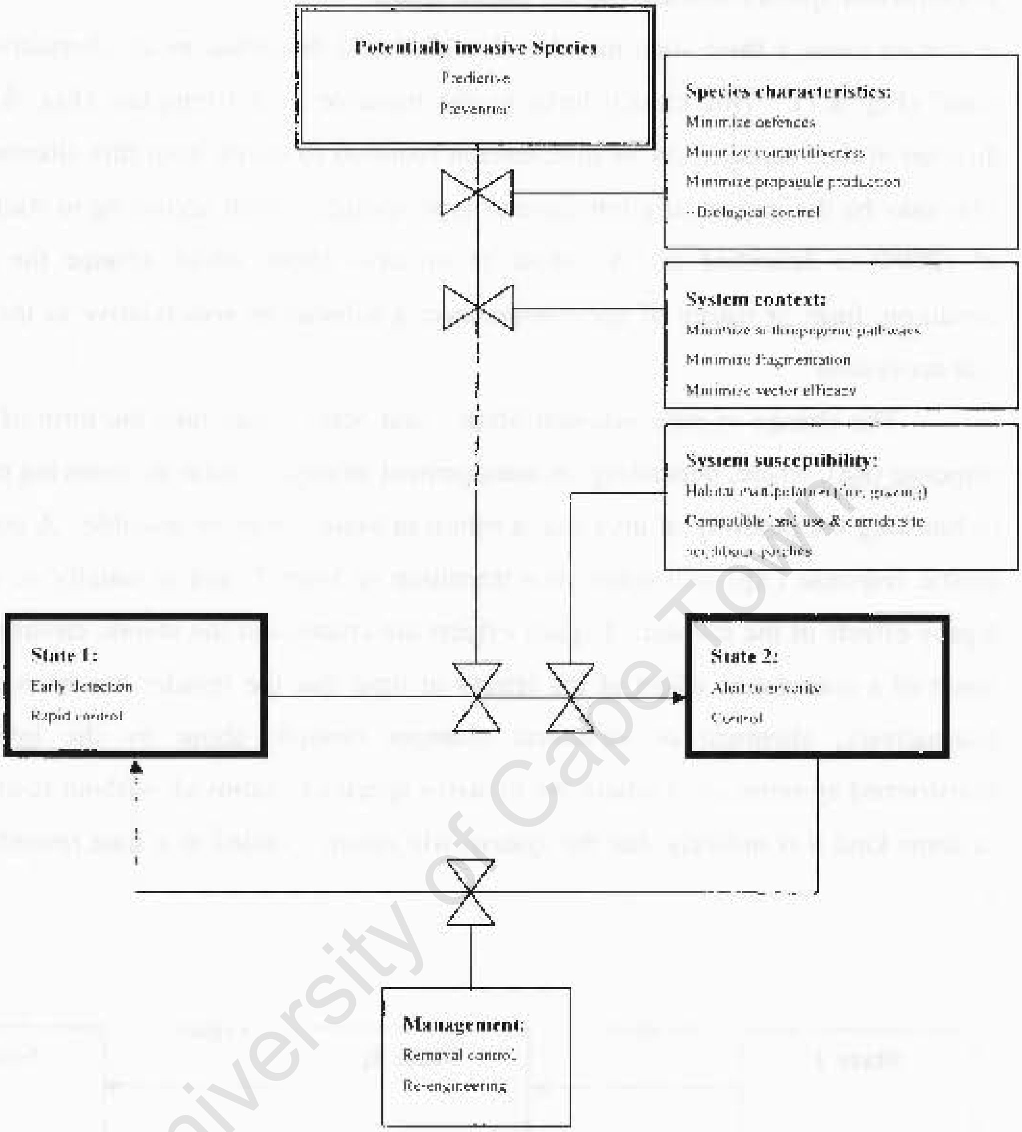


Figure 8.6: A model template for management response to invasions. The management response is applied to the model template (Fig 8.3) to provide an explicit link between management options and the invasion process.

Transformer species and alternative stable-states

In certain cases a third state may be identified and described as an alternative "stable-state" (Fig. 8.7). This clearly links to the invasive model template (Fig. 8.4), but is directed at the management or intervention required to move from this alternative state. This may be the impact of a transformer type species, which according to Richardson *et al.* (2000) is described as "A subset of invasive plants which change the character, condition, form or nature of ecosystems over a substantial area relative to the extent of that ecosystem".

The change in state between State 1 and State 2 may take the form of an elastic response (Re), where, depending on management strategies, such as removing the invader or blocking the pathway of invasion, a return to State 1 may be possible. A persistent or plastic response (Rp) will result in a transition to State 3, and is usually as a result of legacy effects of the invader. Legacy effects are changes in the abiotic environment as a result of a cumulative effect of the length of time that the invader has been present, or alternatively, chemical or structural changes brought about by the invader. In transformed systems, even where the invasive species is removed, without re-engineering of some kind it is unlikely that the system will return unaided to a state resembling State 1.

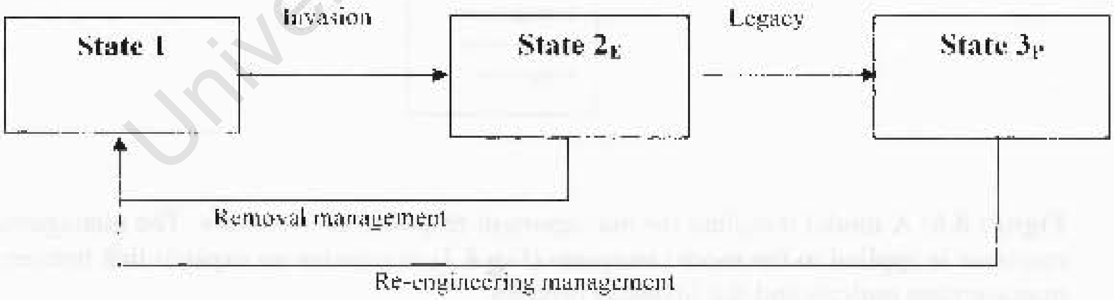


Figure 8.7: A state change model for the impacts of invasions and legacy effects. The model indicates the degree to which management may be effective at reversing the negative impacts of invasion. $_E$ and $_P$ indicate elastic and plastic type responses, respectively.

Conclusion

Conceptual frameworks and models have formed an integral component of developing an understanding of many phenomena in ecological systems. The relatively slow development in understanding the components driving plant invasions has hampered prediction and has limited the scientific basis for management. The various factors that have been proposed as drivers of invasion clearly need to be considered together within an integrated framework. Advances in the understanding of invasions within any given place need explicit consideration of the species traits, the receiving environment and the connections between them. This roster of factors is a logically complete set of features, which rely on explicit temporal and spatial delimitation of the system of interest. To date models have failed to successfully develop general understanding of invasions. The suggested framework provides a structure to facilitate syntheses across scales and situations that might promote generalization. It is general enough to provide a common understanding, while at the same time, providing the mechanisms that can be specified to answer questions about particular invasions.

CHAPTER NINE
GENERAL CONCLUSION

Ecological theory and management applicability

To develop some insights into the mechanisms behind alien plant invasions in an African savanna, I have considered a number of aspects which I believe to play an important role. Certainly the range of important components that require in-depth investigation are beyond the scope of this thesis. However, I have tried to highlight some of these and provide a framework for continued research and learning.

I have consciously tried to use, and advance science (ecological) theory, while developing useful management outcomes, and similarly, use management problems to define and develop science theory (Table 9.1). Clearly, importance of different spatial scales and the inter-linkages between these emerges as a crucial issue.

In the introduction (chapter 1) I related the various components of the thesis to the 'naturalization-transformation' model (Richardson *et al.* 2000). While this approach provides one way of viewing the relationship of various aspects to the invasion process, I suggest an alternative, but complementary, framework and model, which was discussed in chapter 8. I discuss my findings and conclusions in relation to these new conceptual tools.

I argue that to develop a general understanding of invasions requires investigation of three linked components which together constitute the invasion process. These include species characteristics, the system context and the system susceptibility (Fig. 9.1). Each of these higher level contributing processes have a number of specific causes or mechanisms, which may or may not be invoked, in a particular ecosystem. I have for example explored, explicitly or implicitly, the following species characteristics: propagule production, dispersal mode, defences, resource demand and competitiveness (Fig. 9.1). I have considered connectivity, pathways of invasion and vector efficacy as features of the system context, and resource availability, patchiness and other features of system susceptibility. Thus, although I have not considered all the specific mechanisms potentially implicated, I have still been able to contribute to an overall understanding of invasions in savanna systems. This can be applied to a model (Fig. 9.2) which places the three contributing processes into context with each other, indicating the point at which actions may be taken to enhance management strategies.

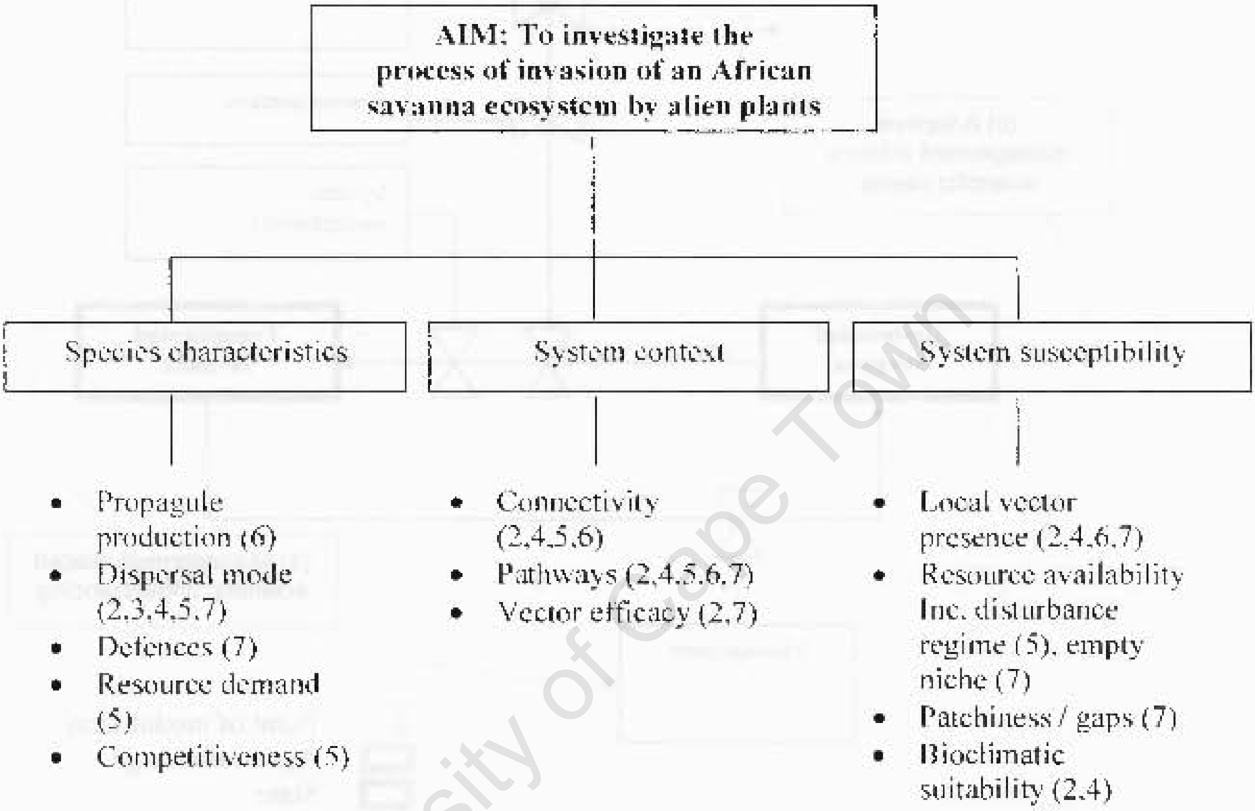


Figure 9.1: Applying the various thesis chapters to a general framework for plant invasion ecology. Numbers in brackets refer to thesis chapters in which the particular aspect was explored.

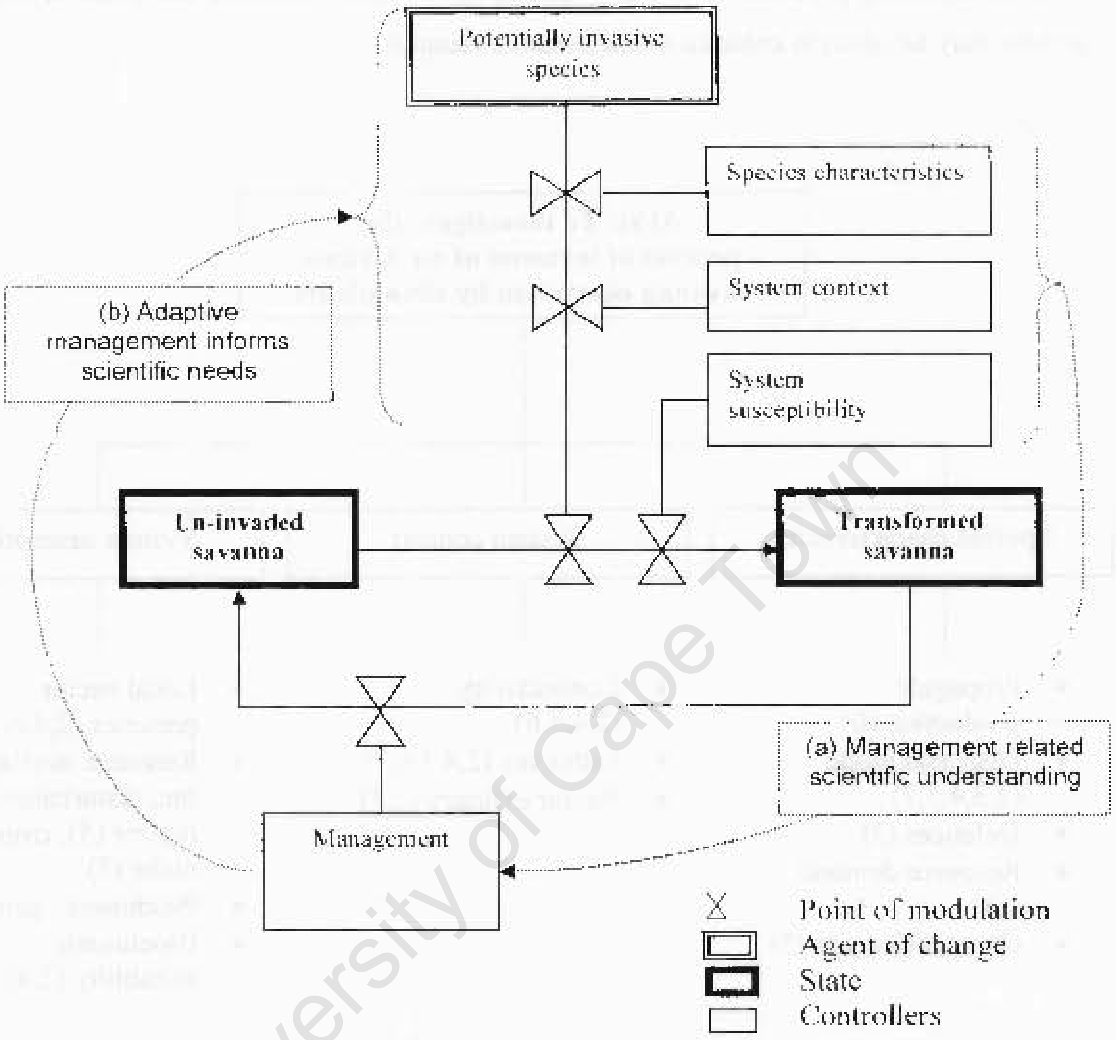


Figure 9.2: A model for exploring the context and role of three composite processes in the invasion process, and the implications for management.

Clearly, if management is to be successful in the long-term, plans need to consider species characteristics, system context and system susceptibility. Chapter 2 indicates the importance of assessing the risk of surrounding areas both on a species- and area-approach, and thus managing both the potential invasion in the most strategic areas, as well as the most important species at specific 'hot-spots'. Chapter 4 considers the human dimension, clearly making a case for the management of intentional introductions of alien plants as a focus of invasion. Although human dimensions of biological invasions are well recognised, I explored these problems in a special microcosm- a protected area- and suggest that insights from this work might be applied to other protected areas before it is too late. I assessed the dynamics of one terrestrial alien plant (*Opuntia stricta*), at two scales, namely the landscape- (chapter 6) and local-scale (chapter 7). I was able to draw on this experience in formulating the conceptual framework and model (chapter 8), and contextualize them with a real example. The work on riparian invasions following a large infrequent disturbance (chapter 5) provides insights into the role of patches and differential resource distribution in patches, in examining the riparian systems' susceptibility to invasion. Specifically assessing alien plant distribution data at multiple scales (chapter 3) provided the scale context and necessary understanding that would allow the above described work to be placed in context spatially.

These components thus provide some insight into the mechanisms invoked by alien plants invading a savanna ecosystem, while collectively, providing some understanding necessary to formulate more advanced management plans (Fig. 9.2a and Table 9.1). But this needs to be taken further. In applying an adaptive management process, management experience must also be used to define research questions, and scientists need to be adaptable in the way they design their research and the ecological paradigms they consider (Fig. 9.2b; see also appendices 1.4 & 1.6).

Scale considerations

Why worry about scale? It may be argued that scale is an intuitive background issue in every ecological investigation (see the discussion in Wiens 1989, p. 385, in his argument for careful explicit consideration of spatial scaling). I would agree; it most often is an intuitive part of ecological research. I also argue that instead of being a background issue, it needs to come to the fore explicitly (as argued by Wiens 1989) for three important reasons specifically, in considering alien plant invasions. First, if an investigator does not consider the grain, extent and time scales carefully in the research design, the design might be inappropriate for the particular arguments that are being investigated. This would lead to incorrect conclusions. For example, the debate surrounding the issue of whether native species richness leads to increased invasion or suppresses invasion (Stohlgren *et al.* 1999) can be resolved to a large extent by scale. At a small scale (1 m^2 plot scale) it indeed appears that areas of low plant species richness are more easily invaded, and at a landscape or biome scale, plant invasions generally occur in areas of high species richness (Stohlgren *at al.* 1999). Second, this would allow replication of techniques and thus direct comparisons in other areas; or, at least allow for carefully considered cross-scale comparisons. Third, a good understanding of the scale issues are needed to apply science theory to conservation management. Management problems and boundaries, for example the size of protected areas, vary enormously and applying strategies at in incorrect scale may lead to failure, frustration and perhaps loss of trust in science or scientists by managers.

Concluding remarks- A personal perspective

This research has been an intense, challenging and immensely satisfying learning experience. I will forever be indebted to my supervisors and various collaborating scientists that have played a role in various ways. While developing a personal thesis on the invasion of alien plants, I have been challenged to broaden my horizons and think widely across sub-disciplines in ecology. This has been extremely exciting process, and a foundation on which I look forward to building.

Table 9.1: The relationship between the thesis chapters: implications for research, management and monitoring.

Chapter	**Research implications**	**Management implications**	[1]**Monitoring implications**
2- Risk assessment of riparian invasions	Provides a new framework which can benefit from refinement and testing its applicability in different situations.	Provides a framework for assessing areas of increased management importance, both from a area- and species-perspective.	Provides zones and areas (I used quaternary watersheds) when monitoring is required to detect an influx of new species or changes in abundance.
3- Patterns at multiple spatial scales	Argues for thorough consideration to be given to the scale at which alien plants are investigated ecologically, as well as for management and monitoring.	Provides understanding of the importance of spatial scale in assessing alien plant distribution and a manner in which to determine the best scale of resolution for exploring these issues in a particular scenario.	Same as for management.
4- Ornamental plants as invasive aliens	Assesses the human dimension in introducing and facilitating alien plant invasions from an ecological perspective. Would be a useful case study to further explore from a sociological approach.	Provides insights into the management and policy procedures that were put in place, and discusses some of the highlights and short-falls.	Indicates the importance of auditing management of alien plants in known and high priority foci.
5- Patterns of riparian invasions	Provides a new approach assesses the roles of patches in a landscape as either promoting or inhibiting the potential for invasion in a river landscape, and which could be further researched	Indicates important patches across a landscape that should be managed due to current or potential increased levels of invasion.	Similar to management.

	to refine this understanding.		
6- Reconstructing *Opuntia stricta* invasion	Provided details into the role of propagule pressure in structuring patterns and the possible process and rate of invasion over the last 50 years. This work contributed to the explanation of the conceptual tools developed in chapter 8.	Reinforces the importance of managing outlying foci as the driving factor in the invasion process.	Provides an idea of where to monitor as well as baseline data to assess changes in distribution and density of *O. stricta*.
7- Local-scale dynamics of *Opuntia stricta* invasion	Provided detailed insights into the importance of vectors, nurse plants and micro-climate in establishment of this species. Indicates that to completely understand a problem, detailed studies of its ecology are needed.	Contributes to the overall understanding of the process of *Opuntia stricta* invasion, which allows improved management of the problem.	Same as for management.
8- A new conceptual framework for invasions	Provides new tools for exploring any invasive plant situation, generalizing across scales and scenarios and thus developing generality in invasion biology. Although designed for plant invasions, is most likely applicable across taxonomic groups.	Provides insights into the important mechanism in a particular scenario, and thus the important attributes that need to be considered in formulation management responses.	By highlighting the important attributes of a particular invasion problem, might provide an indication of the aspects that need monitoring.

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[1] - Monitoring is referred to here as the ability to detect changes in the distribution and abundance of a species over time.

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Plants in National Parks: Perspectives from South Africa and Australia. In: *Plant Invasions: human perception, ecological impacts and management* (eds. B. Tokarska-Guzik, J. Brock, G. Brundu, L. Child, C. Daehler, P. Pyšek), pp. 391–407. Backhuys Publishers, Leiden, The Netherlands. In press.

1.9: Foxcroft L.C. & Freitag-Ronaldson S. 2007. Seven decades of institutional learning: managing alien plant invasions in the Kruger National Park, South Africa. *Oryx* 41: 160–167.

Part 2- Alien plant lists for the Kruger National Park.

This appendix is based on Foxcroft *et al.* (2003), and subsequently updated with data managed by LCF in the SANParks Conservation Services division. The aim of this appendix is to provide an overall list of alien plants for the Kruger National Park, as a reference point.

2.1 Table: Ornamental alien plant species recorded per camp in Kruger National Park, indicating the number of camps in which each species has been recorded, as well as mode of introduction (Chapter 4). Species names, authorities and indications of naturalization are based on Foxcroft *et al.* (2003). Evidence of cultivation means that the taxon was intentionally introduced, propagated, irrigated and tended to. Evidence of naturalization means that the species has naturalised out side of staff gardens and tourist rest camps. It might happen that the species naturalized (naturalized, sensu Pyšek *et al.* 2004) in the village environment, not necessarily in the natural landscapes. * indicates that the species is invasive in KNP.

2.2 Table: Distribution and nestedness of alien plant species between camps (Chapter 4).

2.3: Foxcroft L.C., Henderson L. Nichols G.R. & Martin B.W. 2003. A revised list of alien plants for the Kruger National Park. *Koedoe* 46: 21–44.

2.4: Foxcroft L.C. 2007. Current List of Alien Plants for the Kruger National Park, South Africa. South African National Parks, Skukuza, South Africa.

Metadata:

All data used in this thesis is in the process of being catalogued in the Kruger National Park data (metadata) repository, and is available from http://dataknp.sanparks.org. In addition, the metadata will also be catalogued in the Centre for Invasion Biology, Stellenbosch University data repository, which is available from http://ir.sun.ac.za/cib. Alternatively, you may contact me at LlewellynF@sanparks.org.

APPENDICES

Part 1- Management implications.

1.1: KNP Policy/ Standard operating procedure on alien species management (Chapter 4).

Appendix 1.1:

SOUTH AFRICAN NATIONAL PARKS

THE CONTROL OF ALIEN PLANT SPECIES IN DEVELOPED AREAS OF THE KRUGER NATIONAL PARK

June 2004
Prepared by: Llewellyn Foxcroft

1. INTRODUCTION

Purpose of this document

This standard operating procedure, which falls under the alien species policy for SANParks, provides guidelines for the control of alien plants in all developed areas in the KNP. It provides occupants with information on the regulations, and indicates which species may not be cultivated in developed areas.

Scope of this document

This document refers to all plant species within developed areas in the KNP. This includes all developed and disturbed areas, namely, rest camps, personnel villages, ranger outposts, entrance gates, concessions, offices and any other similar areas.

2. BACKGROUND AND DESCRIPTION OF THE PROBLEM

Researchers have estimated that an effective program to control invasive alien plants in South Africa would cost approximately US$100 million per year for the next 20 years! Although a proportion of invasive plants find their way into areas accidentally (as hitchhikers on other transported goods) intentional introductions of plants through ornamental use, commercial forestry and other means, account for a large number of invasive species worldwide. Invasive plants have clearly been shown to have a serious impact on biodiversity, production ability and ecosystem services (such as water provision and purification).

Unfortunately, most invasions are characterized by a "lag-phase" during which time a species may not invade or cause any disruption at all. Further, this lag-phase may take up to 200 years before the alien species becomes invasive and is recognized as a serious problem. By this point, control is costly and frequently not efficient. Our best defence is to be pro-active and remove any species that do not belong in the area before they have the opportunity to invade. Many of the species currently regarded as serious invasive species in the KNP include species that were used commonly as ornamental garden plants. Examples include the *Opuntia stricta* (sour prickly pear invasion covering 80 000 hectares around Skukuza and still spreading), *Lantana camara* (which has invaded almost all the main rivers in the KNP) and even *Pistia stratiotes* (water lettuce), which for many years has been a problem on the Sabie river and Sunset dam. All these plants were cultivated in the Skukuza village (and others), and were not initially known to be invasive - just as we do not know which species we now cultivate will become invasive in the future.

This document serves as a formal record of the prohibition of alien plant species within KNP personnel villages and rest camps. The document will also form the basis of the KNP Code of Conduct -Alien Plant section and provides clarification of the regulations surrounding alien plant species in the KNP.

In general, the practice of propagating and dispersing prohibited alien plant species in the KNP has continued in contravention of the KNP Code of Conduct and in spite of the Alien Biota Section's efforts to control these species. Many of these species have invaded riverine and other areas of the KNP or have the potential to do so. Millions of Rands (up to R6 million per year in the KNP alone) are being spent annually on removing these plants outside of rest camps and staff villages, while other potentially invasive species are being watered/irrigated (many with higher water needs than indigenous species) and cultivated.

The long-term aim of the current alien plant policy is to promote a corporate understanding of the dangers associated with alien species and to ensure long-term protection from these species by aiming for a KNP where only indigenous species are used in the rest camps and villages.

3. PRINCIPLES AND DEFINITIONS

3.1 Principles

- South Africa (and therefore KNP) as signatories to the Convention on Biodiversity, under Article 8 (II) have an obligation to: **Prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species.**
- Invasive alien species are regarded as one of the greatest threats to the biodiversity of the KNP.
- The KNP shall strive to remove all alien species where possible, and to restore previously invaded or planted areas, in order for these sites to resemble or form part of the functioning landscape and ecosystem.

3.2 Guidelines

- No notions of "naturalization" are taken into account.
- Although all alien species are undesirable and their introduction prohibited, the control of species should be traded off against the impacts and costs (ecological and economic) of control.
- Economic benefits to preventing the introduction of and for controlling species should be developed wherever possible (e.g. Working for Water).
- Efforts should be made to remove all previous introductions (i.e. the removal of alien plants in rest camps and lawn grasses).
- Certain alien species need to be accepted as part of the KNP ecosystem. Although undesirable, it may either be impossible to remove these species due to the scale (spatial and/or temporal) of invasions, the characteristics of certain species or due to it being economically too costly to achieve. With this in mind it is our obligation to continuously study the long-term impact on biodiversity and document such impacts for the benefit of future generations and management of other areas, where the invasion is not as advanced.
- The intentional introduction of any alien species into the KNP is prohibited (unless an approved species, e.g. biological control or approved pet).

- Certain species may be approved for importation into the KNP, where it has been proven that the introduction of such species is beneficial and poses no, or minimum threat. For example, biological control for the long-term management of a particular invasive alien plant.
- Any new introduction of an alien species should be reported and disposed of immediately (in a suitable manner).
- It is the responsibility of all SANParks personnel (and any other affiliated contract employees) to ensure the implementation of this policy.
- All applicable legislation will be adhered to as a minimum guideline, with the aim to further improve thereon and provide an example to all South Africans.
- For those species requiring import and export permits, the State veterinary services and the relevant importing or exporting provincial conservation organizations should be consulted.

3.3 Definition of "indigenous" and "alien" in the KNP context:

The following definitions will indicate the types of species that may be planted in a particular area:

Large rest camps, tourist entrance gates:
Although landscaping and cultivation are allowed. all plants are to be restricted to those known to be indigenous within the landscape in which the camp is situated.

Small camps, such as private and bush camps, concessions and wilderness trail camps etc:
No landscaping or cultivation allowed. Therefore only species occurring in the immediate vicinity of the camp are allowed. These plants are to grow naturally in the camp. Planting of species may only be done in cases where the camps have been cleared of vegetation and then only with plants of the species found in the immediate vicinity of the camp.

Villages and staff gardens:
Trees- any trees found in the KNP may be planted. However. planting of trees should preferably be restricted to types found in the vicinity of the village.
Shrubs and flowers- in general. any shrub or flower from the KNP, lowveld and escarpment ecosystems are allowed.

4. POLICY

1. It is the responsibility of all SANParks personnel (and any other affiliated contract employees) to ensure the implementation of this policy.
2. All applicable legislation (e.g. NEMBA and CARA) will be adhered to as a **minimum** guideline, with the aim to further improve thereon and set a good example to all South Africans.
3. **The introduction, propagation and spread of any alien plant species within the KNP is strictly prohibited.**
4. All vacant gardens will have **all** alien species removed, regardless of their apparent invasiveness.
5. All occupied gardens will have the NEMBA / CARA listed plants, as well as other well known invasive species and fruit trees removed as a minimum. Please see attached list (Table 1-3).

6. Refusal to comply with the regulations as stipulated in the NEMBA / CARA Act is an offence and full co-operation is required. The Executive officer, as defined by the regulations may inspect premises to ensure these regulations are being adhered to.
7. The main source of all plants for cultivation should be the Skukuza Nursery. No other plants will be allowed into the KNP. Inspections at the gate should include checking for plant material to prevent the introduction of alien species through the gates.
8. Prohibited species (i.e. species listed in tables 1-3) that are grown in pots will not be allowed under any circumstance. Any other alien plants growing in pots will only be allowed provided they do not produce any seed or vegetative parts which will allow species to escape from pots and hanging baskets.
9. No alien plant material may be distributed between gardens and be allowed to establish.
10. No alien plants may be dumped over fences or in any other place other than that designated for that purpose. Thereafter, the alien plants shall be killed at the disposal sites to prevent them from establishing and escaping.
11. No alien plant may be planted against or encouraged to grow on and into trees.
12. The Invasive Species Section or the executive officer (as designated by the regulations) may inspect the premises for plants species at any time.
13. Clearing work is an ongoing process and teams will be required to revisit the gardens on an ongoing basis to remove re-growth and follow-up previous operations.
14. The KNP reserves the right to change the declared status of any plant at any time.

6. RELATED POLICIES AND DOCUMENTS

- KNP Water Use Policy. Many invasive alien plants use considerably more water than indigenous plants. In addition, irrigation of lawns and maintaining water intensive garden plants results in further water wastage. Such lawns and gardens should be replaced with indigenous species (rest camps should be planted back to indigenous shrubs and trees to resemble the atmosphere of the lowveld ecosystem).
- Code of Conduct- Kruger National Park.

7. RELEVANT LEGISLATION

- CARA - Conservation of Agricultural Resources Act (Act 43 of 1983)
- National Environmental Management Biodiversity Act (Act 10 of 2004)
- National Environmental Management Protected Areas Act
- The Convention on Biological Diversity, Article 8(H).

APPENDICES

Part 1- Management implications.

1.2: Foxcroft L. & Richardson D.M. 2003. Managing alien plant invasions in the Kruger National Park, South Africa. In: *Plant Invasions: Ecological Threats and Management Solutions* (eds. L.E. Child, J.H. Brock, G. Brundu, K. Prach, P. Pyšek, P.M. Wade & M. Williamson), pp. 385–403. Backhuys Publishers, Leiden, The Netherlands.

APPENDICES

Part 1- Management implications.

1.3: Freitag-Ronaldson S. & Foxcroft L.C. 2003. Anthropogenic ecosystem influences in the Kruger National Park. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity* (eds. J. Du Toit, K.H. Rogers & H.C. Biggs), pp. 391–412. Island Press, Washington, D.C., USA.

Managing alien plant invasions in the Kruger National Park, South Africa

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Abstract

Invasive alien plants were first noted as a problem in the Kruger National Park (KNP) in 1937. Since then, the number of invasive alien species and types of impacts and the overall impact has increased rapidly.

The most widespread terrestrial invaders are: *Lantana camara* L., *Opuntia stricta* Haworth. (Haworth.), *Chromolaena odorata* (L.) R.M. King & H. Rob., and three *Senna* species. Widespread aquatic macrophytes are *Azolla filiculoides* Lam., *Eichhornia crassipes* (Mart.) Solms., *Pistia stratiotes* L. and *Salvinia molesta* D.S. Mitch. These species have dispersed into the Park along the major river systems that originate outside the Park, flowing through agricultural, forestry and urbanized land. The other main pathway of spread has been from gardens in staff villages and rest camps within the KNP. All riparian vegetation along major rivers and most tributaries is invaded to some extent. Many other invaders are widespread and abundant in the catchement areas of the main rivers outside the KNP and thus threaten to invade the park soon.

Some progress has been made in integrating the management of invasive alien species with other management functions in the KNP. A management system based on a framework of Thresholds of Potential Concern (TPCs) has been implemented, and invasive alien species were recently included in this system. TPCs have been defined with limits of acceptable change for spatial and temporal scales. Management actions are instituted when these limits are exceeded. The success of management efforts directed at invasive alien species in the Park depends to a great extent on the success of sustained management campaigns in the catchment areas of the rivers that flow through the Park. Five other innovations implemented to address the increasing scale of threats posed by invasive alien plants are also described.

Introduction

The Kruger National Park ("the KNP" or "the Park") is situated on the eastern side of the Limpopo and Mpumalanga provinces of South Africa, and is bordered along its entire eastern side by Mozambique. The Park, extending 360 km from north to south and covering 20,000 km^2, is one of the largest areas in the world managed primarily for the conservation of biodiversity. The KNP falls in the savanna biome of southern Africa (Scholes 1997). Most of the region experiences a hot wet season of

Plant Invasions: Ecological Threats and Management Solutions, pp. 385-403
Edited by L.E. Child, J.H. Brock, G. Brundu, K. Prach, P. Pyšek, P.M. Wade and M. Williamson

approximately four to eight months duration, and a warm dry season. Thirty-five "landscape types" (Gertenbach 1983) form the basis for dividing the Park into manageable sectors. The KNP is crossed by seven major river systems (Fig. 1), all of which originate to the west of the Park and drain a combined area of about 88,600 km². Large portions of these drainage areas are used for industry, agriculture, commercial forestry, and human settlements. All these rivers flow through the Park and into Mozambique. Because of the importance of the rivers as conduits for dispersal of many invasive alien species, the Park acts as a "filter" between South Africa and Mozambique. Mozambique has less capacity to manage invasive species than South Africa, so the KNP has an important responsibility to prevent the spread of invasive species through the Park across its eastern border.

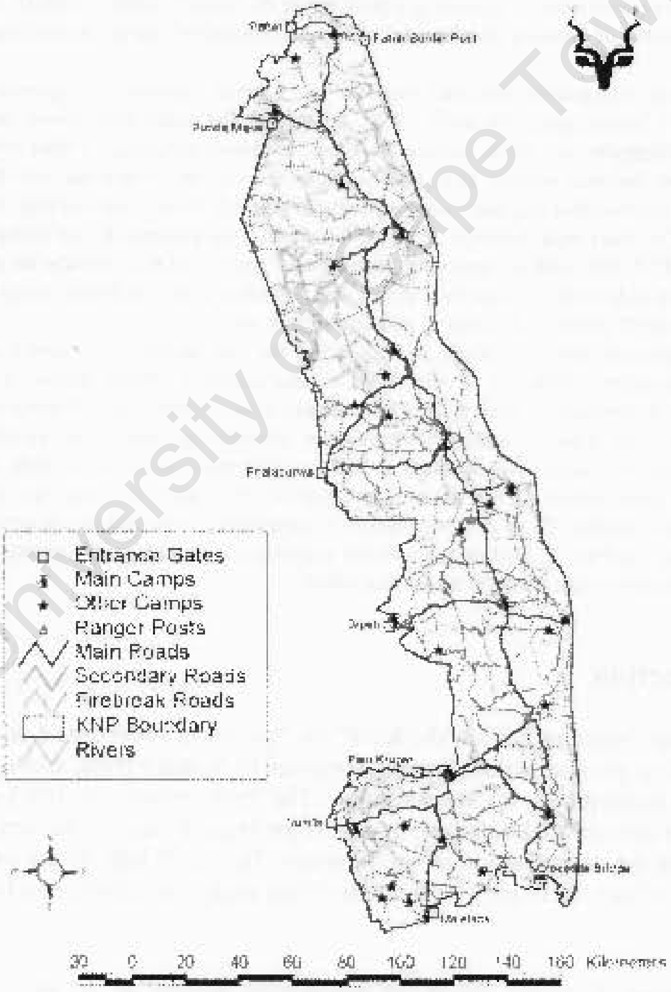

Fig. 1 River systems and infrastructure of the Kruger National Park.

The recent development of a massive Transfrontier Park (incorporating the KNP with Gonerhezou and Gaza parks in Zimbabwe and Mozambique) reinforces the KNP's responsibility in this regard.

The area that is now the KNP was occupied by groups of nomadic hunter-gatherers for thousands of years before Europeans arrived in the early 1700s. The large herds of game attracted European hunters during the winter months when the risk of malaria was lowest. The dwindling numbers of animals in the late 1800s led to the proclamation of the Sabie Game Reserve (now the KNP) in 1898. The establishment of this reserve regulated access to the area. Development within the Park was confined to rest camps for visitors, small villages for staff, and a road system. This prevented the widespread introduction and dissemination of alien plant species. Obermeijer (1937) made the first observations of alien plants species in the KNP and listed six species ("troublesome weeds": *Chenopodium ambrosioides* L., *Tagaetes minuta* L., *Argemone mexicana* L., *Gomphrena celosioides* Mart., *Boerhavia diffusa* L., *and Cocculus hirsutus* (L.) Diels). A gradual increase in the development of rest camps and staff villages within the KNP, and the rapid increase in development and urbanization in the catchments of the major rivers entering the Park, led to an escalation in the rate of introduction of alien plant species. This, and the rising awareness of invasive plant species, their impacts and the increase in general botanical and specific alien plant surveys led to an increase in the number of records of alien plant species. At the end of 2001, 366 alien plant taxa were known to occur in the KNP. This number includes naturalized and invasive taxa (Fig. 2, Richardson *et al.* 2000, Table 1), as well as taxa planted in rest camps and villages but not known to be naturalized (Fig. 2).

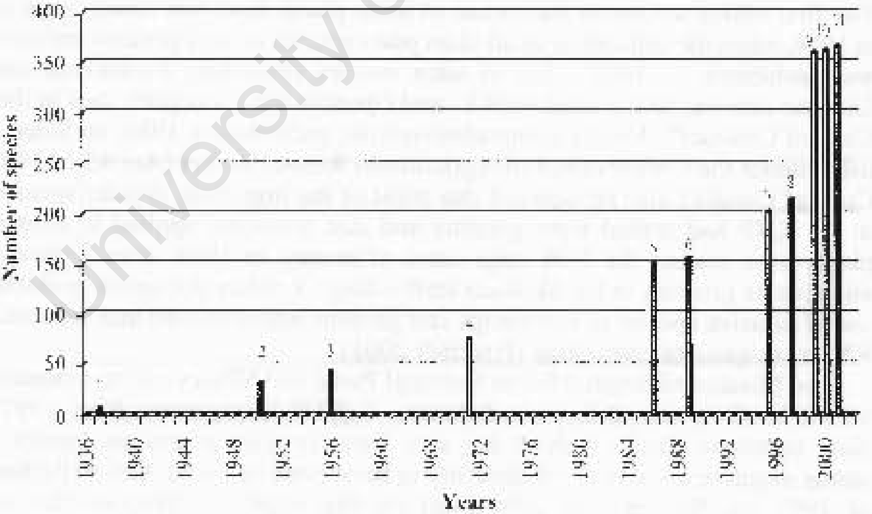

Fig. 2. The number of invasive alien plants reported in the Kruger National Park in surveys between 1937 and 2001. 1. Obermeijer 1937, 2. Codd 1951, 3. van der Schijff 1957, 4. van der Schijff 1969, 5. Gertenbach 1985, 6. Macdonald & Gertenbach 1988, 7. Anon 1995, 8. Anon 1997a, 9. Foxcroft 1999, 10. Foxcroft 2000a, 11. Foxcroft 2001.

The KNP currently maintains 13 main rest camps and 133 smaller camps, ranger's outposts and other infrastructure. The network of roads, comprising 832 km of main/paved roads, 1,726 km of gravel/secondary roads, and 4,229 km of management/firebreak tracks, form important pathways for the introduction and dissemination of alien species (Fig. 1). Notable examples of invasive species whose current range is attributable to the development of staff villages are *Opuntia stricta* (sour prickly pear) and *Pistia stratiotes* (water lettuce). *O. stricta* now occurs in management units covering about 66 000ha centred on Skukuza (Lotter and Hoffmann 1998). *P. stratiotes* has invaded several reaches of the Sabie and N'waswitsontso Rivers and several pans and dams in other parts of the Park (Lotter 1997). *Lantana camara*, the most widely distributed and aggressive invasive alien plant in the KNP, was also grown in rest camps until 1951 (Macdonald 1998). The spread of this species is probably more the result of dispersal into the KNP along rivers from dense stands in the catchment areas than to spread from rest camps. About 240 alien plant species are currently known to occur in staff villages in the KNP; 60 of these species are considered to be potentially invasive (assessment based on reproductive potential and whether the species are known to invade in other parts of the world with similar climate and other environmental conditions).

This chapter describes the evolution of a strategy for managing plant invasions in the Park. Special attention is given to describing attempts to integrate alien plant management within the overall management framework for the Park, and to regulate the spread of species into the Park by targeting important invasion pathways.

Early efforts at alien plant control in the KNP

The first efforts to control the spread of alien plants from rest camps were initiated in 1958, when the cultivation of all alien plant species in staff gardens and rest camps was prohibited. In 1972 a list of alien species (including *Eichhornia crassipes*, *Lantana camara*, *Melia azedarach* L. and *Opuntia* spp.) was published in the "KNP Code of Conduct". A more comprehensive list, published in 1984, included species listed under the Conservation of Agricultural Resources Act (Act 43 of 1983). The Code of Conduct also recognized that most of the important invader species found in the KNP had spread from gardens and that measures applied to control these plants were costing the Park large sums of money. In 1999, after a survey of the alien plants growing in the Skukuza staff village, a policy document prohibiting the use of invasive species in rest camps and gardens was proposed and accepted by the KNP management committee (Foxcroft 2001).

The Mission of South African National Parks (SANParks) is "to maintain biodiversity in all its natural facets and fluxes..." (KNP Management Plan, 1997). Alien plant invasions clearly bedevil this aim. Invasive alien plants are known to have strong negative impacts on biodiversity in most parts of South Africa (Richardson *et al.* 1997, van Wilgen *et al.* 2001), and are thus clearly in direct conflict with this Mission. A workshop on biodiversity conservation held in the KNP in 1997 rated invasive alien species the greatest threat to KNP's biodiversity, ahead of the well-recognized threats of poaching and fragmentation (Anon 1997b). Despite this, much more attention has been given to the other factors that threaten biodiversity in the

Park. For example, the KNP recognizes two regions (far north and south western regions) as botanical reserves where emphasis is placed on managing the negative impacts of large populations of elephants (*Loxodonta africana*) for the benefit of the rare plant species and vegetation types (Whyte *et al.* 1999). Fire management practices in the Park have also evolved as the understanding of the role of fire in savanna ecosystems has developed (van Wilgen, Biggs and Potgieter 1998).

Alien species have lagged behind with respect to sustained attention and the development of sound management policies and strategies. In the last few years, however, biological invasions have been afforded more attention on the management agenda of the KNP.

Patterns, extent and drivers of invasion

Invaded habitats in the Park can be roughly categorized as aquatic (river, artificial dams, natural pans); disturbed areas; moist areas; riparian zones; roadside fringes; rest camp/villages; and upland areas (Table 1). Fig. 3 shows the extent of invasion along rivers and surrounding camps in the KNP. All these habitats are invaded to varying extents, but riparian zones are by far the most severely invaded (40 taxa recorded; Table 1). Rest camps and villages contain 38 taxa, of which many (32 taxa) could invade the riparian habitats. Upland areas are the next worst with nine taxa, roadside areas with six taxa, aquatic areas with five taxa, disturbed areas with three taxa and moist areas with two taxa. *Lantana camara* and *Opuntia stricta* are currently regarded as transformer weeds in thee KNP. In this section we describe salient features of invasions in the main habitats.

Riparian vegetation

Frequently disturbed by minor floods, and periodically by major stochastic flood events (which disperse propagules, denudes riverbanks and stimulates germination), riverbanks and floodplains provide ideal habitats for the establishment of invasive plants. Dense stands of species such as *L. camara* cover very large areas in the KNP.

Problems associated with alien plant invasions in riparian zones of the KNP include direct competition for resources, with many alien plants being able to germinate and establish quicker than indigenous species after floods. The presence of allelopathic properties in many of the plants inhibit the growth of other species. Without substantial management intervention plant communities in these habitats move towards depauperate, alien-dominated communities with important implications for ecosystem functioning.

There is a complex pattern of land ownership in the catchment areas of the major rivers and the KNP has no control over landuse in these areas that serve as the main source of alien plant propagules for riparian systems of the KNP. For the Sabie-Sand River catchment, which covers about 6,500 km², only the bottom third lies within the Park. At least 40 invasive species have been recorded in the upper catchment and about 23% of the catchment was mapped as invaded by alien plants in the late 1990s (Versfeld *et al.* 1988, Le Maitre *et al.* 2001). About 20 of these species have already established in the KNP. The upper reaches support *Pinus* and *Eucalyptus* plantations, many of them highly invaded with *Solanum mauritianum* Scop., *Caesalpinia decapetala* (Roth) Alston and other alien species. The middle reaches consist mainly of commercial agriculture of sub-tropical fruit and, in the lower reaches subsistence farming in densely populated communally owned rural areas. These areas are sources of many alien plant species for the KNP. Regular dispersal of propagules in the Park is a major challenge for management.

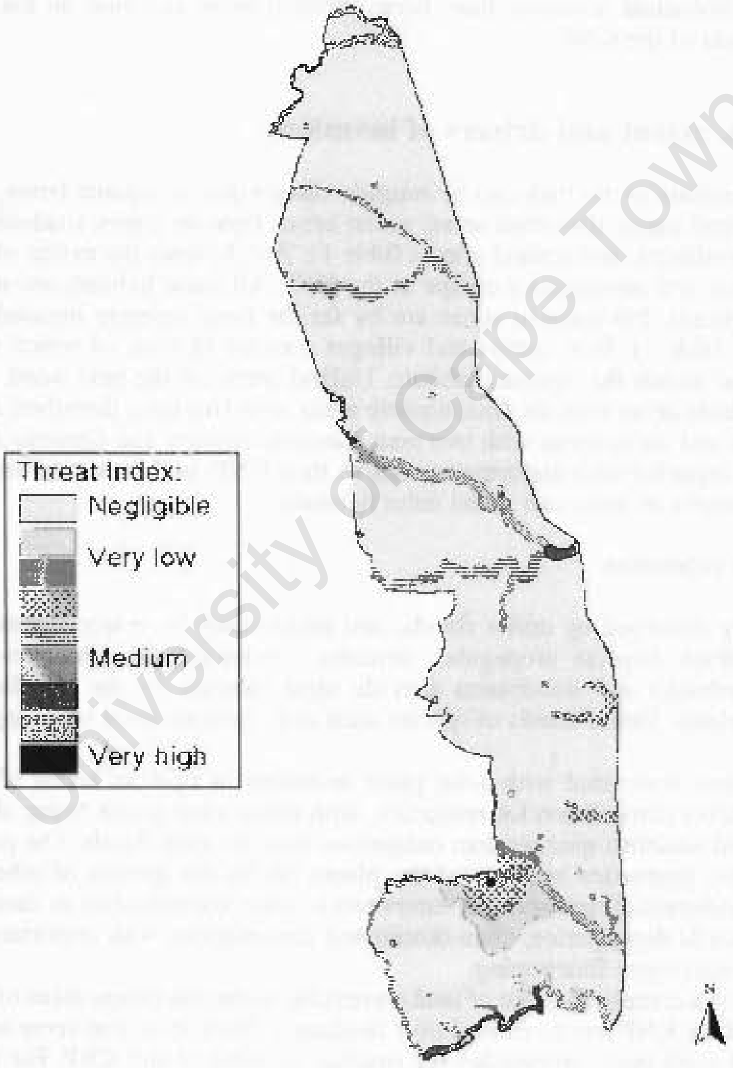

Fig. 3. Distribution of invasive alien plants in the Kruger National Park. Areas were evaluated for number of species present and densities of all alien species. For each (density and species) a score was allocated and then combined to provide the threat index for that region or river.

Table 1. List of invasive alien plant species recorded in the Kruger National Park and also listed in the Conservation of Agricultural Resources Act. **Habitat codes**: Aq = aquatic; Ds = disturbed areas; Ms = moist areas; Rp = riparian; Rs = roadside; RV = rest camp/village; Up = upland). **Functional Classification codes**: Substrate (epiphyte = e; aquatic = a; terrestrial = t), **Longevity** (annual = a; perennial = p; {> 5 years}; variable). **Habit** (upright = u; scandent = s; creeping = c; floating (free) = f(f); floating (attached) = f(a)) (after Richardson *et al.* 1997); **Status** (A = alien; C = casual; N = naturalized; I = invasive (* = transformer species) (after Richardson *et al.* 2000).

Species	Family	Habitat	Growth-form	Functional classification			Status
				S	**Lo**	**H**	
Acacia dealbata Link.	Fabaceae	Rp	Tree	T	p	u	I
Achyranthes aspera L.	Amaranthaceae	Rp/Ms	Shrub	T	p	s	I
Agave sisalana Perrine	Agavaceae	Up	Shrub	T	p	u	I
Ageratum conyzoides L.	Asteraceae	Rp	Herb	T	a	u	I
Ageratum houstonianum Mill.	Asteraceae	Rp	Herb	T	a	u	I
Argemone mexicana L.	Papaveraceae	Rp	Herb	T	a	u	I
Argemone ochroleuca subsp ochroleuca Sweet	Papaveraceae	Rp	Herb	T	a	u	I
Arundo donax L.	Poaceae	Rp/Ms	Emergent reed	A	p	u	I
Azolla filiculoides Lam.	Azollaceae	Aq	Free-floating macrophyte	A	v	f(f)	I
Bauhinia purpurea L.	Fabaceae	RV	Shrub	T	p	u	C
Bauhinia variegata L.	Fabaceae	RV	Shrub	T	p	u	C
Bryophyllum delagoense (Eckl. & Zeyh.) Schinz. (= *Kalanchoe tubiflora*)	Crassulaceae	RV	Groundcover/ semi-succulent	T	p	u	I
Caesalpinia decapetala (Roth) Alston	Fabaceae	Rp	Shrub/Climber	T	p	u	I
Canna indica L.	Cannaceae	Rp	Rhizomatous herb	T	p	u	I
Cardiospermum grandiflorum Sw.	Sapindaceae	Rp/RV	Climber	T	v	u	I
Cereus jamacaru DC.	Cactaceae	Up	Tall perennial	T	p	u	I
Chromolaena odorata (L.) R.M. King & H. Rob.	Asteraceae	Rp	Shrub/Climber	T	p	u	I
Cinnamomum camphora (L.) Siebold	Lauraceae	RV	Tree	T	p	u	I
Cirsium vulgare (Savi) Ten.	Asteraceae	Ds	Herb	T	b	u	N
Convolvulus arvensis L.	Convolvulaceae	Rp	Herb	T	a	u	N
Cortaderia selloana (Schult.) Asch. & Graebn.	Poaceae	RV	Grass	T	a	u	I
Cuscuta campestris Yunck	Convolvulaceae	Rp	Climber	T	p	c	N
Datura ferox L.	Solanaceae	Rp/Rs	Herb	T	a	u	I
Datura innoxia Mill.	Solanaceae	Rp/Rs	Herb	T	v	u	I
Datura stramonium L.	Solanaceae	Rp/Rs	Herb	T	a	u	I
Eichhornia crassipes (Mart.) Solms	Pontederaceae	Aq	Free-floating macrophyte	A	p	f(f)	I
Eriobotrya japonica (Thunb.) Lindl.	Rosaceae	RV	Tree	T	p	u	*
Eucalyptus spp.	Myrtaceae	RV	Tree	T	p	u	*
Eugenia uniflora L.	Myrtaceae	RV	Tree/shrub	T	p	u	I
Grevillea robusta A. Cunn.	Proteaceae	Rp	Tree	T	p	u	I
Hedychium coccineum Sm.	Zingiberaceae	RV	Rhizomatous herb	T	p	u	I

Table 1. Continued.

Species	Family	Habitat	Growth-form	Functional classification			Status
				S	Lo	H	
Hedychium coronarium J. König	Zingiberaceae	RV	Rhizomatous herb	T	p	u	I
Hedychium gardnerianum Ker Gawl.	Zingiberaceae	RV	Rhizomatous herb	T	p	u	I
Ipomoea alba L.	Convolvulaceae	Rp/RV	Climber	T	v	c	I
Ipomoea purpurea (L.) Roth	Convolvulaceae	Rp/RV	Climber	T	v	c	I
Jacaranda mimosifolia D. Don	Bignoniaceae	RV	Tree	T	p	u	I
Lantana camara L.	Verbenaceae	Rp/RV/Up	Shrub/Climber	T	p	u	I*
Leucaena leucocephala (Lam.) de Wit	Fabaceae	Rp/RV	Tree/shrub	T	p	u	I
Ligustrum vulgare L.	Oleaceae	RV	Shrub	T	p	u	I
Litsea glutinosa (Lour.) C.B. Rob. (= *L. sebifera*)	Lauraceae	RV	Tree/Shrub	T	p	u	I
Macfadyena unguis-cati (L.) A.H. Gentry	Bignoniaceae	Rp/RV	Climber	T	v	c	I
Melia azedarach L.	Meliaceae	Rp/RV	Tree	T	p	u	I
Mimosa pigra L.	Fabaceae	Rp	Tree/shrub	T	p	u	I
Morus alba L.	Moraceae	RV	Tree	T	p	u	I
Myriophyllum aquaticum (Vell.) Verdc.	Haloragaceae	Aq	Floating (attached)	A	p	f(a)	I
Nephrolepis exaltata (L.) Schott	Davalliaceae	RV	Fern	Fe	p	s	I
Nerium oleander L.	Apocynaceae	RV	Shrub	T	p	u	I
Nicotiana glauca Graham	Solanaceae	Rp	Tree/shrub	T	p	c	I
Opuntia aurantiaca Lindl.	Cactaceae	Up	Short perennial succulent	T	p	u	I
Opuntia ficus-indica (L.) Mill.	Cactaceae	Up	Tall perennial succulent	T	p	u	I
Opuntia imbricata (Haw.) DC.	Cactaceae	Up	Tall perennial succulent	T	p	u	I
Opuntia monacantha Haw. (*O. vulgaris misapplied*)	Cactaceae	Up	Tall perennial succulent	T	p	u	I
Opuntia stricta	Cactaceae	Up/RV	Short perennial succulent	T	p	u	I*
Parthenium hysterophorus L.	Asteraceae	Rs	Herb	T	a	u	I
Pennisetum setaceum (Forssk.) Chiov.	Poaceae	Rs/Ds	Herb	T	p	s	I
Pereskia aculeata Mill.	Cactaceae	RV	Shrub/Climber	T	p	u	I
Pinus spp.	Pinaceae	Rp	Tree	T	p	u	I
Pistia stratiotes L.	Araceae	Aq	Free-floating Aq macrophyte	p	f(f)	I	
Pontederia cordata L.	Pontederiaceae	Rp/RV	Rooted aquatic	Aq	p	f(a)	I
Psidium guajava L.	Myrtaceae	Up/RV	Tree/shrub	T	p	u	I
Ricinus communis L.	Euphorbiaceae	Rp	Woody Shrub/herb	T	c	u	I
Rubus cuneifolius Pursh	Rosaceae	Rp	Shrub	T	p	u	I
Salix babylonica L.	Salicaceae	Rp	Tree	T	p	u	N
Salvinia molesta D.S. Mitch.	Salviniaceae	Aq	Free-floating macrophyte	A	p	f(f)	I

Table 1. Continued.

Species	Family	Habitat	Growth-form	Functional classification			Status
				S	Lo	H	
Senna bicapsularis (L.) Roxb	Fabaceae	Rp/RV	Tree/climbing	T	p	u	I
Senna didymobotrya (Fresen.) Irwin & Barnaby	Fabaceae	Rp/RV	Tree/Shrub	T	p	u	I
Senna pendula (Willd.) Irwin & Barnaby	Fabaceae	Rp/RV	Tree/shrub	T	p	s	I
Sesbania punicea (Cav.) Benth	Fabaceae	Rp	Tree/shrub	T	p	s	I
Solanum mauritianum Scop	Solanaceae	Rp	Tree	T	p	u	I
Solanum seaforthianum Andrews	Solanaceae	Rp/RV	Climber	T	p	c	I
Syzygium cumini (L.) Skeels	Myrtaceae	RV	Tree	T	p	u	I
Tecoma stans (L.) Kunth	Bignonaceae	Rp/RV	Tree/shrub	T	p	u	I
Thevetia peruviana (Pers.) K. Schum.	Apocynaceae	Rp/RV	Tree/shrub	T	p	u	I
Tipuana tipu (Benth.) Kuntze	Fabaceae	RV	Tree	T	p	u	I
Tithonia diversifolia (Hemsl.) A.Gray	Asteraceae	Rp	Herb	T	v	u	I
Toona ciliata M. Roem.	Meliaceae	RV	Tree	T	p	u	C
Thelechitonia trilobata (L.) H.Rob. & Cuatrec = (*Wedelia trilobata*)	Asteraceae	RV	Herb	T	p	c	I
Xanthium strumarium L.	Asteraceae	Rp/Rs/Ds	Herb	T	a	u	I

Invasions originating from rest camps

Villages and rest camps in the KNP contain many species known to be invasive in other areas, such as *Hedychium* spp. and species of Commelinaceae and Crassulaceae. Many alien species are used for hedging and beautification, with resistance to their removal being met with by personnel who have been living in the KNP and tending to the gardens for a long time. These taxa pose a threat to the surrounding areas and with time may invade the riparian fringes of the rivers on which the camps are situated (Foxcroft 2001).

Upland areas

Upland areas are well suited to invasion by species of the Cactaceae, and 66,000 hectares in the Skukuza has already been invaded by *O. stricta* (Lotter and Hoffmann 1998). Integrated management plans have been implemented to contain and reduce the density and impact of the weed, using biological and chemical control. Other species, such as *L. camara*, are also starting to show their ability to survive in these areas; they survive through the dry periods and proliferate during wet cycles.

Aquatic systems

Four of the five major aquatic weed species in South Africa (Cilliers 1991) are present in the KNP (*A. filiculoides, E. crassipes, P. stratiotes* and *S. molesta*). Most of the invasive stands of these species originated from staff camps near rivers. A few invasions have resulted from the spread of propagules from outside the Park along rivers. Spread within the Park has also been aided by human activities, for example, the introduction of *E. crassipes* into the Letaba and subsequently in Engelardt Dam at Letaba rest camp was through the use of pumps and machinery transferred from the Crocodile to Letaba rivers during the construction of Shimuweni camp. The invasion of dams usually occurred via rivers. Chemical control has targeted all except *A. filiculoides* over the past 25 years at various places in the Park, but no populations have been eradicated and biological control has been instigated (Cilliers 1991, Cilliers, Zeller and Strydom 1996).

Roadsides and other disturbed areas

Disturbed areas include gravel pits, dumping areas, roads, camps, old settlements and other areas which have been impacted in some way by human activities. Ruderal/agricultural weeds generally invade dry riverbeds, disturbed on a seasonal basis by quick flowing water, although species such as *Xanthium* spp., *Datura* spp. and *Bidens* spp. are well represented along roadsides. The road network in the KNP (Fig. 1) is an important pathway for the dissemination of alien species. Disturbance associated with road building provides establishment opportunities, and many species are dispersed in sand (usually collected from river beds) and other materials.

Moist areas

Moist areas are also frequently associated with villages and rest camps, in that the gardens may lead onto small tributaries or densely shaded areas which may also be watered by garden watering and thus remain moist for long periods of time. These areas, in turn, frequently lead onto the riparian zones of the larger tributaries and major rivers.

Management systems of the KNP and integration of considerations for dealing with alien plant invasions

Changing approaches to the management of alien plant invasions in the KNP

The appointment of the first warden of the Sabie game reserve in 1898 started an era of management policies based on a "common sense" appraisal of the situation without any scientific input (Macdonald 1988). Policies largely focused on issues relating to poaching and the need to increase game numbers by controlling carnivores (Pienaar 1982), the manipulation of large-mammal population numbers, water provision, and prescribed burning to manage vegetation composition.

Management was explicit in its acceptance of the "balance of nature" paradigm (Rogers and Bestbier 1997). The 1990s saw a dramatic change in the approach to management, driven primarily through external influences (management decisions being scrutinized by agencies ranging from impoverished neighbouring communities to animal welfare organizations). In the past, invasive alien species were afforded low priority in the KNP with management efforts being directed towards other more traditionally recognised problems and impacts. This resulted in an increase in species numbers and densities of infestations in the Park, while limited resources were provided for alien plant clearing. Until the early 1980s, when the first "pollution control" officer was appointed, rangers were responsible for controlling invasive plants in their sections. The initial focus of the newly formed pollution control section was the mechanical and chemical control of various plants, mainly along the Sabie River (as well as solid waste management). Later, the use of biological control agents and the development of integrated control strategies started taking form. In 2001, following the international trends in terminology, the section adopted the name of the Invasive Alien Species Section, with the aim of developing research and monitoring programmes to support and further develop management strategies. This further implies the monitoring of invasive non-plant species also becoming problematic in the park.

Simply allocating funding was insufficient to have an impact on the alien species presence. For invasive species management to be effective and recognised as a threat to the Park, it needs to be incorporated into a system whereby the system forces recognition to be taken of the problems at the correct level of management. The strategic adaptive management system adopted by the KNP provides a framework for setting (and revising/updating) goals and auditing the extent to which these goals are realized (See appendix 1 for the objectives of the Invasive Alien Species Section for the KNP). Within the KNP management there was also recognition of the new paradigms in ecology and conservation biology and the greater need for accountability and transparency (Rogers and Bestbier 1997). These processes led to the revision of the KNP management plan and the adoption of strategic adaptive management processes. Salient features of the new management process are discussed below.

Strategic adaptive management and Thresholds of Potential Concern (TPCs)

The KNP's management system is based on a hierarchy of objectives, from the coarsest/broadest objective – the Mission statement – down to finer, specific objectives. The higher-level vision and objectives serve upper management levels with statements of strategic intent, while lower-level goals provide managers with specific, spatially and temporally bounded end points (Rogers and Bestbier 1997). Through a combination of these objectives, a strong multi-faceted approach is taken in the overall control programme. These low-level objectives represent measurable goals which are defined as Thresholds of Potential/Probable Concern (TPCs). These TPCs represent the upper and lower limits of acceptable change in ecosystem structure, function and composition over time and at a specified spatial scale. A TPC is reached when one or more of these limits are exceeded. Monitoring determines when the prescribed limits have been exceeded. At this stage, a "TPC exceeded" notification may be submitted to the KNP Conservation Services Management Committee. Table 2 shows the types of management concerns and issues, and Table 3 lists the TPCs tabled to date.

To illustrate how the management system works, we discuss some examples relating to fire management, since much attention has been given to deriving objective TPCs for this sphere of management. TPCs designed for fire management concerns in the KNP are designed to indicate limits in the fire regimes that would signal potential impacts on biodiversity. The prevailing philosophy is that variation in fire regime (frequency, season and intensity or fires) maintains biodiversity (van Wilgen, Biggs and Potgieter 1998). The TPCs are measured through frequency, *i.e.* how frequently is a particular area being burned and whether there is an acceptable variation to frequency. Another TPC theme is that of "Burning, drought and forage availabilty". These are monthly TPCs which are set and measured to determine, as the season progresses, whether rainfall and veld recovery is sufficient to allow fires to proceed or to manage fires that are seen to be deleterious to veld condition. Fire season measures the ratio of fires between late winter/early spring and late spring/summer. Fire intensity TPCs are proposed in order to evaluate whether a range of intensities are reached, as a mosaic of intensities are regarded to provide for increased biodiversity. Other TPCs that are defined include fire size distribution, extent of fires in any year, and the cause of fires as described in van Wilgen, Biggs and Potgieter (1998).

Currently, TPCs dealing with invasive alien species are based on a coarse approach until tightly defined monitoring programmes are established. TPCs listed at this stage may represent a first record for a new species in the KNP or a first record from a new management unit. The list below indicates the TPCs drafted for monitoring invasive alien species as well as the TPC listings for invasive species to date.

Themes of TPCs defined for invasive alien species:

TPCs related to distribution:
- Any new occurrence of an alien species in the KNP
- Imminent external threat by an alien species to the KNP
- Extension of range (first ever report from a new block, or from blocks not contiguous with neighbouring blocks)
- Expansion of blocks, which represents more than a 5% increase in distribution over the number of blocks infected the previous year.

TPCs related to increase in density: (all areas infested – blocks are measured in modified canopy cover estimates to assess plant density. These densities are arranged into a number of classes)
- An increase of density two classes upwards in any block.
- Overall increase in density

TPCs relating to rate of spread vs. rate of clearing:
- Number of new blocks infested greater than number blocks cleared.

Table 2. Management concerns and Thresholds of Potential Concern (TPC's) for each biophysical group. TPC's represent points for each monitored group at which indicators show potential levels of concern for the environment and management needs to examine the causes driving the aspect to this point of concern and provide management recommendations.

Biophysical grouping	**Theme of TPC(s)**
Woody vegetation	% woody cover Structure
Herbaceous vegetation	% perennials Changes in density or community composition
Rare biota	Black Rhino, Wild Dog, Rare antelope, Rare Plants
Large mammal responders	Counts higher or lower than any historical counts (for selected species) Counter-trend behaviour for species where the trends are understood (zebra, wildebeest, buffalo) Range contraction
Spatial heterogeneity	**Riverine/Riparian and waterhole – related:** Intactness of canopy cover; structural heterogeneity of riparian fringe Directional loss of bedrock in rivers (alluviation); Population structure of key riparian species **Terrestrial:** Heterogeneity Indices (= landscape patchiness) Applied physiological indices (e.g. Leaf Area Index)
Invasive Alien Species	New distribution in KNP or increase in distribution Increase in density Rate of spread vs. clearing Impact on biodiversity Outside alien threats
Birds	Surrogacy for vegetation structure
Riverine and riparian	Functional role classes
Terrestrial	Species richness and community statistics
Raptor nesting survey	Drop in nesting rates for larger species
Fire	**Overarching theme is fire pattern (as biodiversity surrogate)** *Sub themes:* – Long-term frequency (inter-fire periods) – Long-term proportion: early vs. late season Long-term spread of intensities – Long-term size distribution Long-term % of unintended fires Proportion of area burnt per month, within each year, as related to biomass
Fish	Integrity of assemblage Habitat assessment
Amphibians	Shrinkage of distributional range Shift in community composition Shift in species richness?
Reptiles (excluding crocodiles)	Shrinkage of distributional range Shift in community composition Shift in species richness
Small mammals	Shrinkage of distributional range Shift in community composition Shift in species richness
Erosion	Sheet erosion Donga erosion
Landscape water	Ratio of areas far and near water
Nutrient cycling	Nitrogen and phosphate status of key grazers ("forage quality")
Water quantity and quality (in rivers)	Flow (in line with Water Act-ecological reserve) & Quality parameters (incl. chemical constituents).
Wilderness qualities	Evidence of other humans (than own trail group) Evidence or visibility of infrastructure Noise pollution Litter Traffic congestion Evidence of invasive or disruptive methodologies

Table 3. Running list of unclosed (unresolved) Thresholds of Potential Concern (TPCs) as on 31 May 2001.

TPC	Dates raised at Standing Comm.	Summary of progress	Next check-point
Silt concentration: Olifants River	Feb 99/March 99	Await acceptable Environmental Management Plan from Lepele Water	May 2001
Poor water quality, various rivers (mainly transient)	July 00	Await detailed report and recommended allowable duration in terms of data matching.	May 2001
Chromolaena odorata (chromolaena) new occurrence	Oct 99/Sept 00/ Mar 01	Control and monitoring action taking place inside and just outside KNP at Phalaborwa; now also below Engelhardt Dam in Letaba.	May 2001 suggest new date in light of increase in range
Rare antelope (roan, tsessebe & sable)	Mar 00, ongoing	Patch burns, enlarge exclosures	After end of dry season 2001
Tithonia diversifolia (Mexican sunflower)	July 00	Concerted control effort: Crocodile River	After end of rainy season, around June 2001
Azolla filiculoides (red water fern)	Oct 99/Jan 00	Implement biocontrol (release agents)	End 2001
Arson Fire	Feb 99 & several returns	Recalibrated over 10 years since 'lightning' system	End 2003.
Varroa jacobsoni (honey bee mite)	NEW: Nov 00	Ongoing monitoring	May 2001 ("regular feedback") – after how many negative feedbacks should we consider a date for closure?
Acridotheres tristis (Indian myna)	NEW: Nov 00 (Lower Sabie) and Jan 01 (Talamati)	Controlled at Lower Sabie. Disappeared from Talamati – monitor	To be decided
Arundo donax (giant reed)	Mar 01	Controled at Crook's corner, Vlakte plaas	To be decided
Cardiospermum halicacabum (balloonvine)	Mar 01	Ongoing monitoring at Mlondozi dam & Ribbokrand	To be decided

However, refinement and calibration of the current invasive alien species TPCs are needed to represent real and meaningful points of concern. TPCs need to show at what rates of invasion, or increases in density, management needs to become concerned and initiate management actions to address the specific problem.

The list of "unclosed" (unresolved) TPCs (Table 3) gives the impression that the main management concerns of the KNP relate to invasive alien species, and rivers. It appears that the KNP management system and processes are now structured in such a manner so as to recognise and record the serious impacts to biodiversity conservation and not the traditionally recognised impacts which are perhaps not of such critical importance in ecosystem processes.

Innovations developed for the management of invasive alien species in the KNP

In an effort to enhance the control of invasive species in a holistic manner, a few key aspects were identified as lacking and efforts were made to implement measures to rectify these situations.

Some of the aspects currently being targeted are:

1) An approved policy governing the systematic removal of invasive alien species from rest camps and staff gardens

In 1999, a policy was adopted by the KNP Management Committee for the control of invasive alien plants in the KNP staff villages and rest camps (see Foxcroft 2001). The policy document included a survey of invasive alien species in the Skukuza staff village. The species assemblage represented any garden in other subtropical towns countrywide and was of serious concern. The most serious species, whose escape into the surrounding areas was imminent were divided into three categories and prioritised according to seed and other dispersal, numbers of plants in the village, and on similar behaviour portrayed elsewhere. These species are systematically removed from the gardens, while indigenous alternatives from the Skukuza nursery are promoted. The policy documented the current applicable legislation as well as other regulations relevant to the propagation of plants in the KNP. Although not well received by all residents, the policy, combined with an aggressive awareness campaign is hoped to develop an ethic of indigenous gardening and restoring the atmosphere of the Lowveld system, while protecting the surrounding areas from escaping invasive species.

2) Implementation of a monitoring programme and a GIS based database

Previously, all recording and knowledge of the distribution of invasive alien species, density responses and the impacts of clearing operations in the KNP were incomplete and poorly documented. The current development of a monitoring programme for IAS in the KNP aims to assess and monitor the extent of invasive alien plants in the KNP according to defined criteria (TPCs).

As there are currently 366 alien plant species listed in the KNP, and managing them all effectively is an impossible task, detailed knowledge of the distribution and density of the most serious species is essential. Battles need to be chosen wisely to maximise benefits and minimize impacts. Efforts will be made to monitor the measurement of change in the abundance and condition of weed populations over time. The chief objectives of the monitoring strategy are to fulfil the requirements of the TPCs as defined by KNP management. They are:

- To monitor the abundance and densities of alien vegetation in relation to indigenous vegetation.
- To monitor the impact of alien vegetation on biodiversity.

These outcomes should provide an indication to assist management in determining strengths and weaknesses in the physical clearing programmes and measure the responses of the weed infestations to the clearing operations.

3) Partnerships with the national *Working for Water* programme
1997 saw the launch of the first 1997 saw the launch of the first project of the Department of Water Affairs and Forestry's *Working for Water* programme (van Wilgen, Le Maitre and Cowling 1998) in the KNP to boost the Park's own alien plant control initiatives. Later the Poverty Relief programme of the South African Government launched a further project in the Park with an amount of R 6 million. This project employed 1000 workers. About R 20 million has been spent in the KNP by the *Working for Water* programme to date on alien plant control, mostly along the major rivers.

4) Co-operation with "weed interest groups" and local government departments
Cooperation with, and maintaining the momentum of, interest groups involved in managing alien plants, or creating awareness of problems associated with aliens is an essential part of the strategy for managing invasive alien plants in the KNP. An example of one group with which the KNP interacts is the Sabie River Coordinating Committee (SRCC). The SRCC, initiated in 1991, comprises local government authorities, municipal authorities, private landowners, forestry and conservation authorities and other interested parties. The main aim of the SRCC is to map the extent of invasive alien plants and co-ordinate a control programme throughout the catchment with the support and involvement of the various landowners. Other aspects facilitated by the SRCC are initiatives to improve water quality and quantity, natural diversity, the promotion of multiple land use through tourism and recreation, and the promotion of environmental ethics and awareness.

Another interest group which was initiated in 1997 is the Alien Invader Task Group (AITG; http://www.elektrikink.net/aitg/framemain.htm), a national project of the SANParks Honorary Rangers association. The AITG has become one of the main projects of the Honorary Rangers, alongside the game capture and relocation programme and anti-poaching projects. The AITG supports the KNP Alien Biota Section through fundraising, awareness and education, providing equipment, and physically clearing invasive alien species in rest camps. The AITG also staffs information displays and provides pamphlets and other materials to the growing game-ranch industry.

5) Promoting the effective control and best management practices and regional strategic planning

Alien plant management plans typically focus on tactics for clearing alien species and logistical arrangements (Moody and Mack 1988), but fail to provide an objective means for prioritising actions. With the recent appearance in the KNP of *Chromolaena odorata*, a threat to the entire Lowveld and escarpment, proactive efforts were made to bring together all main regional programmes to determine how best to tackle *C. odorata* systematically over the entire region. Efforts to consolidate fragmented maps with records of *C. odorata* and to consider the control of the weed, using tested control principles was applied in an effort to co-ordinate and structure the clearing initiatives.

It is hoped that through a combination of these and other aspects of invasive plant management, the Park may embark on an approach to limit the invasion of further species and maintain those species already within the Park to minimum and acceptable levels of infestation.

Conclusions

Managing invasive alien plants in the KNP relies on the integration of research and management in a system that allows for adaptive management in a fluctuating environment. The system allows for setting of defined goals (TPCs) over temporal and spatial scales, monitoring, evaluating responses and implementing management actions, to audit the response of the environment to the actions instituted. Since the revision of the KNP Management Plan and the development of the hierarchy of objectives, invasive alien species have been afforded higher status; this is reflected in the level at which the Alien Impact objective is stated.

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Appendix 1: Objectives of the Invasive alien species section in the Kruger National Park

Alien Impact Objective

To anticipate, prevent entry, eradicate or minimise the influence of non-indigenous organisms so as to maintain the integrity of native biodiversity.

Sub-objectives

Strategic objective: Evaluate the overall scale of threat of alien species, assess organisational and infra-structural capacity in relation to realistic needs, and muster necessary resources to address any shortfall.

Prevention objective: To anticipate imminent or potential risks of entry of alien species into the KNP and set-up effective mechanisms to prevent such entry.

Eradication objective: Plan and implement eradication and/or control campaigns for alien species already within the KNP.

Prohibit/discourage objective: Prohibit the use of invasive alien species and discourage the establishment or utilitarian/recreational use of any alien species. In rest camps the only alien species currently allowed are *Dactyloctenium australis*, *Stenotaphrum dimidiatum* and *S. secundatum* as lawn species.

Research objective: Develop an understanding of the practically relevant aspects of specific alien species and their control, usually in the following areas:

- Autecology of alien species, especially reproduction and dispersal
- Their effect on biodiversity
- Efficacy of control measures, including cost effectiveness and environmental acceptability
- Environmental impact of control operations and practical recommendations to improve the basis of control.

Awareness objective: To promote an awareness of especially the long-term dangers of alien species, by influencing perceptions of staff and public in such a way as to achieve willing active support for counter measures.

The Kruger Experience

ECOLOGY AND MANAGEMENT OF SAVANNA HETEROGENEITY

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Chapter 19

Anthropogenic Influences at the Ecosystem Level

STEFANIE FREITAG-RONALDSON AND
LLEWELLYN C. FOXCROFT

Anthropogenic changes are many and varied, exerting different levels of influence at different scales. In the global environment these changes cause complex responses strongly linked to ecosystem processes and are leading to unprecedented changes in global biodiversity. Sala et al. (2000) identified the main agents of change in savanna ecosystems as land use change, elevated CO_2, increased nitrogen deposition, climate change, and alien biota introductions. At the same time, aquatic systems are expected to be hugely affected by land-use change, alien invasions, and climate change. These drivers increasingly affect Kruger, which is also influenced by regional and local anthropogenic impacts that act at finer scales and over differing temporal time frames.

Kruger, the crown jewel of South African National Parks (SANParks), provides considerable financial revenues. Since its inception and sporadic development, management has been driven by a desire to minimize human influences and maintain "pristine" characteristics, no doubt shaped by the romanticized European view of the natural landscape before twentieth-century modernization (Carruthers 1995). However, even without overarching global influences this noble intention is contradictory because the Kruger ecosystem has been and still is affected by human presence, direct and indirect use, and management policies and actions. The myriad positive and negative human-induced impacts have all played some part in shaping the ecological and spiritual landscape of the Kruger we have today. These are overlaid on the geological template, geomorphological history (Chapter 5, this volume), prevailing climate, and ongoing spatial and temporal redefinition through the forces of nature, which in themselves are being shaped indirectly by humans. This chapter explores the varying human influences not covered by other chapters and examines their influences on heterogeneity.

Humans affect the environment through physical presence and in an intangible social manner through decision making, induced conflict, religion, and other factors. Low population densities and low-intensity resource use by Stone Age hunter-gatherers probably would have constituted a low-impact period in the Kruger's prehistory, and it is accepted that early humans did not shape the environment in a permanent way (Table 19.1). Although savanna burning regimes would have had some influence on the Kruger area, little is known (Chapter 7, this volume). A medium-impact period followed during the Iron Age, dominated by metalworking skills and a more residential lifestyle based on hunting and pastoralism (Plug 1987; Carruthers 1995; Table 19.1). Population numbers in what is today Kruger are thought to have peaked around 15,000 in this period, resulting in localized homogenization of the ecosystem through agricultural practices. Nevertheless, Kruger is considered to have been a marginal or transitional area in terms of cultural-historical occupation and farming, with population fluctuations driven by climatic factors and disease (Meyer 1986).

From Colonialism to Conservation

The first non-Africans influencing the Kruger area were Arabian traders up to the eighteenth century, followed by the Portuguese control of the gold and slavery trade through East African ports and Dutch and Voortrekker pioneers a century later (Pienaar 1990; Carruthers 1995). The tsetse fly, carrying blood trypanosomes, no doubt slowed down exploration, exploitation, and settlement of the lowveld by Europeans in the nineteenth century. Although the tsetse fly was severely decimated during the rinderpest epizootic of 1896–1898 and ensuing drought (Smuts 1982), malaria and horse sickness in the wet summer months also posed a significant deterrent (Chapter 17, this volume).

The development of Kruger had its beginnings in the recognition that the impacts of humans on lowveld game populations and hunting prospects in the late 1800s and early 1900s were unsustainable and that the game needed protection (Chapter 20, this volume). Impacts of professional hunting in the erstwhile Transvaal were enormous (Carruthers 1995), and the decimation of elephant populations must have influenced structural heterogeneity in the region, but to what degree is difficult to assess.

Establishment of the Sabi Game Reserve in 1898 saw the first separation of the human component from the landscape when scattered villages were resettled west of the boundary (Pienaar 1990; Chapter 20, this volume). Over time Kruger became renowned through its wildlife research and management programs, mirrored by staffing structures, but the basic philosophy of protection-

Kruger ecosystem.

PERIOD	LIFESTYLE AND MAIN RESOURCES USED	PREFERRED HABITAT	KRUGER OCCUPATION AND ESTIMATED NUMBERS
Stone Age	Hunting and gathering, using wild fauna and flora, firewood, and probably fire to drive game.	Wooded, hilly, game-rich areas close to water.	Probably the whole park, but southern Kruger concentrations estimated at 1 group per 7,000 ha (*i.e.*, approx. 1 person/700 ha). Minimum of 150 sites (approx. 1,500 persons) and maximum of 300 sites (approx. 3,000 persons).
Iron Age	Hunting, farming, metalworking, and trading. Would have used natural fauna and flora, also for medicinal uses. Started domesticating plants and animals and used firewood, natural building material (wood, thatch, stone, soil), minerals (iron, copper, gold).	Good grazing areas with suitable soils, water, and climate for agriculture such as riverbanks. Suitable places for villages, with a preference for hills and rivers. Availability of wood crucial for domestic and metalworking purposes. Preferred disease-free areas for both humans and animals.	Almost the whole park, with settlement patterns centered on cattle and staple grain production. Settlements consisted of villages, cattle posts, and sometimes capitals. ~350 recorded sites spanning ~1,800 years. Gradual increase in human numbers to ~15,000 people. Occupation commenced by migration along the main rivers. During the earlier period, five high-density centers were located mainly in valleys of the Limpopo, Letaba, and Sabie rivers (Meyer 1986). Later, this era was characterized by conflict and forced migrations, with resettlement in the 1800s in the western parts, including Makahane, Masorini, Pretoriuskop, and Nsikazi and Crocodile rivers. The mid-1800s–1900 were an unstable period, with tribal wars, droughts, and raids resulting in only a few remaining temporary villages. Low human densities with impacts of tsetse flies and rinderpest.

ism prevailed. Nature conservators set the standards and norms based on biotic and abiotic associations, generally excluding the human component from the historical or management landscape. In contrast, it was soon noted that for conservation objectives to be met, the public had to be allowed access to Kruger. This resulted in the development of tourism facilities and infrastructure, in a manner aimed at maintaining the natural qualities of Kruger as far as possible. This essential paradox continues to this day, often with tension between activities (such as road construction) and the intended philosophy (minimum interference) behind them.

Proclamation of Kruger and its forerunners rested on two main drivers, politics and concern about the overexploitation of the region's wildlife (Carruthers 1995), although populations of species such as eland and buffalo were decimated by the rinderpest panzootic, not hunting pressures (Chapter 17, this volume). This resulted in boundary definition, fencing and protection, and road and firebreak development to facilitate much-desired control over the area. Since that time the Kruger ecosystem has been shaped by evolving game management practices, including water provision (Chapter 8, this volume), fire management (Chapter 7, this volume), elephant management (Chapter 16, this volume), and disease (Chapter 17, this volume). Changing management philosophies have affected how these impacts were dealt with and the intensity of their outcomes in time and space (Chapter 4, this volume). Management paradigms evolved with increased understanding of the ecosystem, scientific advances, and theoretical developments. This includes the notion of stable states, the balance of nature versus fluctuations, and the implicit goal of managing for ecosystem health and heterogeneity rather than homogeneity, as well as a perceived notion of untouched primeval naturalness and wildness (Chapter 1, this volume).

Boundaries and Fencing

The Sabi and Shingwedzi reserves were characterized by low species densities, local extinctions, sparse settlement, and seasonal use by humans. In 1926, proclamation of the Kruger National Park resulted in western boundary definition through negotiations with landowners, without considering ecological boundaries. Main drivers of boundary fencing were the protectionist segregation philosophy to conservation (Carruthers 1995; Chapter 20, this volume), veterinary control requirements (Chapter 17, this volume), and political boundary definition with Mozambique and Zimbabwe. By 1976 Kruger was entirely fenced, although segments were again removed from the mid-1990s onward as neighboring conservation-oriented holdings went into agreements with Kruger. Although some boundary adjustments and land swaps have had political implications only, others have resulted in biodiversity losses. Of significance were the 1960–1961 and 1967–1968 southwestern boundary changes that excised areas west of the Nsikazi River, including Numbi Hill, to facilitate provincial road construction. This resulted in loss of unique habitats from Kruger, including the last permanent refuge of red duiker, the only suitable habitat for oribi, and some of the best grey rhebuck and favored roan and sable habitat in Kruger (Pienaar 1990). Fencing not only affected these locally rare species but also affected east-west migratory patterns of wildebeest and zebra populations (Whyte and Joubert 1988).

Compounding impacts of fencing include highly local effects such as injury, maiming, and death of individuals, subpopulation extinctions (Joubert 1986), individual, they are not big when considered at the population dynamics scale. In contrast, positive spinoffs include facilitating boundary patrols through associated road construction, inhibition of poaching activities, prevention of straying or luring of rare or human-conflict species, and barriers to spreading of disease (Chapter 17, this volume). Nevertheless, effectiveness depends on adequate fence maintenance, which often is not the case. Similarly, the exact positioning of Kruger's legal boundary is ill defined along certain rivers and remains a controversial point of friction between Kruger and riparian neighbors.

Fences have separated land management practices, resulting in sharp fence-line contrasts. These are generally unquantified in the Kruger context, and visual interpretation of changes in heterogeneity may appear harsh, although plant diversity (all species weighted equally) may be higher in adjacent communal lands (Shackleton 2000). With or without fences, the effective size of Kruger is gradually shrinking in certain areas through land-use change and encroaching development, whereas the "Greater Kruger Park" expands in other areas as private and provincial conservation areas are incorporated.

Animal Population Management and Poaching

This has historically been a central focus of conservation and research activities in Kruger. Large herbivore responses to protection measures defined management actions, and by 1912 it was believed that most populations responded well. Stevenson-Hamilton's game laws prohibited illegal killing of wildlife, rangers were appointed to enforce legislation, and by 1925 herbivore populations had recovered to pre-exploitation levels of around 1880. Herbivore population fluctuations were monitored and ascribed to environmental conditions or management actions, with severe population declines or increases resulting in population management activities (Joubert 1986).

Population Augmentations

The Game Reserves Commission made provision for reintroductions and artificial regulation of game numbers in 1918, with no formal policy until 1949. This policy vacuum resulted in consideration of exotic species introductions, although these proposals were not implemented because funding was insufficient. Later, numerous introductions, reintroductions, and translocations, particularly of antelope species, took place (Table 19.2). Most occurred after the advances in wild animal capture and care techniques of the 1960s, which paved the way for acceptable and safe means of effecting translocations. Rhino conservation has been at the forefront of these efforts. The last naturally occurring

SPECIES	DATE	REINTRODUCTION	SUCCESS
White and black rhino	Numerous	Numerous	Highly successful.
Crested guinea fowl	1930	20 sent to Kruger	Apparently successful.
Lichtenstein's hartebeest	1985	6 from Malawi	Successful but with much effort: 65 released from Nwatshitsumbe camp, 50 from Hlangwine camp. Still breeding in the camps.
	1986	15	As above.
Roan antelope	Unrecorded	12 from Zimbabwe to Hlangwine camp	Unsuccessful; did not adapt, primarily because of tick burdens. Population depleted by anthrax and drought in 1960s and 1970s.
	1984	To Rietpan area	Unsuccessful.
Mountain reedbuck	1974–1976	370 from Mountain Zebra National Park to Stolznek	Population healthy, often seen.
Grey rhebok	1978	20 from Golden Gate Highlands National Park to Khandizwe plateau	Limited success. Suitable habitat is limited in Kruger; this is probably the only suited area (west of Malelane).
Oribi	1962	29 from Badplaas to Fayi camp (Pretoriuskop)	Unsuccessful. Unsuitable habitat (Novellie and Knight 1994).
	1972–1973	98 from Badplaas released between Stolznek and Pretoriuskop	Unsuccessful. Did not adapt because of limited suitable highveld grassland habitat and fire regimes.
Aardwolf	1962	Badplaas (with the oribi)	Unknown.
	1979	3 released at Punda Maria from Natal	Unknown.

(continued)

white and black rhinos were seen in the region in 1896 and 1936, respectively, and reintroductions of white rhino began in 1960 and were followed by black rhino reintroduction in 1972 (Pienaar 1970; Pienaar 1994). Kruger's healthy, expanding white rhino population, estimated at around 5,000 animals, is now used for translocation to other areas as part of the white rhino conservation program, with 40 to 100 white rhino moved out of Kruger annually. Most other Kruger reintroduction efforts have been unsuccessful (Table 19.2). Although this can be attributed to exclusion of suitable habitat by boundary changes over time in some instances, limited data are available to adequately assess reasons for success or failure. Success rates are highly dependent on habitat suitability and size and composition of the founder group, but documentation of dates, numbers of animals, and success rates remains poor in conservation circles as a whole (Novellie and Knight 1994).

SPECIES	DATE	REINTRODUCTION	SUCCESS
Suni	1982	4 released at Punda Maria from Natal	Unknown.
	1989	20 from Natal, 9 from de Wildt to Skukuza pens	Did not do well in captivity.
Red duiker	1972	27 from Mariepskop to Shabinkop, Newukop, and Sabie River	Unknown.
	1981	21 released between Sabie and Sand rivers	Unknown.
Nyala	1980	21 brought from Natal to Sabie River	Successful. Regularly seen along Skukuza–Lower Sabie tarred road.
Eland	1971	27 from Addo Elephant National Park to Hlangwine camp	Vulnerable to high tick counts and few calves raised; released from the camp and supplemented with bulls from northern Kruger.
	1972	6 from Mountain Zebra National Park to Hlangwine camp	As above.
Sable antelope	1970	19 from Crocodile River Estates at Hoedspruit to northern Kruger	11 released into Nwashitsumbe camp bred well, and 64 animals were released in 1976.
Samango monkeys	1982–1988	95 from Entabeni near Louis Trichardt released along the Luvuvhu River	Sometimes seen in the Pafuri area.
Cheetah	1968–1969	34 from Namibia to Tshokwane, Malelane, and Crocodile Bridge areas	Very limited success.
Tsessebe	1972	Unrecorded numbers taken from the north of Kruger and Hoedspruit to Hlangwine enclosure	Heavy mortalities, but 4 survived.
	1978	2 bulls from Percy Fyfe Reserve to Hlangwine camp	Unrecorded.

Population Reductions

With an early approach to management described as pragmatic intervention, population reductions of various species were a regular feature. Initially this targeted predators (considered overabundant vermin, threatening stock, human lives, and conservation efforts), with control peaking in 1911–1920 and 1951–1960 in response to concerns about small or declining ungulate populations (Figure 19.1). Aims and objectives of culling changed under the influence of different wardens (Smuts 1982), officially ceasing in 1975. Impacts of these actions on lion and other predator populations in Kruger are speculative. Although they would have led to reduced populations at specific times, high reproductive rates and turnover may have buffered the population from extreme impacts, and knock-on effects probably were not significant in changing herbivore densities and structures. This contention is based on the outcomes of intensive lion and spotted hyena culling between 1975 and 1980, which resulted in negligible population impacts on lions and their prey populations (Smuts 1978; Whyte 1985; Chapter 18, this volume). Today, carnivore populations on Kruger's boundaries result in antagonistic encounters with neighboring communities. Costs of repatriation of animals are high, and often "problem animals" are killed or hunted on or along the boundaries. This edge effect probably is symptomatic of the Kruger source area not having a sink to which excess animals can migrate and naturally be removed from the system.

The 1960s and 1980s were characterized by large herbivore population control (Figure 19.1). In 1965 the board authorized artificial control of elephant (Chapter 16, this volume), buffalo, hippo, giraffe, wildebeest, zebra, and impala, based on the principles that large herbivores are limited by water and grazing during droughts and that high-density species could affect habitat and species diversity and compete with rarer species. Similarly, culling during high-rainfall periods was motivated by the constant fear of drought. From 1985 onward, an alternative to culling, providing financial return, became standard practice through the capture, sale, or donation of species. Numerous animals have been translocated from Kruger, increasing the budget available to SANParks for land acquisitions. The most significantly affected species is the white rhino, with an annual sale and translocation of 1–2 percent of the population. Black rhino are removed on a limited and ad hoc basis, usually to boost populations in other national parks or for political reasons. Although elephant translocations have been limited in the past because availability of alternative ranges is limited, the recent transfrontier agreement has resulted in the initiation of large-scale translocation of this species to Mozambique. Impacts of such actions on the overall Kruger ecosystem are unknown but are surely limited in the current framework of operations.

Poaching and Illegal Exploitation

Poaching has received attention since Sabi Game Reserve proclamation, with Stevenson-Hamilton establishing the first antipoaching unit in 1903. Common practices of snaring and fishing became illegal with the protectionist approach at the end of the eighteenth century and resulted in conflict around access to natural resources (Carruthers 1995; Chapter 20, this volume). These practices

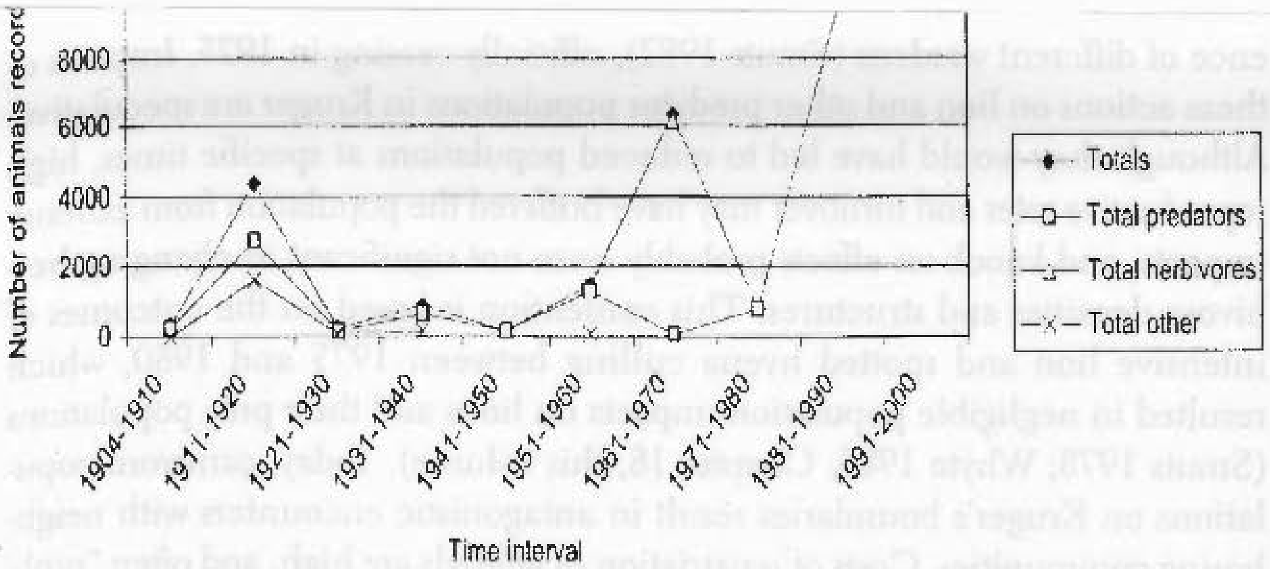


Figure 19.1. Total recorded numbers of animals culled in Kruger (excluding elephant). Data from Joubert (1986).

would have had an insignificant impact on game populations, but this changed with the advent of organized rhino and elephant poaching in the late 1970s and early 1980s. Poaching incidences have fluctuated in recent times, linked to increasing poor populations on Kruger's borders and a high demand for rhino horn and ivory (Figure 19.2). Today's antipoaching operations are highly organized and logistically and financially well supported and play a deflective and proactive role outside Kruger's boundaries. Success has been achieved through informer networks, general education, and counterincentives, with poaching operations well under control at present (relative to other conservation areas in Africa) and considered to have limited population effects (Figure 19.2).

Even rough estimates of illegal exploitation of plant resources in Kruger are difficult (Botha 1998). Although Botha et al. (2001) allude to occasional noncommercial harvesting, it is speculated that substantial amounts of medicinal plant materials leave Kruger. The annual South African trade in medicinal plants has been estimated at around $500 million, with an estimated 494–741 tons from 176 species used in Mpumalanga per year (Botha 1998; Botha et al. 2001). Some resources are harvested in Kruger because they have become scarce elsewhere, and others are collected by resident staff with easy access (e.g., bark in Skukuza staff village). Harvesters generally select for size to maximize their returns (Botha et al. 2001), which may affect population recruitment in rarer or slow-growing and maturing species. Increasing demand for such products will exert increasing pressures on wild populations if long-term resource management programs are not established. The exact impact of these practices is unknown but has the potential to lead to local species extinction, as has happened in areas outside Kruger (Botha 1998).

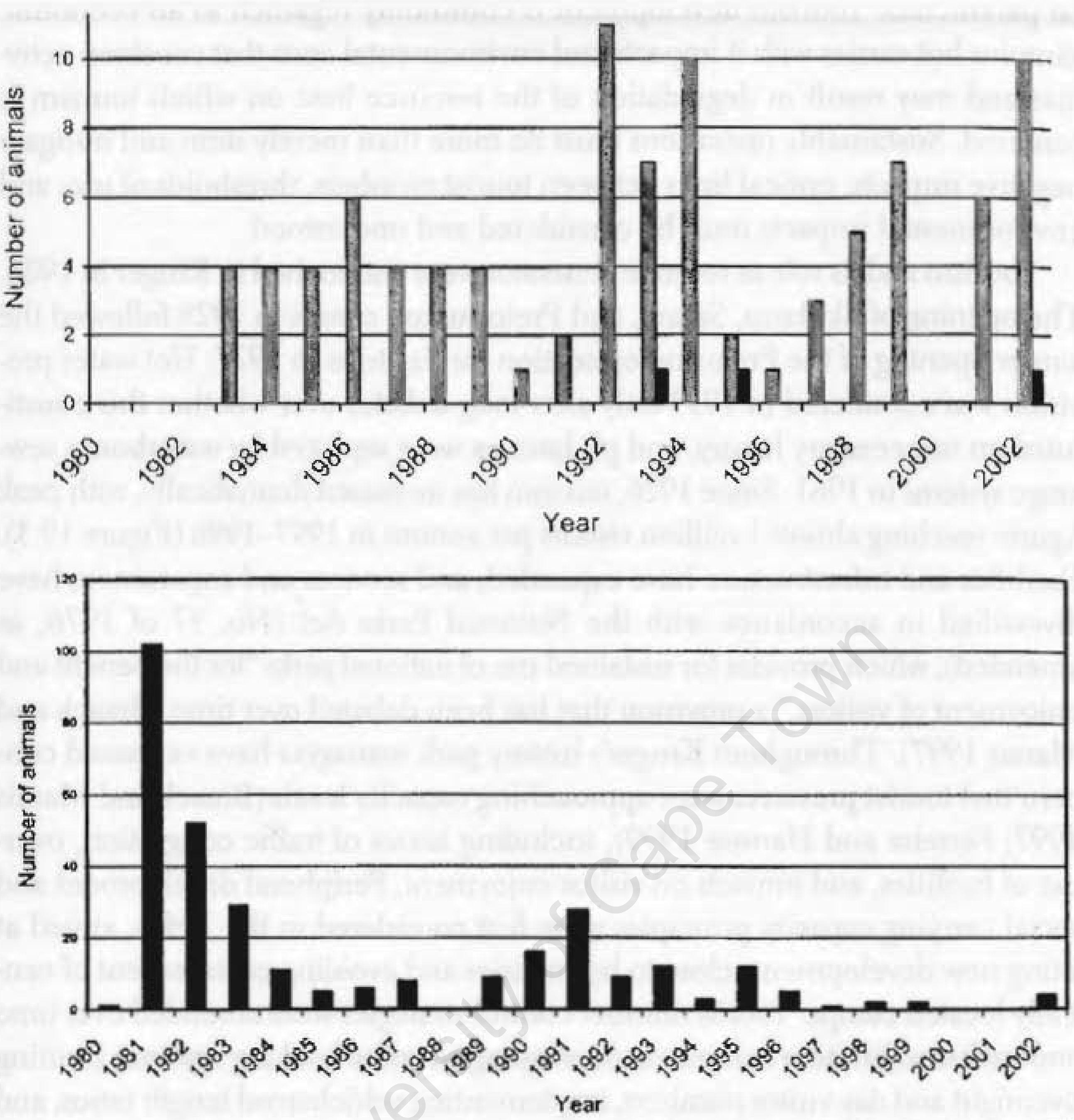


FIGURE 19.2. *(a)* Kruger rhino poaching incidents between 1980 and October 2002. White and black rhino numbers are indicated by gray and black bars, respectively. *(b)* Elephant poaching incidents in Kruger between 1980 and October 2002. The Convention on International Trade in Endangered Species ban came into effect in 1989–1990.

Tourism

Kruger's appeal as a tourist destination is enormous, and it is a major driver of economic development in the region. This, together with its annual net income, has led to Kruger being perceived as the goose that lays the golden egg (Ferreira and Harmse 1999). Economic and political pressures to increase revenue generation, attract more visitors, provide benefits to neighboring communities, and become more accessible often are juxtaposed to maintenance of attraction integrity and long-term sustainability of economic and environmental parameters. Tourism development is commonly regarded as an economic stimulus but carries with it impacts and environmental costs that constrain activities and may result in degradation of the resource base on which tourism is centered. Sustainable operations must do more than merely stem and mitigate negative impacts; critical links between tourist numbers, thresholds of use, and environmental impacts must be considered and understood.

Tourism and its role as revenue generator were entrenched in Kruger in 1926. The opening of Skukuza, Satara, and Pretoriuskop camps in 1928 followed the winter opening of the Pretoriuskop section for day trips in 1927. Hot water provision was considered in 1933 only after long debates over whether this constituted an unnecessary luxury, and pit latrines were replaced by waterborne sewerage systems in 1961. Since 1926, tourism has increased dramatically, with peak figures reaching almost 1 million visitors per annum in 1997–1998 (Figure 19.3). Facilities and infrastructure have expanded, and services and experiences have diversified in accordance with the National Parks Act (No. 57 of 1976, as amended), which provides for sustained use of national parks "for the benefit and enjoyment of visitors," a provision that has been debated over time (Braack and Marais 1997). Throughout Kruger's history park managers have expressed concern that tourist pressures were approaching capacity levels (Braack and Marais 1997; Ferreira and Harmse 1999), including issues of traffic congestion, overuse of facilities, and impacts on visitor enjoyment. Peripheral development and social carrying capacity principles were first considered in the 1940s, aimed at siting new developments close to boundaries and avoiding enlargement of centrally located camps. Tourist number control strategies were amended over time and included limiting camp size, developing advance booking systems, limiting overnight and day visitor numbers, implementing vehicle:road length ratios, and zoning Kruger for development and use (Ferreira and Harmse 1999).

Balancing Conservation with Tourism

The importance of balancing conservation achievement, scientific value, economic viability, and cultural value was recognized in 1962. It was argued that conservation success entailed economic returns and that nature conservation was for the benefit of humans rather than for its own protection. The importance of recreational value in its widest sense included spiritual, intellectual, and physical renewal. Therefore, in the mid-1970s interpretive services' role included disseminating knowledge and increasing visitor sensitivity for conservation issues, arguing that the ill effects of tourism could be reduced by reducing visitor ignorance (Joubert 1986).

More recently, the needs of tourism and conservation have been addressed through zoning techniques. Nevertheless, zoning has been a source of debate,

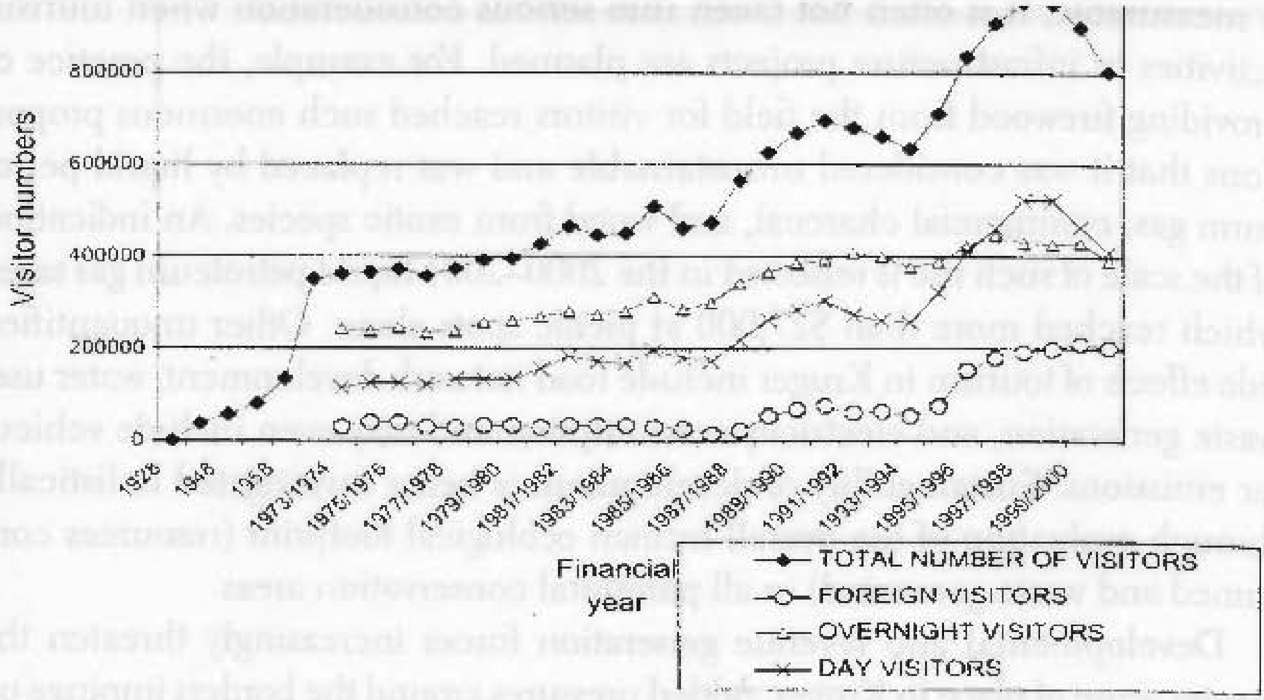


FIGURE 19.3. Numbers of annual visitors to Kruger since 1928. The total includes all foreign, local, overnight, and day visitors, but foreign visitor numbers are included in both the overnight and day categories.

with contention revolving around the basis, definition, and size of zones, their desired qualities, use, and management (Freitag-Ronaldson et al. in press). Perceptions, expectations, and interpretation of zoning no doubt have resulted in much of the debate. Wilderness management and zoning have become a cornerstone objective of the Kruger management framework (Braack 1997) and resulted in the Recreational Opportunities Zoning (ROZ) policy, which guides infrastructural and ecotourism development. This provides a heterogeneous template for directing levels of management and tourism activities. It is based on the premise that grades of wilderness experience and opportunities should be made available to visitors without impeding biodiversity management goals (Venter et al. 1997). This policy is under review because of ongoing challenges and a perception by some that it restricts tourism expansion.

Dealing with Tourism

An annotated list of visitor-influenced wildlife impacts in Kruger points toward some effects on the structural, functional, and compositional aspects of biodiversity (Freitag-Ronaldson et al. in press). Although <3 percent of Kruger is directly disturbed by infrastructure, the overall impact of tourism activities on all aspects of biodiversity is poorly understood and often is not recognized explicitly. Although direct resource use (water, wood, gravel, waste generation) is measurable, it is often not taken into serious consideration when tourism activities or infrastructure projects are planned. For example, the practice of providing firewood from the field for visitors reached such enormous proportions that it was considered unsustainable and was replaced by liquid petroleum gas, commercial charcoal, and wood from exotic species. An indication of the scale of such use is reflected in the 2000–2001 liquid petroleum gas sales, which reached more than $27,000 at picnic spots alone. Other unquantified side effects of tourism in Kruger include road network development, water use, waste generation, and electricity consumption and may even include vehicular emissions. Sustainability of development is being investigated holistically through evaluation of the overall human ecological footprint (resources consumed and waste generated) in all parastatal conservation areas.

Developmental and revenue generation forces increasingly threaten the greater sense of place in Kruger. Added pressures around the borders impinge on this conservation area, effectively reducing the nonimpacted core area and the distribution of wilderness attributes sought by visitors. A zoning system alone will not provide a holistic approach to the protection of tourism qualities, an integrated environmental management approach is needed. Kruger must consolidate a balanced plan to guide further development, combining societal values, biodiversity conservation, precautionary principles, and sustainable development.

Roads

Road ecology (Foreman and Alexander 1998) has received little attention, even though the conspicuous presence of roads fragments the Kruger landscape. Road impacts operate on two primary levels: the individual, species, and population level and the ecosystem process and landscape level. The former impacts influence abundance, distribution, mortality, and colonization rates (Tshiguvho 2000) and includes road kills (with spates of mortality, probably in seasons when vulnerable species forage more frequently on roads or night traffic rates are higher), road avoidance by animals because of noise, and barrier effects with possible demographic and genetic consequences of population subdivision (Forman and Alexander 1998). At the process level, hydrological, erosion, sedimentation, and chemical effects, nutrient cycling, and alien invasion impacts are operating. From observations in Kruger, this seems to be limited mainly to the road edge zone, although this is worthy of investigation. Similarly, little is known about the wider scale effects of habitat and landscape fragmentation, which may affect a variety of species, communities, and ecosystem functions. Certainly the impacts of roads will be species, ecosystem, or landscape specific, varying with road type and associated characteristics (Tshiguvho 2000).

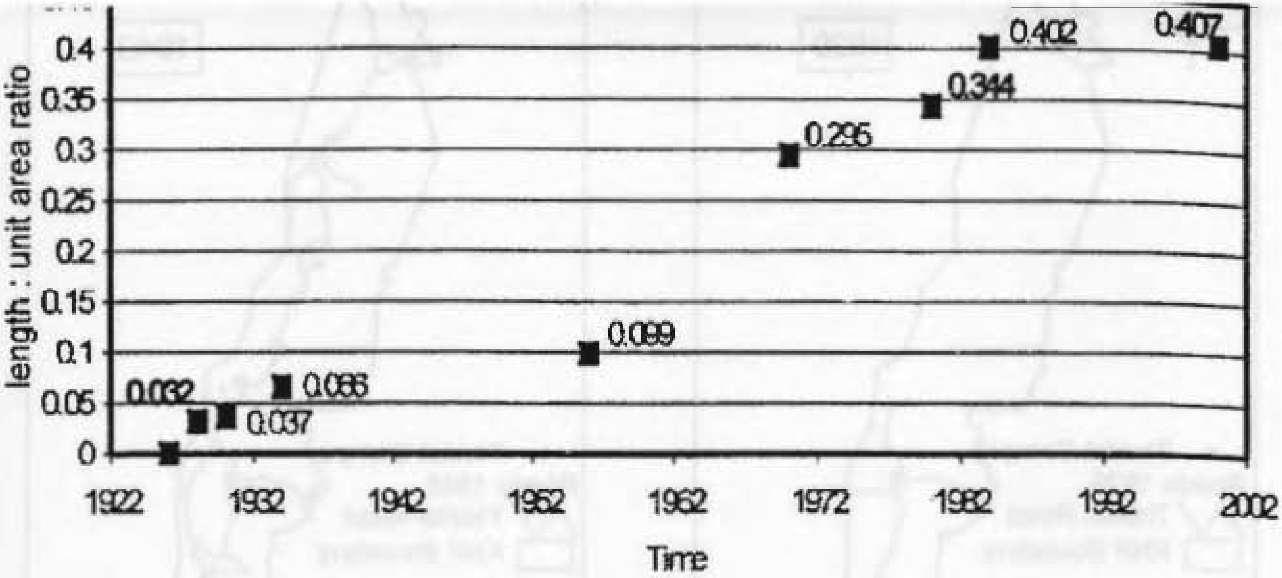


FIGURE 19.4. Kruger road development over time, measured as a length:unit area (km/km^2) ratio. Data taken from Joubert (1986) and information supplied by Kruger Technical Services Division.

There were no vehicles in Kruger in 1926, and the Selati railway, pack donkeys, and horses were used for transportation. The need for roads accompanied increasing management requirements and the advent of tourism, with the first car tracks opened in 1928 and the first road tarred in 1961. Since then, the road network (including firebreaks, management roads, and airstrips) has expanded to 7,926 kilometers, dramatically increasing between 1956 and 1970 (Figures 19.4 and 19.5). Here we conservatively estimate the immediate road verge effect by buffering roads by twice their width (an arbitrarily selected buffer width, with gravel road width = 6.5 m and tar road width = 12 m, compared with maximum road verge transect widths of 20 m in the Tshiguvho et al. [1999] study). This results in a corresponding immediate road-affected area of 29,751 ha, or 1.5 percent of Kruger's surface area. Generally these effects operate at the local and individual scale, with negative effects mainly on invertebrates, small mammals, and timid game species (Pienaar 1968) and positive effects on species such as scavenging ants (Tshiguvho 2000) and plants (e.g., *Colophospermum mopane, Dichrostachys cinerea*), which have encroached road verges.

Of greater environmental consequence are fragmentation effects, poorly drained or badly planned road networks, and erosion problems as well as the impacts of maintenance and construction activities such as gravel use. Although no quantitative data exist, a high proportion of unnatural erosion is associated with road-building activities in Kruger, most severe in duplex soil types. Gravel pits reflect the environmental costs of road building in Kruger, with more than 12.5 million m^3 of gravel excavated over the years (Table 19.3). Annual maintenance estimates of 713,000 m^3 of gravel are influenced by rainfall and flood

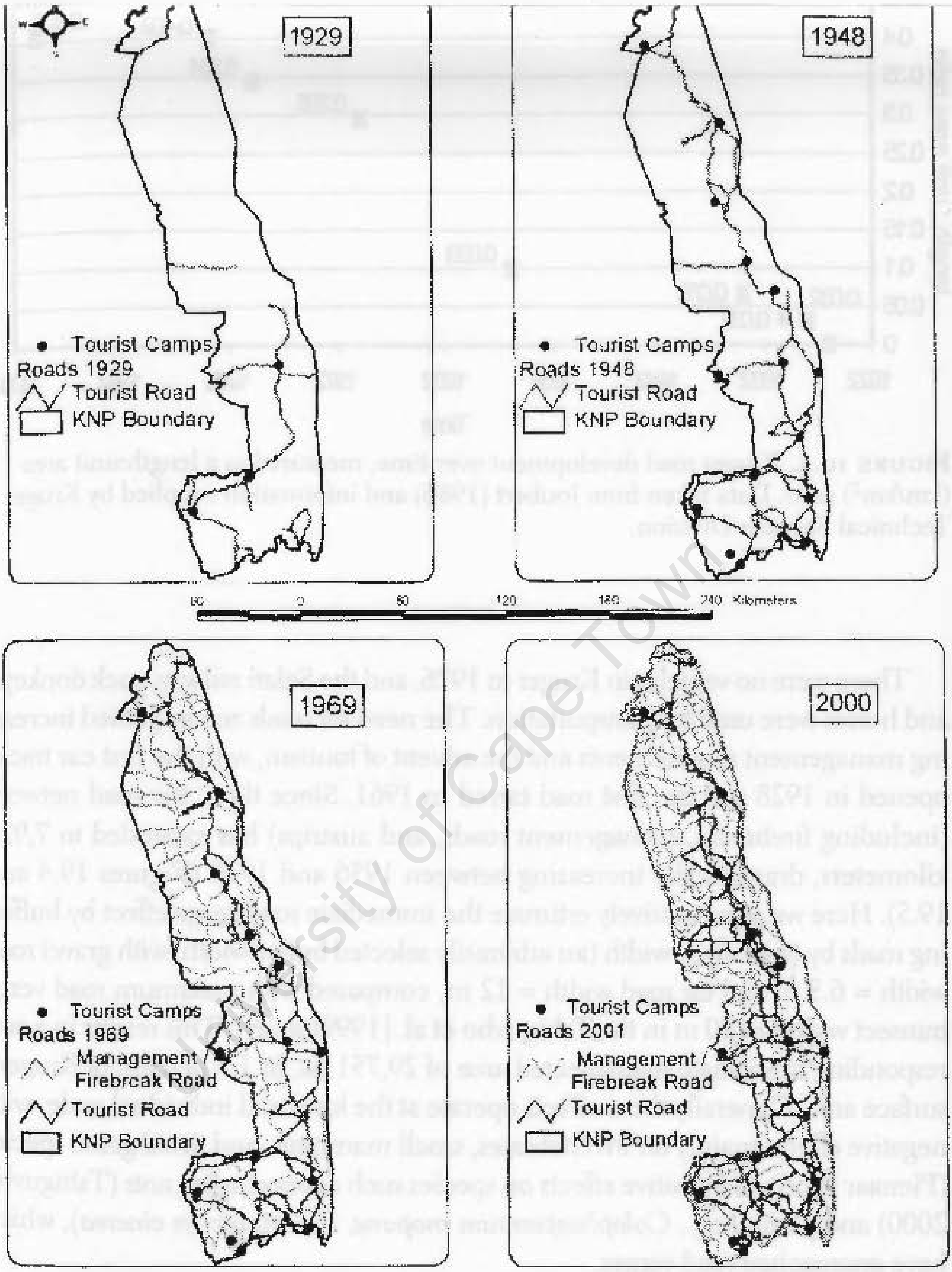


FIGURE 19.5. Tourist and management road networks of Kruger at different times.

events; almost 500,000 m³ gravel was used after the February 2000 floods. Approximately 1,000 gravel pits of differing sizes, depending on gravel content, construction needs, and locality, are largely unrehabilitated. They are unsightly and have other detrimental effects such as withholding water and acting as unnatural water sources throughout the year, sometimes in areas that animals would have otherwise vacated in the dry season (Chapter 8, this volume).

ing 4,164 hectares. Road decommissioning has resulted in an increased block size, with three or four old blocks now constituting new burn units. However, not all roads have the same ecological impact, and fragmentation levels may become meaningful only if considered in light of specific policies (e.g., fire policy) or road type. At first glance Figure 19.5 appears to show that all areas of Kruger have been developed with roughly the same density of roads since 1969. However, if main paved roads are considered to have the highest impact, the southern area has been affected longest and has the highest fragmentation levels. Therefore, homogenization of spatial processes probably has been greatest in the south. Road use for fire management has also affected the system. Burn blocks and fire regimes and policies (Chapter 7, this volume) no doubt played a part in vegetation homogenization in blocks (especially during the perimeter burns placed around blocks) with sharply defined, linear burn boundaries. Even point burns are affected by firebreak and tourist roads, which will continue to shape burn boundaries, although to a lesser degree.

Road networks and gravel pits have a variety of ecosystem impacts that may be of extremely long duration, even after decommissioning and rehabilitation efforts. Therefore, Pienaar (1968) urged the utmost care during road construction, noting that "wherever a road is built through wild country, this area can never again be the same, and whether the influence of such a road is beneficial or detrimental to the ecosystem, it is bound to be profound" (p. 174).

Limited research efforts have addressed the effects of powerlines, or the combined impacts of roads and powerlines, on Kruger biodiversity. Overhead powerlines are unattractive, and ongoing pressure against any such expansion is evident. Reticulation lines may result in raptor electrocutions (van Rooyen and Grantham 1998), although some remedial action (design features or additions to prevent electrocution) has been taken.

Kruger would benefit from development of an overall framework on road impacts and road ecology research, designed to better quantify and understand these effects, particularly with ongoing pressure to build more roads and tracks in concession areas (Chapter 1, this volume).

Invasive Alien Species

Invasive alien species pose the second greatest threat to global biodiversity (IUCN 1997). Impacts include replacement of diverse systems with single (or mixed) species stands, alteration of soil chemistry, geomorphological processes, fire regimes, hydrology, extinction of compositional diversity, and threats to indigenous fauna (Cronk and Fuller 1995), displacement by competition, *Conservative estimates of gravel quantities used for construction and maintenance of the Kruger road network (as supplied by the Kruger Roads Department).*

ROAD TYPE	DISTANCE (M)	AVERAGE WIDTH (M)	AVERAGE CUMULATIVE GRAVEL DEPTH USED OVER TIME (M)	GRAVEL USED (M^3)
Gravel tourist roads	1,768,000	6.5	0.25	2,873,000
Tar roads	885,000	12	0.8	8,496,000
Graveled management roads (firebreaks)	737,000	6.5	0.25	1,196,000
Airfields	12,800	30	0.5	192,000
Total				12,757,000

reduced structural diversity, increased biomass production, and disruption of prevailing vegetation dynamics (van Wilgen and van Wyk 1999). Furthermore, Richardson et al. (1997) suggest that in southern Africa the destruction of riparian habitats is a key impact, and alien plant invasions have directly resulted in the extinction of species.

Kruger has been invaded by numerous taxa, particularly plants. Undesirable effects of alien plant species were first recognized in 1937 by Stevenson-Hamilton, who stated that the introduction of exotic types of fauna and flora "should be religiously avoided" (Stevenson-Hamilton 1937, p. 260). Nevertheless, policy proposals over time (prohibiting cultivation of exotic species and supporting their removal from Kruger) did not significantly affect resident staff attitudes toward their gardening habits or the growing threat of alien plant invasions. The first alien plant list of six species was compiled by Obermeijer in 1937, and the current Kruger estimate stands at 367 species (Foxcroft and Richardson 2001; Figure 19.6). Most habitat types have been invaded, with disturbed habitats most affected (rivers, rest camps, staff villages, and road verges). In 1997 invasive alien species were highlighted as posing a great threat to biodiversity conservation in Kruger, highlighting the general lack of institutional learning and recognition over time of the long-term threats posed by alien plants (Foxcroft and Richardson 2001).

The overemphasis on compositional diversity has been accompanied by an inadequate awareness of structural and functional diversity and the role of invasive species in driving systems into more heterogeneous or homogenous states. Similarly, Kruger research surveys are not designed to specifically explore direct biodiversity impacts but implicitly assume that such impacts are negative and undesirable. One measured biodiversity response came through an experiment on efficacy of control methods for *Lantana camara,* which showed that there was a significant increase in biodiversity after its chemical removal (Erasmus et

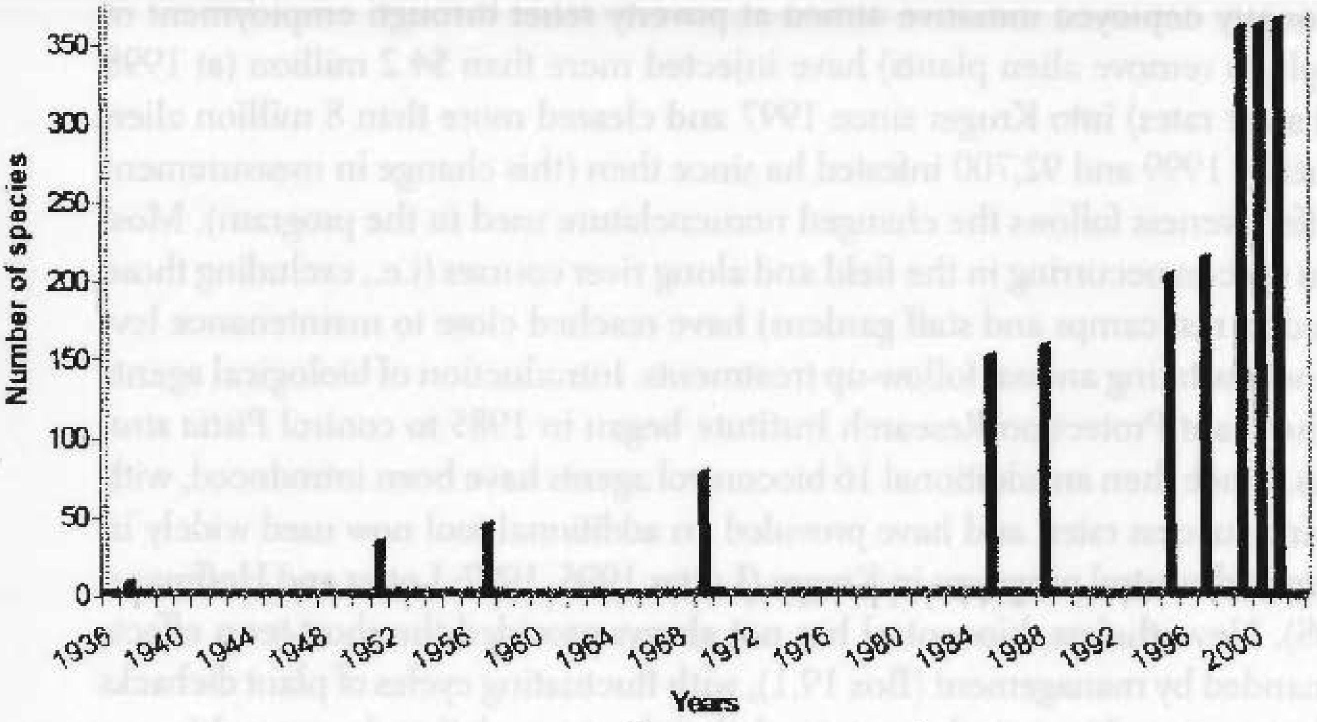


FIGURE 19.6. The number of invasive alien plants reported in Kruger surveys between 1937 and 2001 (data from Obermeijer 1937; Codd 1951; van der Schijff 1957, 1969; Gertenbach 1985; MacDonald and Gertenbach 1988; Anon. 1995, 1996; Foxcroft 1999, 2000, 2001).

al. 1993). At this point *Lantana camara* is considered the most serious riparian invader, covering an area of 30,028 ha, with some patches having attained 100 percent cover in the past. Ongoing control efforts and frequent flooding limit its proliferation, although propagule pressure from surrounding areas facilitates reestablishment. The impact of terrestrial invasives such as the Cactaceae (specifically *Opuntia stricta* in Kruger) is pronounced. It has been shown that *Opuntia stricta* affects vegetation structure in densely infested areas of Kruger (Lotter and Hoffmann 1998). Experiential evidence indicates that in a fire-dominated savanna such species disrupt natural ecosystem cycles where they form dense infestations, excluding other plants such as grasses, affecting fuel loads, fire frequency, and intensity. What we don't yet know is whether species with allelopathic properties inhibit establishment of indigenous species in their close proximity, increasing the disturbance effect and providing a niche for other invasive species or for the expansion of their own range.

Control efforts initially were aimed at eradication, beginning with *Melia azedarach* in 1956 (Joubert 1986). Eradication attempts generally have been unsuccessful. Control efforts now recognize the more realistic target of maintaining infestations at acceptably low levels (the definition of *acceptable* is not rigorously defined but varies by species and refers to the logistical resource needs for controlling alien plant populations). Management operations involved mechanical and chemical means and were improved by the use of registered herbicides, with initial research and funding addressing herbicide efficacy and nationally deployed initiative aimed at poverty relief through employment of people to remove alien plants) have injected more than $4.2 million (at 1998 exchange rates) into Kruger since 1997 and cleared more than 8 million alien plants by 1999 and 92,700 infested ha since then (this change in measurement of effectiveness follows the changed nomenclature used in the program). Most alien species occurring in the field and along river courses (i.e., excluding those found in rest camps and staff gardens) have reached close to maintenance levels, necessitating annual follow-up treatments. Introduction of biological agents by the Plant Protection Research Institute began in 1985 to control *Pistia stratiotes*. Since then an additional 16 biocontrol agents have been introduced, with varying success rates, and have provided an additional tool now used widely in integrated control programs in Kruger (Lotter 1996, 1997; Lotter and Hoffmann 1998). Nevertheless, biocontrol has not always provided the short-term effects demanded by management (Box 19.1), with fluctuating cycles of plant diebacks and recovery as biocontrol agents track their host population demographics.

Management by Objectives

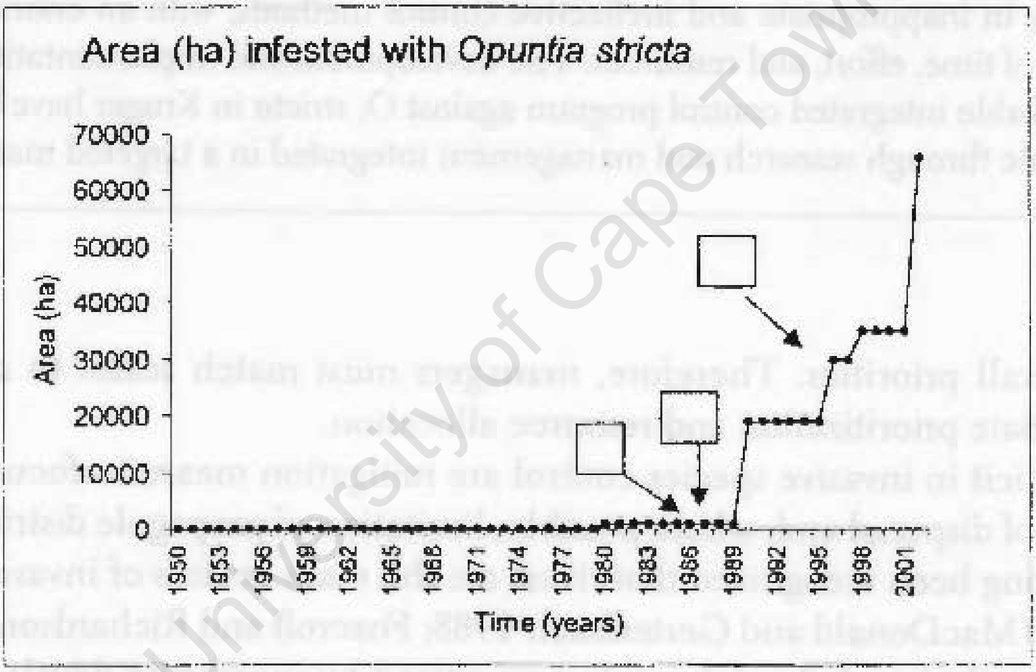
Until recently, charismatic aspects of wildlife management received disproportionate attention and budget allocation, with alien control operations receiving lower priority (Foxcroft and Richardson 2001). The 1997 management-by-objectives approach in Kruger sparked a strategic adaptive management response to invasive alien research and control, integrating science and management more tightly than before. A monitoring and goal maintenance system (Bestbier et al. 2000) provides a structured approach enabling multitiered threshold of potential concern (TPC) assessment (Figure 19.8; Chapter 4, this volume). The first-order TPC states that all invasions into Kruger are undesirable and must be prevented where possible. Therefore, TPC notification follows the first record of an invasive alien plant approaching or entering Kruger. As these plants disperse, second-order prevention-of-spread TPCs are activated, aimed at reducing the dispersion of the species. These are followed up at the third level, which strives for suppression of plant densities (i.e., TPCs come into effect when densities increase by a predetermined amount). Consideration is given to priority taxa most likely to become troublesome, maintaining them at minimum levels, whereas other species are not controlled and fluctuate without intentional intervention. Scale issues are important in successful control program implementation because the definition of priorities changes at different scales. Species significant at the Kruger level therefore may not be as important to control at the regional or national level, and species reported at the level of a ranger section may not carry much weight when viewed across the entire park and weighed against

BOX 19.1

Biological Control in Managing Alien Plants in Kruger

LLEWELLYN C. FOXCROFT AND JOHN H. HOFFMANN

Biological control has been used to manage several alien invasive species in Kruger, including *Opuntia stricta, Lantana camara, Pistia stratiotes, Salvinia molesta, Eichhornia crassipes,* and *Azolla filiculoides. O. stricta* is the most problematic invasive species in Kruger, with more than 30,000 ha in the Skukuza region invaded to various extents (Lotter and Hoffmann 1998). Historically, the invasion displayed a typical lag phase, with plants remaining scarce and limited in geographic distribution. However, in recent years the dispersal and densification of the species have been rapid despite intensive control efforts (Figure 19.7). Initial control efforts relied on chemical herbicides, but they failed to produce satisfactory results, largely because of the extent of the infestation and shortage of labor.



To improve control and limit expansion, biological control was initiated in 1988 with the introduction of *Cactoblastis cactorum* (Lepidoptera: Phycitidae). The release was successful, and the moth readily became established in Kruger although, for unknown reasons *C. cactorum* has not reached effective levels of abundance for *O. stricta* control (Hoffmann et al. 1998a, 1998b). Nevertheless, *C. cactorum* plays a major role in curtailing regrowth of *O. stricta* in infestations treated with herbicides. This strategy provides a rare example of the successful integration of biological and chemical control methods and has achieved substantial savings for Kruger.

A particular biotype of cochineal, *Dactylopius opuntiae* (Hemiptera: Dactylopiidae), was obtained from Australia and released in May 1997 into Kruger, where it readily established in the vicinity of Skukuza. Large, dense clumps of cactus were completely destroyed within 18 months, although cochineal populations declined dramatically during the extreme rainfall experienced in 2000–2001. Cochineal populations have recovered slowly, but periodic heavy rainfall and limited dispersal abilities of the insects have slowed progress (Foxcroft and Hoffmann 2000).

To date the combined impact of *C. cactorum* and *D. opuntia* has not been able to prevent the spread of *O. stricta* (Figure 19.7). However, the insects have curbed the rate of long-range dispersal and densification of *O. stricta* (Hoffmann et al. 1998a, 1998b). Precedents elsewhere indicate that cochineal insects effectively destroy target weeds during periods of below-average rainfall (Moran et al. 1987; Moran and Hoffmann 1987), and it is anticipated that the same will happen in Kruger in the next dry period. Currently *D. opuntiae* is being mass reared under hothouse conditions and released throughout *O. stricta* infestations in and around Kruger.

In general, too little effort is expended on research to evaluate the effectiveness of control strategies for alien invasive plants and other pests. This often results in inappropriate and ineffective control methods, with an enormous waste of time, effort, and resources. The development and implementation of a workable integrated control program against *O. stricta* in Kruger have been possible through research and management integrated in a targeted manner.

the overall priorities. Therefore, managers must match scales to achieve appropriate prioritization and resource allocation.

Implicit in invasive species control are mitigation measures focusing on vectors of dispersal and, where possible, limitation of propagule distribution. It has long been recognized that rivers are the main vectors of invasion into Kruger (MacDonald and Gertenbach 1988; Foxcroft and Richardson 2001), with heavily invaded catchments pressurized by increasing development, commercial farming, and forestry. Until infestations in upper catchments are better controlled, control efforts in Kruger will, at best, remain an attempt to maintain populations at the lowest possible levels. However, internal sources are also important if long-term effective control is to be achieved. Propagule movement by animals and birds implies that before dispersal of an exotic plant species can be successfully limited, all flowering and fruiting populations must be controlled and followed up before the next season of setting seed, as is done in the management of *Opuntia stricta* (Lotter and Hoffmann 1998; Hoffmann et al. 1998a, 1998b).

Human-assisted invasion in Kruger is discussed by Foxcroft (2001), highlighting the role played by staff in introducing species into restcamps and gardens for ornamental and other uses. In 1935 ranger Hoare objected to the planting of flam-

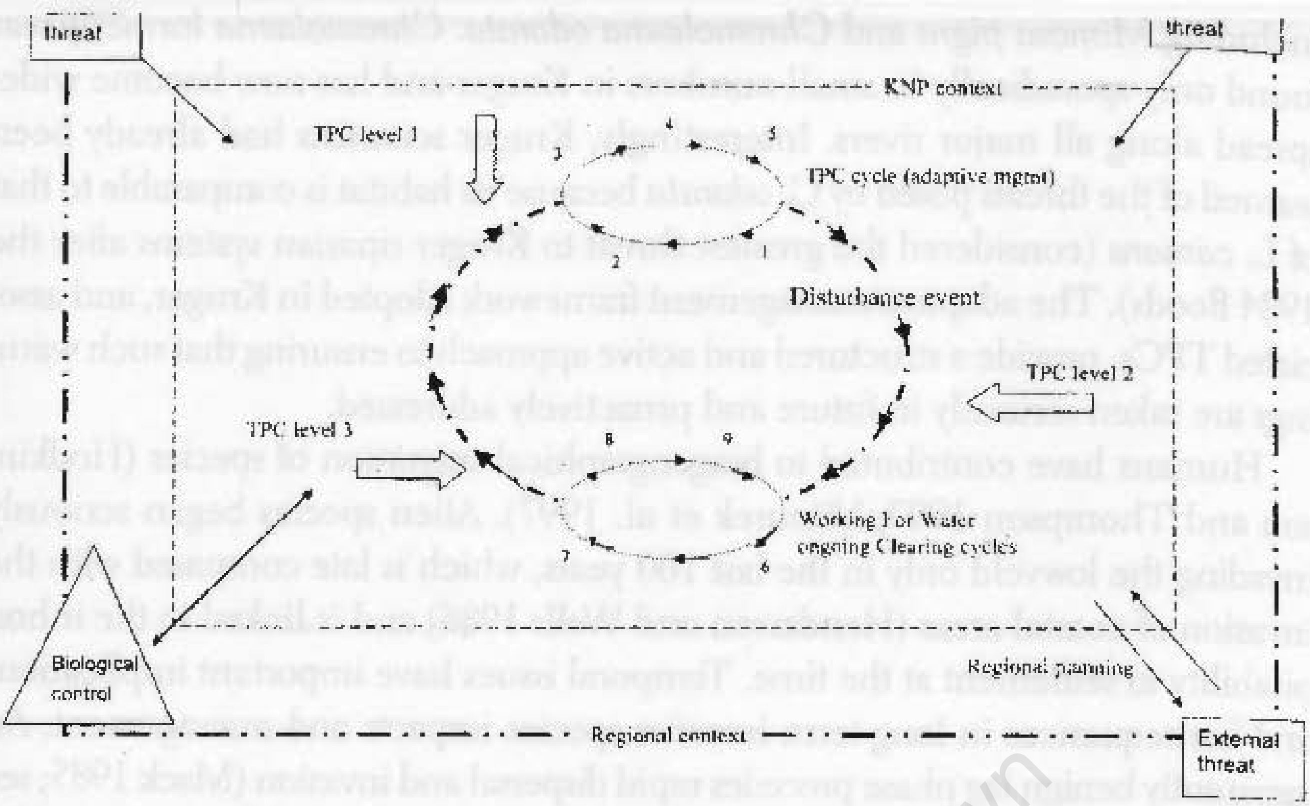


Figure 19.8. The flow of thresholds of potential concern (TPCs) indicating the various TPC levels for invasive species management: 1, analyze; 2, notify TPC reached; 3, take management action; 4, provide feedback; 5, measure; 6, contract; 7, clear; 8, monitor; 9, follow up. TPC levels: 1, prevention; 2, measuring dispersal in Kruger; 3, measuring density of species.

boyant *Delonix regia* at Pretoriuskop; this is one of the first efforts to actively prevent an intentional introduction of an alien species (Joubert 1986). MacDonald and Gertenbach (1988) state that 13 of the 156 alien species recorded were in cultivation in gardens and camps, with 2 of those species (*Lantana camara*, *Melia azedarach*) considered to have high impact on the Kruger system. A survey of the Skukuza camp and staff gardens in 1999 listed approximately 240 exotic species and culminated in a policy that prioritizes species for removal in a phased approach.

Spatial Structure, Lag Periods, and Uncertain Trajectories

Invasive species spread depends on point of origin, transport, and ability to establish and spread into new habitats. Riparian systems are especially sensitive to invasions because they combine high disturbance rates with high fertility and propagule influx (Prieur-Richard and Lavorel 2000). The February 2000 floods altered the structure of the Sabie and other rivers in Kruger, affecting vegetation structure and alien vegetation composition. The initial riparian aliens were quickly replaced by stands of annual herbaceous *Ageratum conyzoides* and *A. houstonianum*, followed and replaced by others. In addition to rapid colonization, the including *Mimosa pigra* and *Chromolaena odorata. Chromolaena* formerly was found only sporadically in small numbers in Kruger and has now become widespread along all major rivers. Interestingly, Kruger scientists had already been warned of the threats posed by *C. odorata* because its habitat is comparable to that of *L. camara* (considered the greatest threat to Kruger riparian systems after the 1984 floods). The adaptive management framework adopted in Kruger, and associated TPCs, provide a structured and active approach to ensuring that such warnings are taken seriously in future and proactively addressed.

Humans have contributed to biogeographical migration of species (Hodkinson and Thompson 1997; Vitousek et al. 1997). Alien species began seriously invading the lowveld only in the last 100 years, which is late compared with the invasion of coastal areas (Henderson and Wells 1986) and is linked to the inhospitability to settlement at the time. Temporal issues have important implications and consequences in long-term invasive species impacts and management. An apparently benign lag phase precedes rapid dispersal and invasion (Mack 1985; see Box 19.1), after which invasive species rapidly occupy all available niches at the greatest density allowed by physical and environmental constraints. This sequential trend may be broken in certain cases but is the exception rather than the rule. Hypothetically, when all available space is occupied and a dense monoculture of invasive species exists, the system should be regarded as transformed (space 4, Figure 19.9a), with little chance of reclaiming it to former composition and function. With Kruger's history of alien plant control, geographic distributions and densities of invasive species have been limited, but whether this will hold in the long term remains to be seen. If left unchecked, invasive species exhibit abilities to move ecological systems from natural heterogeneity to homogeneity over a large scale and time frame. However, serious alien invasives (i.e., transformers and others) that are controlled effectively should be suppressed to maintenance levels with tolerable impact, effectively staying within or reverting to the lag phase condition (Figures 19.9b, 19.9c). Species not controlled will fluctuate as environmental conditions dictate, switching between scattered and locally dense infestations.

Variations in temporal invasion are not always fully understood, particularly for seasonal species. Distinctive cycles of recurrence have long been noted, with extensive stands in some years followed by a complete absence in others (e.g., *Abutilon angulatum, Zinnia peruviana,* and *Nicotiana glauca*). Are such species responding to environmental parameters that allow them to flourish at some stages but not others, and, if so, how long are these cycles? The extent of species displacement and rearrangement of floristic patterns during invasive cycles are unknown but would help management assessments maximize use of limited resources. The real question therefore is whether fluctuating infestations of some species such as *N. glauca* on sandy stretches

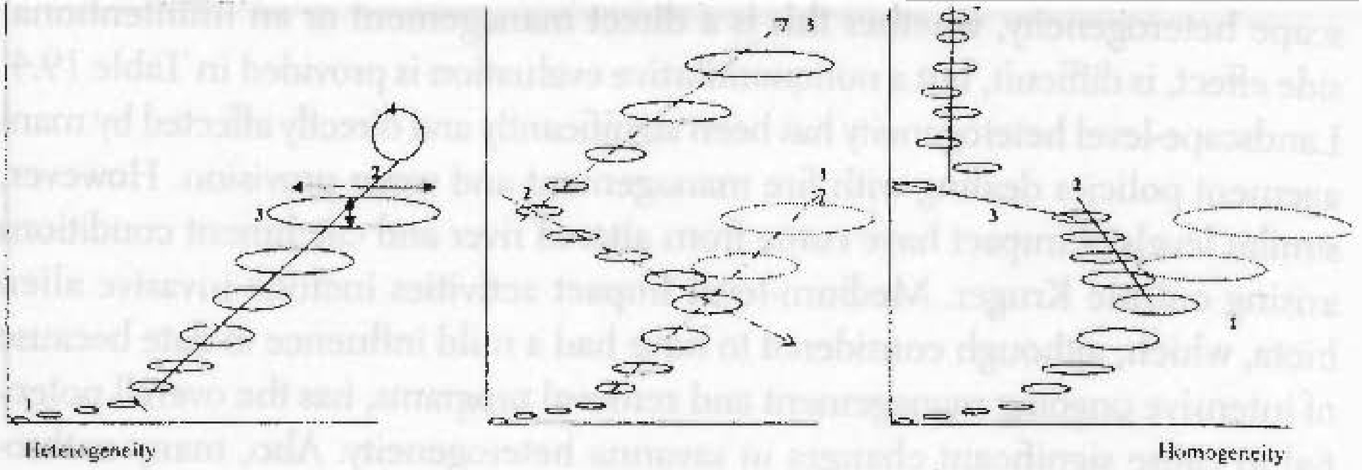


FIGURE 19.9. Scenario A: Trend of plant invasion over time and space, with fluctuations between heterogeneity and homogeneity: 1, lag phase; 2, trend line (tending toward 4); 3, invasion covers a wide area as a homogenous stand but can fluctuate within certain parameters on a local or heterogeneity scale; 4, transformed system with homogeneous stand of invasive plants over a wide area, with little fluctuation in homogeneity (fluctuation would have little impact because of propagule pressure and the seed bank in the entire area). Scenario B: Trend of plant invasions over time with mechanical and chemical control options: 1, trend line heading for transformed state; 2, implementation of mechanical or chemical control operations; 3, trend toward altered state when operations stop for any reason. Scenario C: Trend of plant invasion over time with the release of effective biological control agents: 1, introduction of biocontrol agent; 2, establishment of biocontrol phase; 3, rapid collapse of host plants; 4, tending to central point of fluctuations through seasonal variations of low impact and densities of host plant. Circles represent spatial scale or extent.

of the Olifants and Letaba rivers warrant attention other than for aesthetic reasons. The cyclic nature of these invasions and our lack of understanding of the main drivers make effective control of these species difficult. Control efforts may be better applied by focusing on plants established above the annual flood line, with the rest of the infestation following cycles dictated by environmental influences.

The overall conclusion is that disturbance (both natural and human-induced) drives alien plant invasions in Kruger. Important for management of this problem is an understanding of the temporal lag periods that are both species dependent and environmentally driven. Research and experience in other regions assist management in distinguishing between the long-fuse–big-bang species and those that are unimportant, with limited ecological impacts.

Ranking Anthropogenic Agents of Change

Influences on Kruger have been many and varied, and the majority of them have an anthropogenic origin. Teasing out the exact influences of each agent on landscape heterogeneity, whether this is a direct management or an unintentional side effect, is difficult, but a nonquantitative evaluation is provided in Table 19.4. Landscape-level heterogeneity has been significantly and directly affected by management policies dealing with fire management and water provision. However, similar levels of impact have come from altered river and catchment conditions arising outside Kruger. Medium-level impact activities include invasive alien biota, which, although considered to have had a mild influence to date because of intensive ongoing management and removal programs, has the overall potential to cause significant changes in savanna heterogeneity. Also, many anthropogenic agents of change have had cumulative and synergistic effects, interacting with each other and with natural phenomena such as droughts and floods.

What has been learned over time is that management of this ecosystem must go beyond the fence and incorporate new paradigms of boundary softening such as buffer zone comanagement (e.g., Makuleke and Mdluli Contractual Parks, Marietta Buffer Zone). Nevertheless, Kruger cannot be expected to bear the costs of external impacts and resource use, and techniques must be developed to measure and predict levels of impacts and rates of resource flow. Quantitative estimates of the economic value of the conservation land-use option must also be made and value assigned to the human benefits flowing out of Kruger's continued existence (Chapter 23, this volume).

The Imperative of Responding to Global Environmental Change

Although not specifically discussed elsewhere in this chapter and not ranked in Table 19.4, Kruger recognizes the potential paramount importance of global environmental change. Unprecedented changes in global climate and biogeochemical cycles have resulted in collaborative initiatives at both Kruger (Chapter 22, this volume) and national levels. At a wider level, our participation in the Assessments of Impacts and Adaptations to Climate Change in Multiple Regions and Sectors (AIACC) initiative will lead to improved understanding of the impacts of climate change on the biodiversity sector of southern Africa. The project aims to enhance scientific and technical capacity and provide scenario-planning tools to project climate change vulnerabilities and test and facilitate adaptation strategies. Linked to these are the wide-scale land use and land cover changes and biodiversity reduction. Here Kruger is involved in initiatives aimed at addressing desertification in South Africa and in a carbon emission offset initiative for natural resource rehabilitation in rural areas. Although this is a new response to an objective of Kruger (see Table 4.1, this volume), it is starting to attract the requisite attention.

Ranking anthropogenic agents of change in Kruger.

AGENT OR IMPACT	MAIN EFFECTS AND OUTCOMES	HETEROGENEITY INCREASED OR DECREASED	RELATIVE MAGNITUDE
Fire management	Rigid triennial burn policies between 1957 and 1992 led to homogenization of vegetation; shift from open to closed woodland in higher-rainfall areas through earlier fire suppression; encroachment of some species; structural changes to mopane regions; decline in large trees.	Homogenization at landscape scale	High, especially in conjunction with effects of herbivory, notably by elephants
Water provision policies	Resulted in changed species composition and structure in immediate area of artificial water and impacts of elephant in particular on the woody vegetation; increased patchiness at local level but overall homogenization of Kruger system.	Increased heterogeneity at fine scale; homogenization at Kruger scale	High
River flows and catchment management	Upstream abstractions reduce Kruger surface water, with some perennial rivers becoming seasonal in some years, affecting riparian vegetation and recruitment processes; effects of eutrophication, sedimentation, and decreasing water qualities affect downstream (Kruger) biotic responses.	Homogenization through biodiversity loss and structural and habitat reduction	High
Alien biota	Has high homogenization potential, but this has been severely limited by control efforts, and infestations have still been predominantly within the latent lag phase.	Increased species diversity (although undesirable); local and habitat homogenization (especially riparian systems)	Medium to date (but very high potential)
Tourism activities	Varied effects through associated infrastructure, although biggest concerns are environmental costs not necessarily associated with heterogeneity impacts (through direct and indirect resource use).	Some local homogenization (e.g., wood collection), some local heterogeneity (e.g., effects of artificial wetlands)	Low to medium

(continued)

AGENT OR IMPACT	MAIN EFFECTS AND OUTCOMES	HETEROGENEITY INCREASED OR DECREASED	RELATIVE MAGNITUDE
Population management and culling	Synergistic effect with fire management; stabilized elephant numbers had an overall homogenization effect at the broadest level; population reductions of herbivores and carnivores had uncertain effects.	Local-scale variability increased, larger-scale homogenization through population stabilization	Medium to high (in conjunction with fire policies)
Disease and disease management	Natural disease assists in maintenance of patchiness by its cyclic nature, operating at focal, local, or regional levels; alien disease generally has homogenizing local effects but may contribute to large-scale heterogeneity.	Ecosystem effects linked to other drivers and may then act synergistically in increasing patchiness or homogenizing at various scales	Medium to low
Roads	Fragmented Kruger into blocks, homogenizing within blocks because of fire effects. Small and localized barrier effects, but large implications for gravel use and effects of resource use.	Localized homogenization, although larger-scale synergistic effect with fire management	Medium to low
Fencing and boundaries	Mainly affects large mammal movements and cuts off migratory routes, resulting in unnatural pressure on vegetation.	Homogenizing effects	Small to medium
Poaching	Large effect at turn of century by extirpating dominant herbivores, but more recently has more localized effects with limited impacts on heterogeneity.	Limited effects	Small (but possibly medium before Kruger proclamation)
Population augmentation and reintroductions	Resulted in increased species diversity, but often attempts were unsuccessful.	Negligible	Small
Early humans	Heterogeneity effects through burning and local-scale enhancement of patchiness.	Increased heterogeneity	Assumed to be small

In a recent study assessing effectiveness in protecting biodiversity, Brunner at al. (2001) noted that parks were generally successful at mitigating the anthropogenic impacts of land clearing, hunting, fire, and grazing. Park effectiveness was most strongly correlated with density of guards and inversely with levels of illegal activities in parks. These findings appear to hold for Kruger. They will also lead to increased motivations for more field staff to patrol and combat activities such as poaching along boundaries. However, this narrow focus may result in short-term protection but longer-term biodiversity loss. Far greater threats that tend to be overlooked are already exerting their invisible forces on the ecosystem. Many of them are linked to global change in its broadest sense and are changing the composition and functioning of ecosystems. Of immediate and direct consequence are the escalating biological invasions. Threats from global environmental agents of change probably will dominate in future and attract increased attention and focus. Human-induced changes in atmospheric deposition, greenhouse gases, and nitrogen deposition must be afforded greater concern and consideration to facilitate a pragmatic and adaptive approach to attaining conservation goals.

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APPENDICES

Part 1- Management implications.

1.4: Foxcroft L.C. 2004. An Adaptive Management Framework for Linking Science and Management of Invasive Alien Plants. *Weed Technology* **18**: 1275-1277.

APPENDICES

Part 1- Management implications.

1.5: Foxcroft L.C. 2005. Alien Impact Objectives. In: *A Hierarchy of Objectives for the Kruger National Park- Kruger National Park Management Plan* (ed. S. Freitag-Ronaldson), South African National Parks, Skukuza, South Africa. South African National Parks, Skukuza, South Africa.

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Symposium

An Adaptive Management Framework for Linking Science and Management of Invasive Alien Plants[1]

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Abstract: The development of effective linkages between science and management centers on the smooth integration of three pillars serving common objectives. Science, monitoring, and management all play a role in the overall success of managing natural areas. Control of invasive alien species (IAS) has generally followed rigid principles, built on a foundation of developing mechanisms for re-active, physical control techniques. As the numbers of IAS continue to grow, predictions are needed to manage the most serious species only. This approach requires a management framework that allows ecosystem flux and thus acceptance of invasive species as part of ecosystem dynamics. The management system must allow change within an envelope of predefined limits of acceptable change but must effectively highlight points exceeding these limits. A suitable framework needs flexibility to incorporate new research and thinking in a manner that is fundamentally proactive in approach. This article elucidates the development of the Kruger National Park strategic adaptive management system, allowing for the development of a conceptual framework for exploring science and management links for invasive species management.

Additional index words: Strategic adaptive management, thresholds of potential concern.

Abbreviations: KNP, Kruger National Park; SAM, strategic adaptive management; TPC, threshold of potential concern.

INTRODUCTION

A Complex System View. New paradigms in ecology emphasize complex adaptive systems and heterogeneity at multiple temporal and spatial scales (Levin 1999; Pickett et al. 1997). Within large conservation areas, mind-set changes are required to reflect new thinking and translate them into management actions. In dynamic ecosystems where fluxes are inevitable, managers must institutionalize new paradigms, reinventing themselves through purposeful knowledge diffusion, if control programs are to be efficient in the long term (Biggs and Rogers 2003). Where previously the "balance of nature," was the focus, without explicit reference to scale, acceptance of the "flux of nature" paradigm, over multiple spatiotemporal hierarchies is now required (Bestbier et al. 2000). Management previously strived to "maintain balance" through a "command and control" approach, where adaptive management to "learn by doing" is now considered as a proactive, forward-thinking approach (Bestbier et al. 2000; Rogers 2003). However, learning by doing certainly does not simply imply trial and error management (Walters and Green 1997). Arguments demanding more data before decisions can be made are often unrealistic, the alternative being to place emphasis on what is already known, thereby providing a basis for starting.

Contrary to this, invasive species management has remained in a paradigm of command and control, as a result of a legacy of eradication programs. Managers do not consider invasive species as a part of the system and therefore are governed only by rules of control actions. However, evidence of the failure of control programs because of various reasons, as well as the increasing pressure from new invasions, forces management to consider the most deleterious species only and focus thereon. This approach implies that invasive species will need to be accepted as part of the system, maintained, however, through control programs at minimal levels, where their minimized effects will form part of the system function.

Translating Scientific Understanding into Management Practice. Cognizance certainly needs to be made

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of the fact that many institutional designs are not developed to promote an adaptive management culture and ethic (Rogers et al. 2000). Institutional design and the behavior of individuals tend to retard the process of adaptive management, preferring to rely on "tried and trusted" methods of problem solving (Rogers 2003). Ecologists frequently have a vastly better theoretical understanding of ecosystems and this is contrasted with the availability of managers' tools and resources (Rogers 2003). This aspect is clearly evidenced by the relatively well-developed understanding of vectors of invasions as well as effects thereof; however, invasions are escalating and management programs are not capable of curtailing or successfully managing the problems.

DISCUSSION

Linking Science and Management through Strategic Adaptive Management. Adaptive management is a process of managed learning which steers strategic action to achieve desired endpoints in a complex ecosystem (Biggs and Rogers 2003). Although there are many varieties of adaptive management, the version used in the Kruger National Park (KNP) is referred to as strategic adaptive management (SAM). Biggs and Rogers (2003) provide a detailed description of the development of the SAM system in the KNP, whereas Foxcroft and Richardson (2003) and Freitag-Ronaldson and Foxcroft (2003) detail the development of the invasive species aspects. Consistent throughout these frameworks are feedback loops, which provide opportunity for continuous self-assessment and revision. Developing an objectives hierarchy sets an achievable set of goals for a future desired state. The development of objectives begins with the setting of a mission statement. The highest-level objective, the mission, is a statement of strategic intent and guides the development of the detailed objectives. The higher-level objectives also reflect societal values, whereas the lower levels represent scientific endpoints compatible with the values of the higher-level statements, which translate into ground-level conservation goals. The objectives are arranged in an inverted tree, decomposing to finer objectives at the lower levels (Du Toit et al. 2003).

Thresholds of Potential Concern. A key component in the functioning of SAM is the threshold of potential concern (TPC). TPCs are those "upper and lower levels along a continuum of change in selected environmental indicators" (Biggs and Rogers 2003). They therefore provide a set of operational goals that define variability or heterogeneity of the KNP ecosystem, over multiple spatiotemporal scales (Biggs and Rogers 2003). TPCs form the basis of an inductive approach to SAM because they are invariably hypothesis of limits of acceptable change in ecosystem structure, function, and composition (Rogers 2003). They are therefore a compatible and well-articulated set of adaptive management goals and endpoints (Biggs and Rogers 2003). As such, their validity and appropriateness are always open to challenge, and they must be adaptively modified as understanding and experience of the system being managed increases (Biggs and Rogers 2003). An important aspect of the TPC is that they are preagreed goals, and thus, consensus has already been reached on possible sets of future actions, once the TPC is reached. This therefore implies that management is prevented from stalling or procrastinating at such point. When a TPC is reached or preferably when modeling predicts that it will be reached, it prompts an assessment of the causes of the extent of change (Biggs and Rogers 2003). In this manner, the exceeded TPC represents one dimension of the composite desired envelope represented by all the objectives together.

Foxcroft and Richardson (2003) documented the use of TPCs for invasive alien species in the KNP. However, since the publication of the early TPCs, further learning and refinement has taken place. The previous TPCs failed to deal sensibly with repeat invasion events, which were often no longer cause for concern (Biggs and Rogers 2003; Freitag-Ronaldson and Foxcroft 2003). The development of a multitiered layer of TPCs, closely following the invasion process provides for a more functional listing of TPCs. Level 1 TPCs deal with new invasions in the KNP or those species likely to invade in the near future. However, because it is very unlikely that a species, which may have a high propagule source close to the KNP, will be eradicated, it is counterproductive to list TPCs on a continual basis. Rather, a second and ultimately a third level of TPC are evoked, dealing with increase in distribution and then density.

The current list of TPCs is as follows: (1) TPC level 1—TPCs that deal with new invasions of a species in the KNP (a) Imminent external threat (a species on the boundary is likely to invade within 12 mo) and (b) a species being reported as having invaded the KNP for the first time; (2) TPC level 2—TPCs that deal with an increase in distribution of a species. (a) Any new grid cell not contiguous with the previous distribution, (b) expansion of contiguous grid cells that represent more than a 5% increase over the number of grid cells recorded as invaded the previous calendar year, and (c) total number of grid cells cleared vs. total number of new grid cells invaded; (3) TPC level 3—TPCs that deal with an increase in density of a species. (a) Any increase by two density classes upward in any grid cell and (b) any increase of one density class upward of medium in any grid cell.

The use of TPCs in general has facilitated a migration in focus of traditional wildlife management issues because TPCs have been raised, which highlight current biodiversity concerns (Biggs and Rogers 2003). The majority of these TPC listings have concerned the invasion of alien organisms, bringing about a change in the attitude and approach to invasive species. Invasive organisms are now regarded as one of the greatest threats to the integrity of KNP biodiversity and as a major driver of change. Furthermore, the KNP is approaching management of invasive organisms in a more sustainable manner, with stronger links to real points of concern.

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Alien Impact Objective

To anticipate, prevent entry and where feasible and/or necessary control invasive alien species in an effort to minimize the impact on, and maintain the integrity of indigenous* biodiversity

*indigenous: notion or understanding of indigenous to be developed in the regional KNP context

Note: Alien Impact objectives include all alien organisms and diseases (plants, diseases, fish, birds, insects etc.)

Preamble

The incorporation of the "Alien Impact Objectives" into the 1997 objectives was the first high level recognition of the seriousness invasive alien species in the KNP. This was a milestone in the KNP management's history and a critical step to ensuring future developments on the invasive alien species front. It has also been stated that one of the main reasons that the issues of invasive species have been embraced by management is due to the fact that invasive species were streamlined into overall KNP management, in such a manner so as to demand attention from KNP managers, and not be considered as a sideline issue.

Although stated as "alien biota" objectives, they were largely interpreted as being alien plant orientated. The current objectives have incorporated all forms of biological invasions.

The 1997 objectives were also quite far thinking in that they embodied, before widely discussed and appreciated, the wide range of issues necessary in a comprehensive invasive species plan (such as found in the Global Invasive Species Programme book: A toolkit of best prevention ad management practices). The current objectives have strived to evaluate the 1997 objectives and couple those with the emerging strategies, to provide for a more holistic and complete approach to invasive species management.

The emergence of the basic philosophy that invasive species are undesirable in a national park as filtered through most of the KNP, even to non-conservation orientated persons. This has assisted management in control in a number of develop areas (notably residences such as Skukuza). Acknowledgement of the fact that invasive species are a part of the system and will remain so has also been accepted and allowed, in certain areas, efforts to concentrate on the most damaging species only, not taking a broad and costly approach to attempting to control everything. This is embodied in the changing of one of the higher level objectives from "eradication" to "control", and acknowledges both long-term maintenance and rapid response control.

In the 1997 objectives, the "eradication", "Prohibit/discourage" and "awareness" objectives were reasonably well engaged, with the "strategic" perhaps a bit less and the "research" somewhat less (until recently however, where much energy has been placed on this), and little done on the "prevention" objective.

Alien Impact Objective

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*Indigenous: notion or understanding of indigenous to be developed in the regional KNP context

Note: Alien Impact objectives include all alien organisms and diseases (plants, diseases, fish, birds, insects etc.)

Strategy and Support Objective

To develop a long-term strategy for the management of IAS, by evaluating the current and projected future overall scale of threat, addressing organisational and infrastructural capacity, developing policy and building support for continued high level commitment

- Long-term strategy
- Contingency planning
- Assessment and priority setting
- Building support
- Policy development

Prevention Objective

To anticipate and evaluate imminent or potential risks to the KNP, as well as pathways of invasion and develop effective mechanisms to monitor, manage or mitigate these

- Identify Pathways
- Exclude, prohibit, discourage
- Early detection
- Risk assessment

Control Objective

To ensure the effective and timely development and implementation of integrated control strategies, in such a manner that both rapid response and long-term maintenance goals are met

- Implementation
- Best management practices

Research Objective

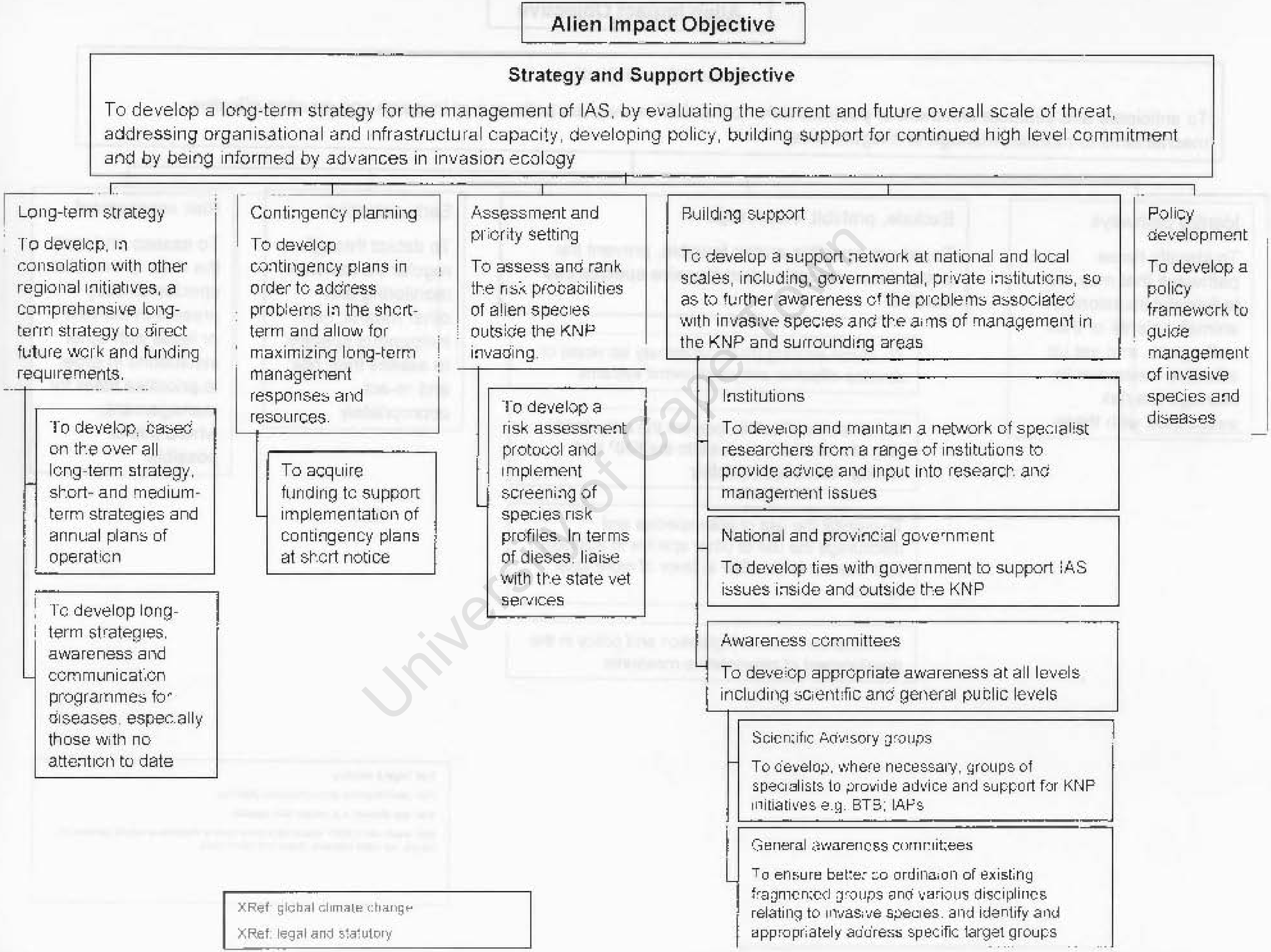
To promote and develop a coordinated research programme in order to develop a clearer understanding of the dynamics and impacts of alien species invasions

- Impacts
- Efficacy of control
- Ecology

Awareness Objective

To develop an awareness programme to inform and educate on especially the dangers and consequences of invasive alien species, in order to facilitate global invasive alien species initiatives

- Activities
- Training
- Funding



Alien Impact Objective

Strategy and Support Objective

To develop a long-term strategy for the management of IAS, by evaluating the current and future overall scale of threat, addressing organisational and infrastructural capacity, developing policy, building support for contioued high level commitment and by being informed by advances in invasion ecology

Long-term strategy

To develop, in consolation with other regional initiatives, a comprehensive long-term strategy to direct future work and funding requirements.

To develop, based on the over all long-term strategy, short- and medium-term strategies and annual plans of operation

To develop long-term strategies, awareness and communication programmes for diseases, especially those with no attention to date

Contingency planning

To develop contingency plans in order to address problems in the short-term and allow for maximizing long-term management responses and resources.

To acquire funding to support implementation of contingency plans at short notice

Assessment and priority setting

To assess and rank the risk probabilities of alien species outside the KNP invading.

To develop a risk assessment protocol and implement screening of species risk profiles. In terms of dieses: liaise with the state vet services

Building support

To develop a support network at national and local scales, including, governmental, private institutions, so as to further awareness of the problems associated with invasive species and the aims of management in the KNP and surrounding areas

Institutions

To develop and maintain a network of specialist researchers from a range of institutions to provide advice and input into research and management issues

National and provincial government

To develop ties with government to support IAS issues inside and outside the KNP

Awareness committees

To develop appropriate awareness at all levels including scientific and general public levels

Scientific Advisory groups

To develop, where necessary, groups of specialists to provide advice and support for KNP initiatives e.g. BTB; IAPs

General awareness committees

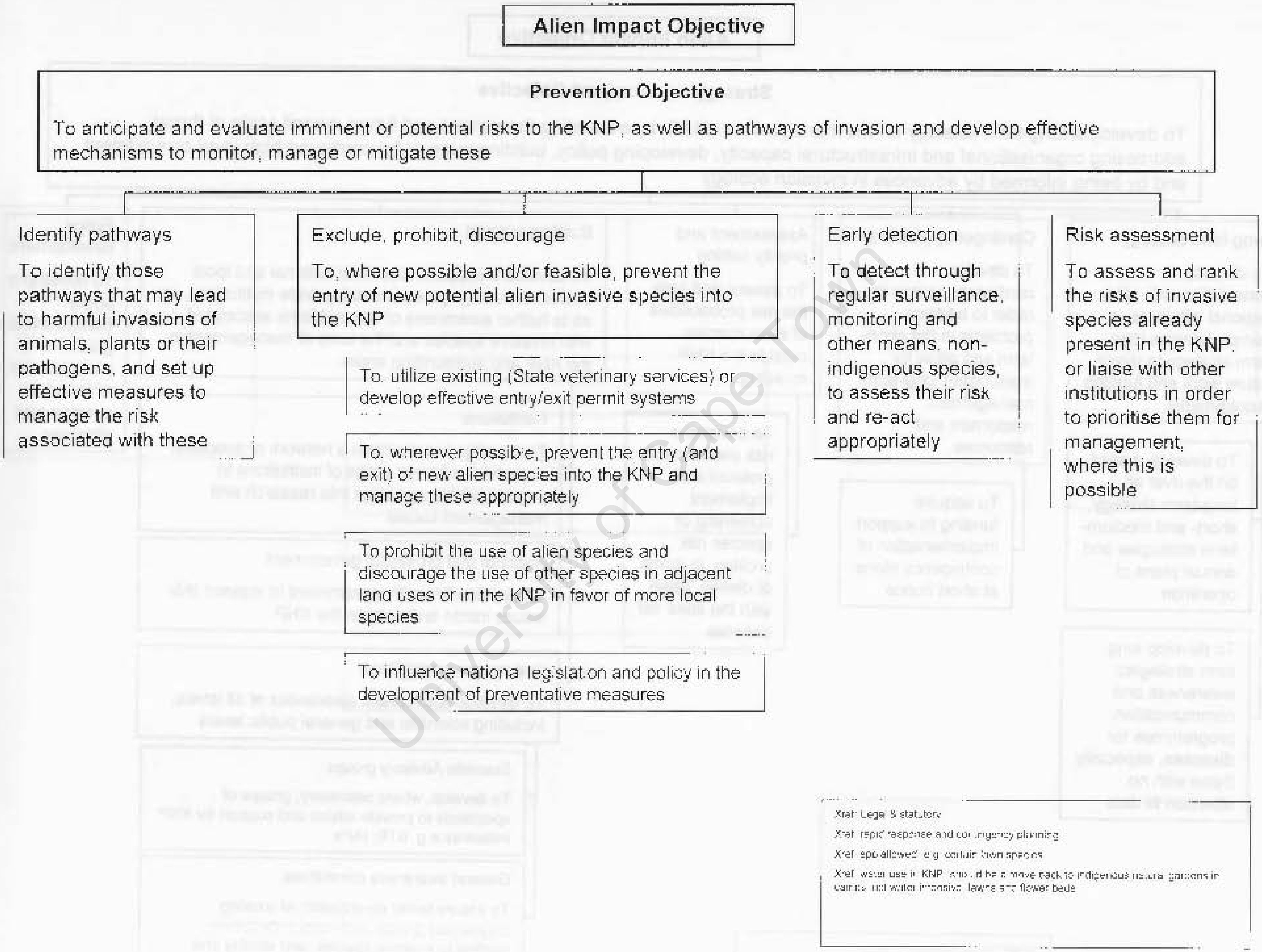
To ensure better co ordinaion of existing fragmented groups and various disciplines relating to invasive species, and identify and appropriately address specific target groups

Policy development

To develop a policy framework to guide management of invasive species and diseases

XRef: global climate change

XRef: legal and statutory



Alien Impact Objective

Prevention Objective

To anticipate and evaluate imminent or potential risks to the KNP, as well as pathways of invasion and develop effective mechanisms to monitor, manage or mitigate these

Identify pathways

To identify those pathways that may lead to harmful invasions of animals, plants or their pathogens, and set up effective measures to manage the risk associated with these

Exclude, prohibit, discourage

To, where possible and/or feasible, prevent the entry of new potential alien invasive species into the KNP

To utilize existing (State veterinary services) or develop effective entry/exit permit systems

To, wherever possible, prevent the entry (and exit) of new alien species into the KNP and manage these appropriately

To prohibit the use of alien species and discourage the use of other species in adjacent land uses or in the KNP in favor of more local species

To influence national legislation and policy in the development of preventative measures

Early detection

To detect through regular surveillance, monitoring and other means, non-indigenous species, to assess their risk and re-act appropriately

Risk assessment

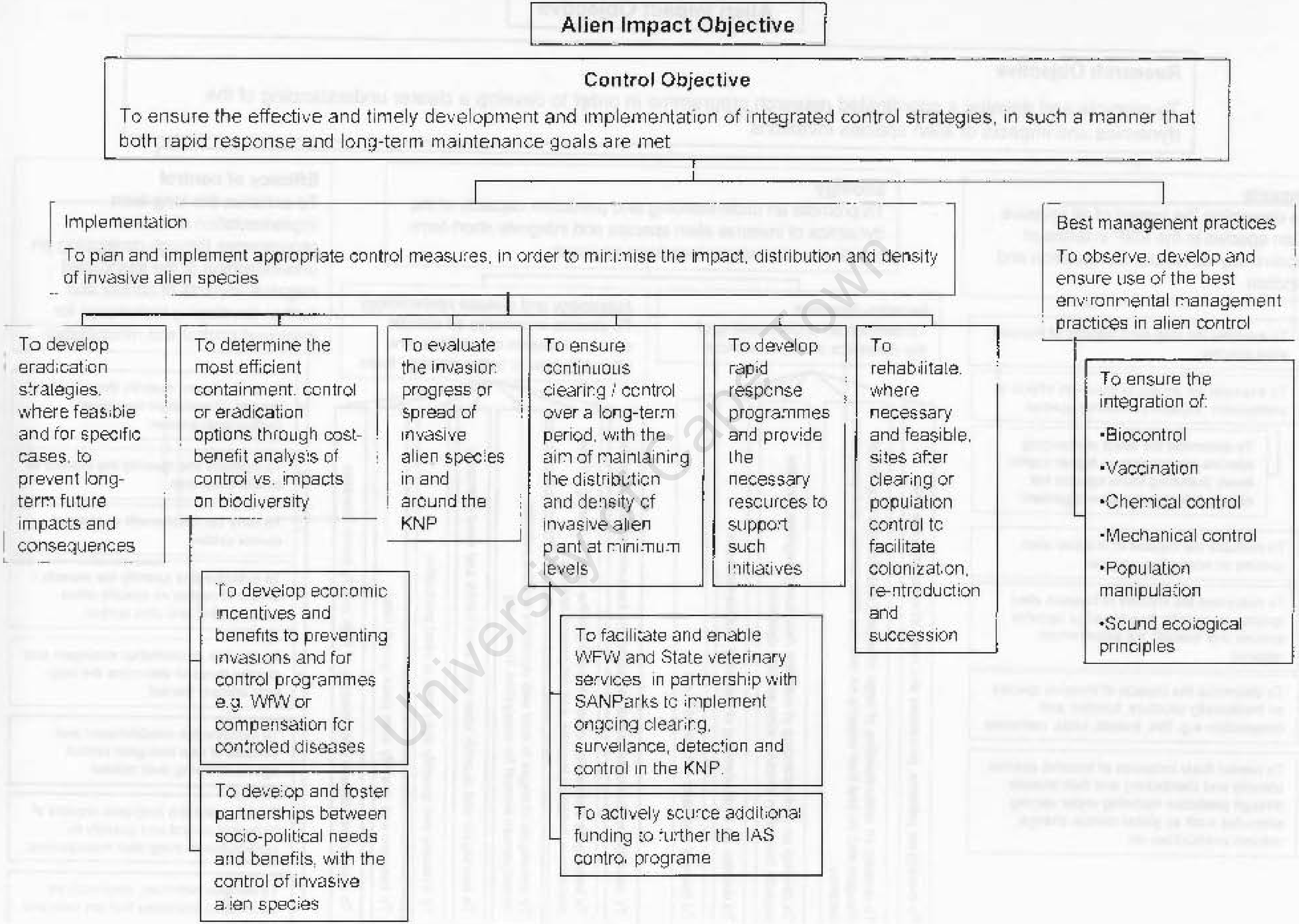
To assess and rank the risks of invasive species already present in the KNP, or liaise with other institutions in order to prioritise them for management, where this is possible

Xref: Legal & statutory

Xref: rapid response and contingency planning

Xref: spp allowed, e.g. certain town species

Xref: water use in KNP: should be a move back to indigenous natural gardens in camps, not water intensive lawns and flower beds



Alien Impact Objective

Control Objective

To ensure the effective and timely development and implementation of integrated control strategies, in such a manner that both rapid response and long-term maintenance goals are met

Implementation

To plan and implement appropriate control measures, in order to minimise the impact, distribution and density of invasive alien species

- To develop eradication strategies, where feasible and for specific cases, to prevent long-term future impacts and consequences
- To determine the most efficient containment, control or eradication options through cost-benefit analysis of control vs. impacts on biodiversity
  - To develop economic incentives and benefits to preventing invasions and for control programmes e.g. WfW or compensation for controled diseases
  - To develop and foster partnerships between socio-political needs and benefits, with the control of invasive alien species
- To evaluate the invasion progress or spread of invasive alien species in and around the KNP
- To ensure continuous clearing / control over a long-term period, with the aim of maintaining the distribution and density of invasive alien plant at minimum levels
  - To facilitate and enable WFW and State veterinary services in partnership with SANParks to implement ongoing clearing, surveilance, detection and control in the KNP.
  - To actively source additional funding to further the IAS control programe
- To develop rapid response programmes and provide the necessary resources to support such initiatives
- To rehabilitate, where necessary and feasible, sites after clearing or population control to facilitate colonization, re-introduction and succession

Best management practices

To observe, develop and ensure use of the best environmental management practices in alien control

- To ensure the integration of:
  - •Biocontrol
  - •Vaccination
  - •Chemical control
  - •Mechanical control
  - •Population manipulation
  - •Sound ecological principles

Alien Impact Objective

Research Objective

To promote and develop a coordinated research programme in order to develop a clearer understanding of the dynamics and impacts of alien species invasions

Impacts

To determine the impact of all invasive alien species in the KNP in terms of biodiversity: structure, composition and function

- To evaluate the long-term impacts of invasive alien species
- To evaluate the impact of knock-on effects of undesirable impacts of invasive species
  - To determine the effect of changing species composition on higher trophic levels (including those species not directly linked to the alien organism)
- To evaluate the impacts of invasive alien species on ecosystem services
- To determine the impacts of invasive alien species on specific threatened or valuable species and quantify the extent where required
- To determine the impacts of invasive species on biodiversity structure, function and composition e.g. fish, insects, birds, mammals
- To predict likely increases of invasive species (density and distribution) and their impacts through predictive modeling under varying scenarios such as global climate change, nutrient availabilities etc

Ecology

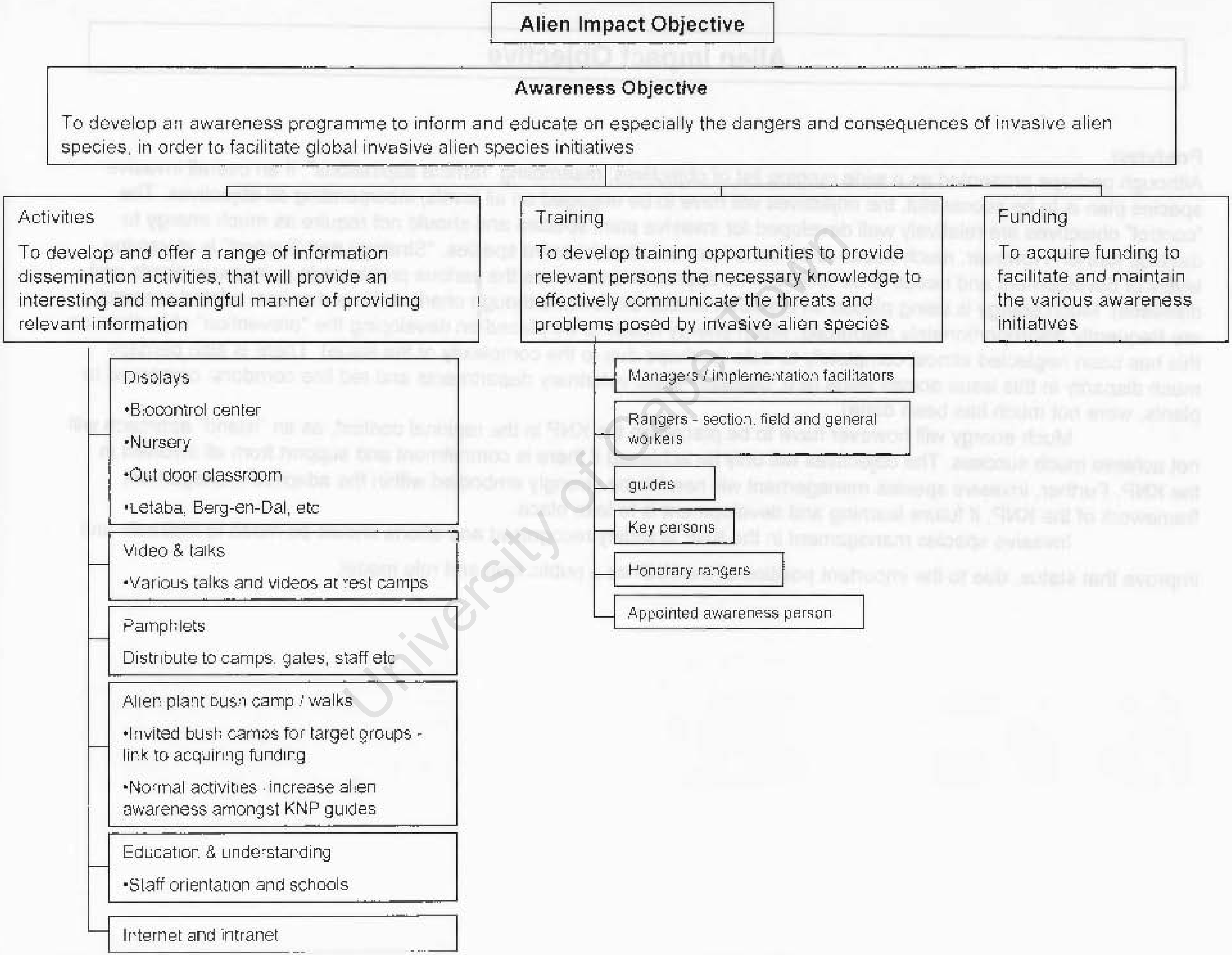
To promote an understanding and predictive capacity of the dynamics of invasive alien species and integrate short-term practical and strategic long-term research

- Invasion dynamics
  To develop an understanding of the dynamics of alien invasions
  - To investigate patterns, processes and rates of invasion in the KNP
  - To develop an understanding of large infrequent disturbances (e.g. floods, droughts etc) on and their impacts on invasive alien species and ecosystem recovery
  - To develop an understanding of modified disturbance regimes, and the impacts thereof on invasive alien species dynamics
  - To develop an understanding of dispersal and transmission
  - To develop and carry out risk analysis
- Autecology and disease epidemiology
  To develop knowledge on specific species, invasion capabilities, and ultimately how to better manage them
  - To develop an understanding of reproduction, transmission and dispersal
  - To investigate competition (and allelopathy in the case of plants) and the interactions between invasive and indigenous species
  - To investigate changes in food web dynamics and the potential consequences thereof for ecosystem functioning
  - To investigate and quantify alien plant seed banks and seed dormancy
  - To evaluate and quantify age / time to seed production
  - To evaluate and quantify alien plant growth rates
  - To understand disease epidemiology of high priority exotic diseases

Efficacy of control

To enhance the long-term implementation of control programmes through developing an understanding of the associated negative impacts of control and further developing techniques for improved control and rehabilitation

- To evaluate and quantify the potential impacts of control on non-target (indigenous) species
- To evaluate and quantify the efficacy of control measures
- To carry out cost/benefit analysis of control options
- To evaluate and quantify the impacts / effects of control on specific areas under control and after control
- To develop rehabilitation strategies and monitor these to determine the long-term efficacy thereof
- To evaluate the establishment and success of new biological control agents following their release
- To determine the long-term impacts of biological control and quantify its contribution to integrated management
- To develop detection, diagnostic and vaccination strategies that are safe and effective



Alien Impact Objective

Awareness Objective

To develop an awareness programme to inform and educate on especially the dangers and consequences of invasive alien species, in order to facilitate global invasive alien species initiatives

Activities

To develop and offer a range of information dissemination activities, that will provide an interesting and meaningful manner of providing relevant information

Training

To develop training opportunities to provide relevant persons the necessary knowledge to effectively communicate the threats and problems posed by invasive alien species

Funding

To acquire funding to facilitate and maintain the various awareness initiatives

Displays
- Biocontrol center
- Nursery
- Out door classroom
- Letaba, Berg-en-Dal, etc

Video & talks
- Various talks and videos at rest camps

Pamphlets

Distribute to camps, gates, staff etc

Alien plant bush camp / walks
- Invited bush camps for target groups - link to acquiring funding
- Normal activities - increase alien awareness amongst KNP guides

Education & understanding
- Staff orientation and schools

Internet and intranet

Managers / implementation facilitators

Rangers - section, field and general workers

guides

Key persons

Honorary rangers

Appointed awareness person

Alien Impact Objective

Postview

Although perhaps presented as a wide ranging list of objectives, resembling "remote aspirations", if an overall invasive species plan is to be successful. the objectives will have to be engaged on all levels, incorporating all objectives. The "control" objectives are relatively well developed for invasive plant species and should not require as much energy to develop further. However, much needs to be done here on other invasive species. "Strategy and Support" is at varying levels of development and needs to be unified in its approach and across the various problems (e.g. invasive plants and diseases). Much energy is being placed on research across all fronts, although charismatic and animal related research are frequently disproportionately resourced. Much energy needs to be placed on developing the "prevention" objectives as this has been neglected almost completely to date (perhaps due to the complexity of the issue). There is also perhaps much disparity in this issue across fields (e.g. disease –state veterinary departments and red line corridors- compared to plants, were not much has been done).

Much energy will however have to be placed on the KNP in the regional context, as an "island" approach will not achieve much success. The objectives will only be achieved if there is commitment and support from all involved in the KNP. Further, invasive species management will need to be strongly embodied within the adaptive management framework of the KNP, if future learning and development is to take place.

Invasive species management in the KNP is widely recognised and efforts should be made to maintain and improve that status, due to the important position of the KNP as a public icon and role model.

APPENDICES

Part 1- Management implications.

1.6: Foxcroft L.C. 2006. *Developing Thresholds of Potential Concern For Invasive Alien Species Monitoring: Hypotheses and Conceptual Understanding.* South African National Parks, Skukuza, South Africa.

APPENDICES

Part 1- Management implications.

1.7: Foxcroft L.C., Lotter W.D., Runyoro V.A. & Mattay P.M.C. 2006. A review of the importance of invasive alien plants in the Ngorongoro Conservation Area and Serengeti National Park. *African Journal of Ecology* **44**: 404–406.

DEVELOPING THRESHOLDS OF POTENTIAL CONCERN FOR INVASIVE ALIEN SPECIES MONITORING: HYPOTHESES AND CONCEPTUAL UNDERSTANDING

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Abstract

The Kruger National Park has developed and refined a system of management called Strategic Adaptive Management. This is built on the construct of the Threshold of Potential Concern (TPC). This paper describes the TPCs developed for monitoring invasive alien species. More importantly though, it describes the conceptual understanding, principles and hypotheses adopted as the foundations for setting these TPCs. In accordance with adaptive management practices, as the conceptual understanding of invasions grows and information is gained through research in the KNP and elsewhere, the TPCs will be revised.

Introduction

Thresholds of potential concern (TPCs) are similar to the term 'Limits of acceptable change' (Stankey et al. 1985). However, the TPC, as embraced and developed by the Kruger National Park (KNP) provides a closer fit to the management paradigm in use in the KNP, namely 'Strategic adaptive management' (SAM). Strategic adaptive management is simply a variation on the widely used concept of adaptive management (Biggs and Rogers 2003). However, an important philosophical departure of SAM from standard adaptive management is the focus on 'forward' or strategic thinking and assessment. Thresholds of potential concern thus form an important component of SAM, representing goals against which success of ecosystem management can be measured. Biggs and Rogers (2003) provide a succinct definition of TPCs: "those upper and lower levels, along a continuum of change in selected environmental indicators that provide the basis for decisions on the acceptability of that change". The TPC approach allows for fluctuations in the ecosystem, but highlights exceedences in ecosystem change over defined space and time scales; thereby defining the desired state of the system being managed. Thus, TPCs in effect provide an indication of whether management actions are currently, or preferably, will in future have an unacceptable biodiversity impact.

TPCs form the basis of an inductive approach to SAM, as they are invariably hypothesis of limits of acceptable change in ecosystem structure, function and composition (Rogers 2003). They are therefore a compatible and well articulated set of adaptive management goals and endpoints (Biggs and

Rogers 2003). As such their validity and appropriateness are always open to challenge, and they must be adaptively modified as understanding and experience of the system being managed increases (Biggs and Rogers 2003). An important aspect of the TPC is that they are pre-agreed goals and thus consensus as already been reached on possible sets of future actions, once the TPC is reached. This therefore implies that management is prevented from stalling or procrastinating at such point. When a TPC is reached or preferably when modelling predicts that it will be reached, it prompts an assessment of the causes of the extent of change (Biggs and Rogers 2003). In this manner, the exceeded TPC represents one dimension of the composite desired envelope represented by all the objectives together.

The invasive species TPCs, while already having undergone revision (see Biggs and Rogers 2003, Foxcroft and Richardson 2003, Freitag-Ronaldson & Foxcroft 2003, Foxcroft 2004, Foxcroft and Downey in prep,) do not yet fully incorporate biodiversity impacts. Rather, the current TPCs represent management or operational TPCs, which have loosely been termed "tracking" TPCs. These TPCs follow a conceptual understanding of the process of invasions (Richardson et al 2000) and highlight changes in distribution within and on the KNP boundary (Fig. 1). The invasion of an alien species into an area follows a general pattern, overcoming a series of barriers which impede the invasion of some species and result in a smaller subset becoming transformer weeds. Each stage in the process presents the KNP with a particular threat and suggests appropriate management actions. Therefore, this means that the TPCs are focussed on the alien species rather than on their biodiversity effects. This therefore means that the negative biodiversity impacts are implied and the presence of alien species unacceptable to the biodiversity conservation values of the organisation.

Management by objectives

The KNP management plan is arranged in a series of objectives, cascading down from the higher, coarser level objectives to the lower, on-ground level goals (Du Toit, Rogers and Biggs 2003, Foxcroft 2004a). The revised objectives provide for a holistic approach to invasive species management (KNP 2005) and include all alien species. We deliberately use the term "alien" as opposed to various synonyms such as "exotic", due to the potential confusion it creates. Alien species that actively invade are termed "invasive" and the most serious invasive species that change the character or function of the system are termed "transformers" (Richardson et al. 2000). Falling under the 'ecosystem objective', the main aim of the 'alien impact objective' is "To anticipate, prevent entry and where feasible and/or necessary control invasive alien species in an effort to minimize the impact on, and maintain the integrity of indigenous biodiversity". For the purposes of the KNP, alien species are defined as "Any species or organisms which have been introduced into, or entered the park on its own accord, from outside its borders". The implication of this would therefore be that:

1) any species from outside the boundaries of South Africa would be considered alien (except in the case of the Mozambique and Zimbabwe sections of the Trans Frontier Conservation Area (TFCA)- which is a natural extension of the KNP ecosystem),

2) any species that may be indigenous to South Africa, but not occur within the KNP ecosystem, would be considered alien to the KNP ecosystem.
3) any species within the KNP, but moved from within one particular landscape to another where it does not naturally occur, would be considered alien in that landscape.

Although the list of objectives is fully described in KNP (2005), the five main alien impact objectives are summarised here. These objectives closely follow the principles advocated by international best management practice standards (see Wittenberg and Cock 2001, 2005).

1. *Strategy and support*: To develop a long-term strategy for the management of IAS, by evaluating the current and projected future overall scale of threat, addressing organisational and infrastructural capacity, developing policy and building support for continued high level commitment.
2. *Prevention*: To anticipate and evaluate imminent or potential risks to the KNP, as well as pathways of invasion and develop effective mechanisms to monitor, manage or mitigate these.
3. *Control*: To ensure the effective and timely development and implementation of integrated control strategies, in such a manner that both rapid response and long-term maintenance goals are met.
4. *Research*: To promote and develop a coordinated research programme in order to develop a clearer understanding of the dynamics and impacts of alien species invasions.

5. *Awareness*: To develop an awareness programme to inform and educate on especially the dangers and consequences of invasive alien species, in order to facilitate global invasive alien species initiatives.

The current TPCs link directly to prevention and control, in that acceptable limits of spread are set. The research objectives cover the development of programmes to evaluate the impacts of invasions at various scales and levels.

Scientific principles for the basis of TPCs

The principle that the KNP is not an island and is substantially impacted upon by actions beyond its borders is a central tenet of understanding and managing alien species invasions (as is river management). Working in concert with this is the acceptance of the paradigm of spatial and temporal flux within the ecosystem (Pickett, Cadenasso and Benning 2003, Rogers 2003). This needs to be embraced in the context of invasions as well (Foxcroft 2004a). Although desirable, the eradication or control of all alien species is neither feasible nor practical. Thus fluxes in invasions and alien species populations must be accepted as well, although this is contrary to most alien species ideals. This means that most managers concerned with alien species would strive to eradicate or manage all alien species and suppress the populations to as close to zero as possible. We contend that this approach is not possible in the KNP, due mainly to the size of the KNP, and the number of species present. We suggest that management will be more effective by placing its resources on the most problematic species only and in the areas where they are becoming problematic. As long the species is present at below acceptable thresholds, for a determined period of time, the species should not be a management priority. Thus, the TPC system allows for the system to fluctuate, including alien species, but highlights critical 'turning points' of concern in biodiversity effects of aliens (Foxcroft 2004a).

The first invasive species TPCs (Foxcroft & Richardson 2003) provided a list of various criteria for evaluation. Experience however highlighted the need to adapt the system due to repeat exceedences of the same TPCs. In other words, the TPC system was not able to sensibly deal with repeat invasions, which were no longer cause for the same level of concern. This led to the development of multiple-level TPCs to avoid raising 'false alarms' (Foxcroft 2004a).

The basis of the principles adopted for the development of these TPCs is captured in the 'barriers' model of Richardson et al. (2000). Using this approach, the 'points of concern' are reflected as the barriers or filters to invasion, and overcoming the barrier invokes the next level TPC (Fig. 1). As a species approaches the KNP, the management response will be to prevent the introduction (point **a** in Fig. 1). This will entail, where possible, the KNP controlling the population itself, or partnering with institutions such as provincial alien clearing project (for example Working for Water) or by co-operative agreements with landowners. Once the species has invaded the KNP, the next level of TPC monitors the spread of the species, where eradication (if possible) or containment strategies are called into force (point **b**). There may however be examples where the tabling of a TPC would lead to a well considered "do nothing" option. Theoretically at least, the next level will be once all available habitat has been invaded. At this point the main concern will be the abundance of the species (point **c**). However, although a species may not have expanded its range to include the entire available habitat in the KNP, it is assumed that at a local scale, patches will have reached a density that will have some level of impact on biodiversity (composition or function) (point **d**).

Although all the TPCs are nested within the framework outlined, the following section discusses the hypotheses and theory behind each of the individual TPC criteria.

Level 1 TPCs: TPCs that deal with new invasions of a species in the KNP

- Imminent external threat (a species on the boundary, that will invade within 12 months)
- First ever record in the KNP

Principles:

1) The introduction of any new alien species is contrary to the mandate of SANParks (KNP 2005, Foxcroft 2005b).
2) The potential negative impacts of biological invasions far outweigh the risk that the alien species will be benign (for example see Mooney et al. 2005, and the numerous references therein).
3) A 12 month period of likely entry into the KNP should provide sufficient time for developing management strategies and controlling the population appropriately outside of the KNP. This should however be considered per species and adjusted accordingly where necessary. Although this is not stated as a hypothesis backed by a body of

scientific literature, this is based on experience gained by the author working in the KNP managing alien plant invasions.

Level 2 TPCs: TPCs that deal with an increase in distribution of a species (or all species combined) in the KNP, over a 12 month period.

- First ever record from a new grid cell
- Any new grid cell invaded that is not contiguous with the previous distribution
- Expansion of invasive species through contiguous grid cells which represent more than a 5% increase over the number of grid cells recorded as invaded in the reference (base) year.

Principles:

1) The early detection of new incursions of invasive species will allow timely response and potential for eradication. This principle is widely accepted (Wittenberg and Cock 2001, 2005) as a standard procedure for the successful control of invasions. Further, studies suggest that once an invasion has increased to an area of over 100ha, the chances for eradiation are minimal (Rejmanek & Pitcairn 2002). The increase of propagule pressure will at some stage reach a critical mass, at which point management will be compromised. This is based on the "long-fuse, big bang" theory, which states that although a build-up of alien species may be slow initially, this is followed by a rapid and exponential increase in the population and propagative individuals and is seldom manageable once reaching this point (Wilkinson 1995, Chapman, Le Maitre and Richardson 2001).

2) The eradication of newly formed invasion foci will increase the probability of containing the invasion at its current extent (Moody and Mack 1988). Although the criteria stated above were already determined in the first iteration, only the 'first ever record from a new grid cell was used'.
3) Although expansion and contraction of alien species is expected to occur through natural processes (the acceptance of a flux paradigm), the total area of the invasion should not be allowed to increase above a stated maximum tolerable "ceiling" level, from the base scenario. This level is currently stated as 5%, but is a guess and requires refinement.

Level 3 TPCs: TPCs that deal with an increase in density of a species (or overall alien species density) in the KNP. These TPCs are not yet operational however, due to the lack of data and efficient cost-effective monitoring options to date. They are nonetheless described hypothetically and may in future have the potential to be used as surrogates for biodiversity impacts.

- Any increase by 2 density classes or more in any grid cell
- Any increase of 1 density class upwards of "medium density" in any grid cell.

Density is currently measured in the following classes, but will be reviewed as monitoring options are evaluated:

- Rare: The species is present in the area but at very low densities with individuals being seen here and there; density = 0.01%
- Occasional: Plants are widely spaced, occurring here and there – on average more than 10 canopy covers apart; density = 0.02 – 1%

- Very Scattered: The plants average 3 - 10 canopy diameters apart; density = 1.1 - 5%
- Scattered: The plants average 1 - 3 canopy diameters apart; density = 5.1 - 25%
- Medium: There are clear and plentiful gaps between the canopies of the plants and other vegetation is still present and vigorous; plants average 0.3 - 1 canopy diameters apart; density = 25.1 - 50%
- Dense: There are small gaps between canopies and no canopy overlap and the other vegetation is still present; plants average 0.1 - 0.3 canopy diameters apart; density = 50.1 - 75%
- Closed: Plant canopies are closed, touching or overlapping and other vegetation is generally suppressed, sparse or lacking; the plants average less than 0.1 canopy diameters apart; density > 75%

Hypothesis:

1) The increase in density of invasive species will lead to an impact on indigenous biodiversity, in terms of composition, function or structure. However, this hypothesis has not been tested in the KNP and only arbitrary density values have been assigned as evaluation criteria thus far.

Future work

An important issue that will need attention in the next five years is developing an understanding of invasions in the KNP context (in terms of ecology and impacts). From this we can then refine or develop new "biodiversity impact" TPCs that either directly, or through use of appropriate surrogates, address the issue of negative biodiversity impacts. This was highlighted in the 'postview' of the objectives hierarchy as an important avenue of future research (KNP 2005). A start has been made on this through research that aims to quantify impacts on selected biodiversity indicators. This however clearly needs to be expanded to measure impacts on other ecosystem components such as ecosystem services and provisions. Useful studies have been done on the water use impacts of various land-use practices (commercial forestry using alien trees) and naturalised and invasive plant species (for examples see Versveld 1998, Le Maitre 2000, 2001). Similarly, we need to develop an understanding of the relationship between abundance, distribution and impacts on the ecosystem. Do you mean you need to develop the ability to express impacts in terms of biodiversity loss?

The idea of 'rate of change' and 'buffer capacity' TPCs has also been suggested. 'Rate of change' refers to the speed at which the system is approaching the point of ecosystem change. The concept of 'buffer capacity' should address the ability of the system to respond to the suite of potential management actions before changing to an undesirable state. This is a philosophical change in and refinement of the 'old' TPCs and requires more careful consideration and modelling approaches. For example, if we gained an understanding of the time it takes to reach an alternative state, dominated by alien species, we could model potential invasions and set TPCs according to these rates. Following control or removal of the invaders, the legacy effects, for example persistent nutrient or soil chemistry changes, would determine the buffer capacity of the ecosystem to recovering from invasion.

Conclusion

The development of TPCs for managing invasive species presents an approach to management, which is fundamentally proactive in nature. The system allows for natural ecosystem flux, but within pre-defined thresholds of acceptability. This represents a pragmatic approach to a substantial biodiversity concern over a vast area.

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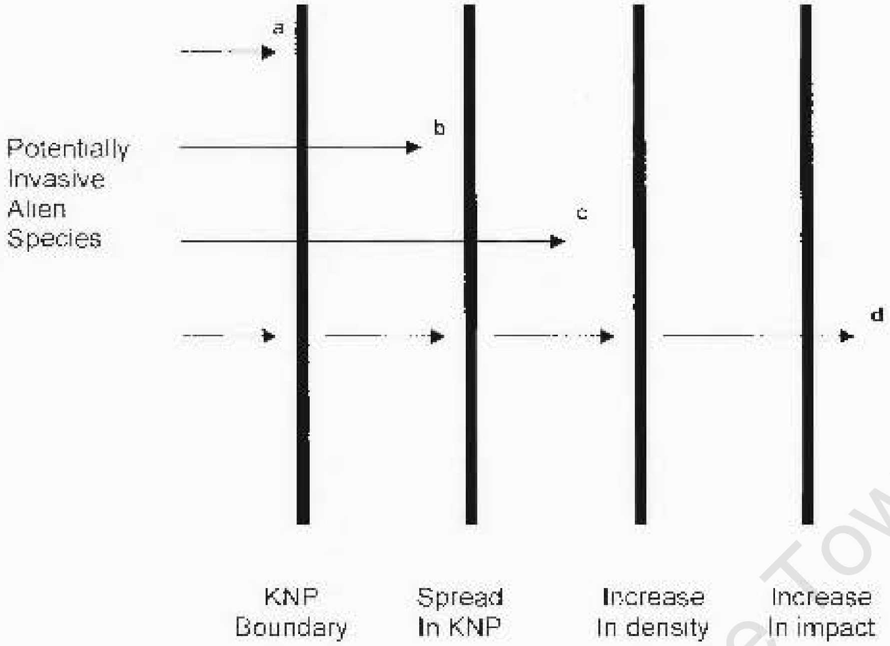

Figure 1: Model hypothesis underpinning the development of TPCs for understanding invasion process in the KNP. a) arrival of a potentially invasive alien species at the boundary of the KNP, b) invasion into the KNP, c) successful invasion into and spread within the KNP, and d) occupation of all available habitat, increase in density and increase in impacts on ecosystem services and processes. However, due to the patchy nature of species, an increase in density and impact may be observed at any scale (thus the broken arrow line) and not necessarily only once densities are high across the KNP landscape. Substantial impacts are expected at this point though. (This framework follows the model approach by Richardson et al. 2001).

Notes and records

A review of the importance of invasive alien plants in the Ngorongoro Conservation Area and Serengeti National Park

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Introduction

Regarded as the second greatest threat to global biodiversity, invasive alien species pose a real and significant threat to many of Africa's conservation areas (Cronk & Fuller, 1995). Little work has been carried out to document and mitigate the increasing threats posed by alien plants in either the Ngorongoro Conservation Area (NCA) or Serengeti National Park (SNP). The invasion by alien plant species in the NCA and SNP has not yet reached a level where control and, in the case of some species, eradication are impossible. The main focus of control in the NCA so far has been on *Datura stramonium* L. and *Argemone mexicana* L. SNP is managing large areas of *Opuntia monocantha* Haw. and *Opuntia stricta* var. *dillenii* (Ker Gawl) Haw. However, urgent attention should be paid to re-assessing the situation in both of these areas and re-setting priorities based on current knowledge. This paper provides a brief review of relevant literature and the status of invasive alien plants within the NCA and SNP and makes recommendations pertaining to management needs.

Results and discussion

Problems associated with alien plant invasions

Alien plant invasions currently affect conservation areas on every continent except Antarctica (Cronk, 1995). All ecosystems, including those in well-protected national parks are potentially invasible (McNeely *et al*., 2001). The impacts of invasive alien species frequently affect more than one aspect of an area's ecology, causing a ripple effect. These impacts include the replacement of diverse ecological systems with stands of alien plants, the alteration of soil chemistry, geomorphological processes, fire regimes and hydrology, and the extinction of indigenous fauna (Cronk & Fuller, 1995). Richardson *et al*. (1997) suggested that the destruction of riparian habitats in southern Africa is a key impact of invasive alien plants. Other impacts noted are species loss because of direct competition, reduced structural diversity, increased biomass production and disruption of the prevailing vegetation dynamics (van Wilgen & van Wyk, 1999).

Trade and travel are well-recognized pathways of accidental introductions of invasive alien plants, enabling species to overcome various geographically isolating barriers. A possible means of introduction of alien species in NCA is through the importation of construction materials, especially sand from Karatu. Alien species are frequently observed at construction sites, such as buildings and culverts (for example *D. stramonium* L. and *A. mexicana* L.). Further, intentional introductions may arise in the NCA through developing exotic gardens at the lodges and at the homes of staff and other residents. Many of these introductions took place at a time where their effects and consequences were not well known.

The main problems in the NCA and SNP

Following a survey of the invasive alien plants in and around the NCA by L. Henderson in November 2002 (Henderson, 2002). LCF conducted a further survey there and in the SNP during July 2003 and provided management recommendations for both areas (Foxcroft, 2003a,b). During September 2003, WDL participated in a Rhino management workshop (Mills *et al*., 2003), providing additional recommendations (Lotter & Foxcroft, 2003). Henderson (2002) listed 39 species in the NCA and a further eleven species in Tanzania. The main priorities for NCA include *Acacia mearsii* De Wild. (Australia), *Caesalpinia*

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*Correspondence: E-mail: llewellynf@sanparks.org *decapetala* (Roth) Alston (Asia), *Eucalyptus camaldulensis* Dehnh. (Australia) and *Lonicera japonica* Thunb. var. *halliana* Nichols (East Asia, Japan, Korea, China). In the SNP, Foxcroft (2003b) indicated the most serious invasive plant species to be *Cylindropuntia exaltata* (A. Berger) Backeb., *O. stricta* var. *Dillenii* (Ker Gawl) Haw., *O. monacantha* Haw. and *Pistia stratiotes* L.

Management recommendations

In order to maximize the benefits from management interventions and the chances of success over the long-term, a strategic plan is required to ensure resources are deployed as wisely as possible. It is frequently recorded that much energy and effort is expended on the techniques of controlling and removing invasive plants, while little attention is paid to the strategic planning of control operations and use of resources (Moody & Mack, 1988). Typically, emphasis is placed almost solely on logistical planning and a fixed amount of funding is provided on an annual basis, with as much work being carried out as possible – until the money runs out. Such an approach is not conducive to sustainable control programmes, which maximize return on investment. Rather, the extent of the problem and the costs and logistics involved need to be known. Thereafter, careful planning can be carried out and finally, the funding sought to implement this plan. In this manner, if the funding is insufficient, additional funds can be added later to ensure all the necessary results are achieved.

It is suggested that priorities are set by grouping the alien species according to the following four characteristics (McNeely *et al.*, 2001):

- the current extent of the species in or near the area;
- current and potential impacts of the species;
- the value of the habitats that the species has or may invade and
- the difficulty of control.

The following are recommended.

Alien species management objectives should be set, which are in line with the broader conservation objectives of the NCA and the SNP. An early detection and monitoring programme should be developed and implemented. Regular surveys need to be conducted of known infestations and key areas or habitats should be monitored. The introduction of known and potentially invasive alien species should be prohibited and existing ones phased out. Simultaneously, educational awareness programmes should be instituted to curb further introductions and should cover NCA staff, members of other institutions and the resident communities. Following the confirmation of management priorities the implementation of control actions should be integrated, where possible, with existing management programmes such as controlled burning, to complement weed treatment efforts. Comprehensive alien plant management plans should be compiled for both the NCA and SNP, with external expert help if necessary, and with a special funding proposal if available budgets are limiting. Biological control options should be investigated, in collaboration with appropriate institutions, especially for highly invasive species in areas in close proximity to the SNP and the NCA. Appropriate research should be conducted to allow for and inform management.

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APPENDICES

Part 1- Management implications.

1.8: Foxcroft L.C. & Downey P.O. 2007. Protecting Biodiversity by Managing Alien Plants in National Parks: Perspectives from South Africa and Australia. In: *Plant Invasions: human perception, ecological impacts and management* (eds. B. Tokarska-Guzik, J. Brock, G. Brundu, L. Child, C. Dachler, P. Pyšek), pp. 391-407. Backhuys Publishers, Leiden, The Netherlands. In press.

APPENDICES

Part 1- Management implications.

1.9: Foxcroft L.C. & Freitag-Ronaldson S. 2007. Seven decades of institutional learning: managing alien plant invasions in the Kruger National Park, South Africa. *Oryx* **41**: 160–167.

Protecting Biodiversity by Managing Alien Plants in National Parks: Perspectives From South Africa and Australia

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Abstract

Conservation of biodiversity, in all its facets and fluxes, is the primary motivation for the development of protected areas. However, designating land as a protected area does not necessarily result in the conservation of biodiversity, as a range of threats to biodiversity may still be active. For example, invasive alien plants pose a significant threat to biodiversity composition, structure and function, irrespective of protected area status. Thus the threat of invasive species to biodiversity needs be addressed as part of a holistic conservation strategy for any protected area. Such a holistic approach must not only consider the invasive species within such areas, but also those species that transcend park boundaries. Here we describe the approaches developed by two organisations that manage protected areas, namely, South Africa's Kruger National Park and the National Parks of New South Wales Australia, and detail their progress towards the management of invasive alien plants for conservation. The key components of the various management frameworks are presented here to illustrate how each has independently addressed the problem of alien plant management and how components from each could be used collectively.

Introduction

While major periods of biodiversity loss have occurred previously, for example the five great extinction events between 500 and 65 million years ago, the current rate of loss is substantially higher (Wilson 1992). Human actions have accelerated the loss of species (Wilson 1992) and are therefore a major contributor to the decline in global biodiversity (WRI *et al.* 1992). Several major human-mediated causes have been identified, namely habitat destruction (loss and fragmentation) and accelerated introductions of alien species (WRI *et al.* 1992, IUCN 2005). Predictions of impacts are dire, especially when the wider impacts (e.g. alteration of soil nutrients,

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atmospheric CO_2 and alteration of disturbance regimes) are incorporated (Tilman & Lehman 2001).

One approach to biodiversity protection is to designate land as a protected area (e.g. National Parks). While the selection of such areas is typically based on the biodiversity value they contain, not all biomes are evenly represented. For example, the native grasslands in Australia (Kirkpatrick 1995) and the succulent Karoo, grasslands and fynbos lowlands of South Africa (Driver *et al.* 2005) are under-represented, while savanna systems are generally over-represented. Irrespective of the selection process, such designations do not guarantee biodiversity protection, as the processes that threaten biodiversity are often still present. Of these, invasive alien species pose a substantial threat (Mooney *et al.* 2005). Encompassing all taxonomic groups, e.g. viruses, fungi, algae, mosses, ferns, higher plants, invertebrates, fish, amphibians, reptiles, birds and mammals (Bright 1995), and with all landscapes being potentially invasible (Lonsdale 1999), the management of alien species for biodiversity conservation presents a range of challenges.

A vast wealth of knowledge has been accumulated in the field of alien species management since the SCOPE (Scientific Committee on Problems in the Environment) programme of the 1980s (Drake *et al.* 1989) asked the questions: which species invade; which habitats are invaded, and how can we manage invasions? However, the number of alien species on all continents continues to increase. In many cases this increase has been much faster than historical invasion patterns (di Castri 1989, Reichard & Hamilton 1997, Groves & Hosking 1998). Such increases place further demands on already limited resources, outpace research, and in many cases limit control options. In addition, many alien species introductions are irreversible, with eradication only feasible for new invasions (Rejmánek 2001) or under special circumstances (Myers *et al.* 2000). While there have been several successful eradication programs carried out on islands (Veitch & Clout 2002), few such successes have occurred on continents or for widespread alien species.

If the invasion of alien species cannot be halted or established invasions eradicated, then we need to understand how to limit their spread, proliferation and impacts on invaded ecosystems. Such knowledge is needed to further develop management strategies and monitoring protocols for protected areas, which are often the last bastion for native species or populations.

This chapter focuses on the management of alien plants for the protection of indigenous biodiversity within protected areas. Despite the management of alien plants in protected areas being a global need, few details have been published on the comparative approaches of different management structures; here we present both an Australian and South African perspective. South Africa and New South Wales (NSW) Australia share a similar climate and cover similar topography (e.g. coastline, temperate rangelands and semi-arid regions). Further, they have many of the same invasive alien plants (e.g. *Lantana camara* L.), as well as alien plant species that are native to the other country (e.g. the South African plant *Chrysanthemoides monilifera* subsp. *rotundata* (DC.) T. Norl. and the Australian alien plant *Acacia cyclops* A.Cunn. ex G.Don).

While we present two different management approaches, we do not believe that the scale of the organisations (one large park, Kruger National Park (KNP) vs. many smaller parks, NSW; Fig. 1), or the different economies and cultures of the countries, prevents generalization across systems. The management frameworks and strategies presented are generic and many of the components can be tailored for more specific situations.

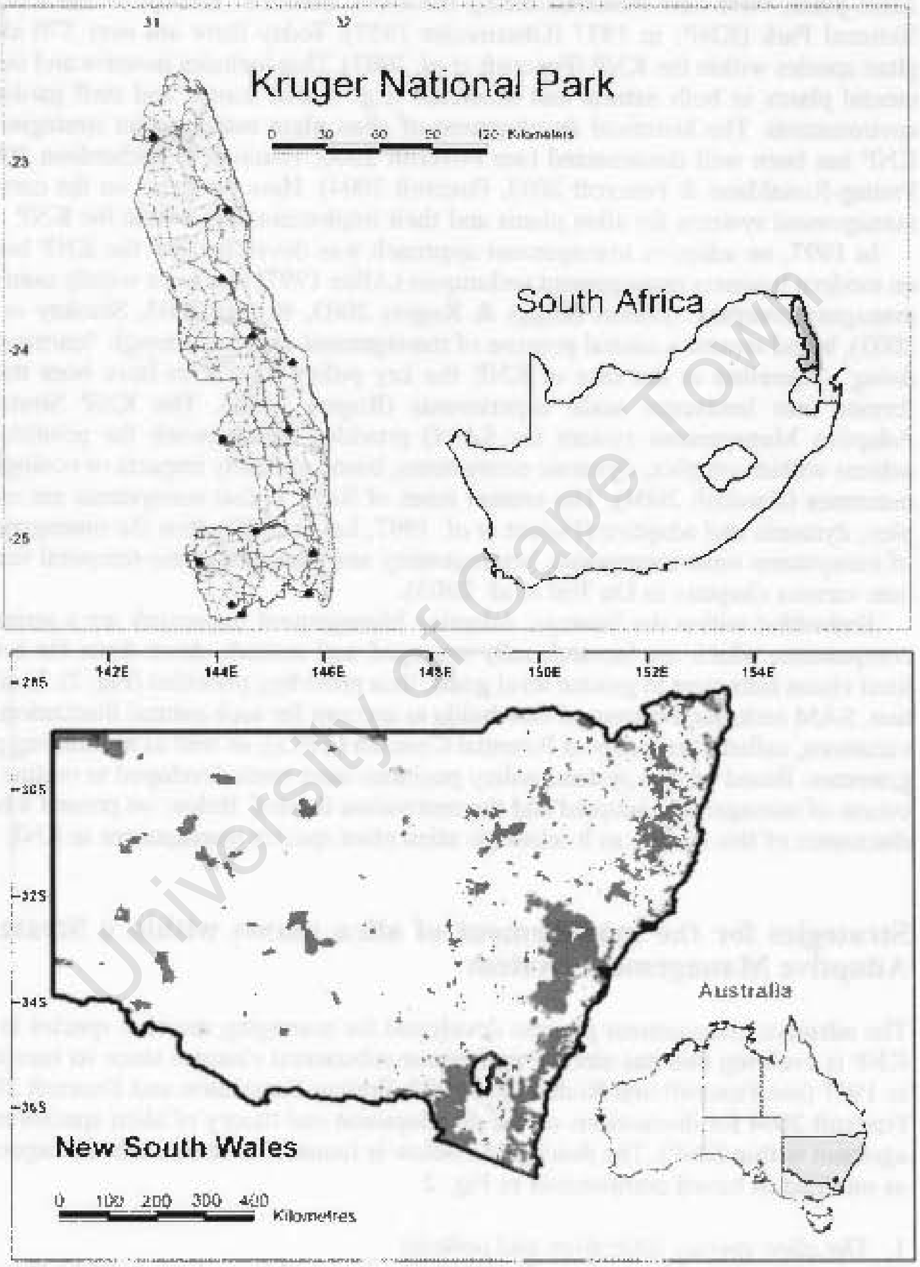

Fig. 1. (a) A map of Kruger National Park, in relation to the rest of South Africa, and (b) National Parks within New South Wales, Australia.

Managing alien plants within the Kruger National Park, South Africa

Alien plants were first recorded during the initial botanical surveys of the Kruger National Park (KNP) in 1937 (Obermeijer 1937). Today there are over 370 alien plant species within the KNP (Foxcroft *et al.* 2003). This includes invasive and ornamental plants in both natural and modified (e.g. tourist camps and staff gardens) environments. The historical development of alien plant management strategies in KNP has been well documented (see Foxcroft 2000, Foxcroft & Richardson 2003, Freitag-Ronaldson & Foxcroft 2003, Foxcroft 2004). Here we focus on the current management systems for alien plants and their implementation within the KNP.

In 1997, an adaptive management approach was developed for the KNP based on modern business management techniques (Allee 1997) that were widely used for managing complex systems (Biggs & Rogers 2003, Rogers 2003, Stankey *et al.* 2003), based around a central premise of management directed through 'learning by doing'. Therefore in the case of KNP, the key policy objectives have been transformed into landscape scale experiments (Rogers 2003). The KNP Strategic Adaptive Management system (or SAM) provides a framework for prioritising actions within complex, dynamic ecosystems, based on likely impacts or ecological outcomes (Foxcroft 2004). The central tenet of SAM is that ecosystems are complex, dynamic and adaptive (Pickett *et al.* 1997, Levin 1999), thus the management of ecosystems must incorporate heterogeneity and multiple spatio-temporal scales (see various chapters in Du Toit *et al.* 2003).

Embedded within the Strategic Adaptive Management framework are a series of components, which are hierarchically arranged and cascade down from the broad level vision statement to ground level goals, thus providing priorities (Fig. 2). In addition, SAM includes a system of thresholds to account for such natural fluctuations or variations, called Thresholds of Potential Concern (TPCs), as well as monitoring programmes. Based on this system, policy positions have been developed to outline the course of management adopted and the motivation thereof. Below we present a brief discussion of this system as it relates to alien plant species management in KNP.

Strategies for the management of alien plants within a Strategic Adaptive Management System

The adaptive management process developed for managing invasive species in the KNP is evolving and has already undergone substantial changes since its inception in 1997 (see Foxcroft and Richardson 2003, Freitag-Ronaldson and Foxcroft 2003, Foxcroft 2004 for discussions on the development and theory of alien species management within KNP). The description below is focused on the current management as outlined in boxed components in Fig. 2.

1. *The alien species objectives and policies*

The management objectives of the KNP are arranged in an inverted tree (Fig. 3), with a value laden vision statement at the top and technically orientated specific goals lower down. While this provides direction for the organisation, specifics are

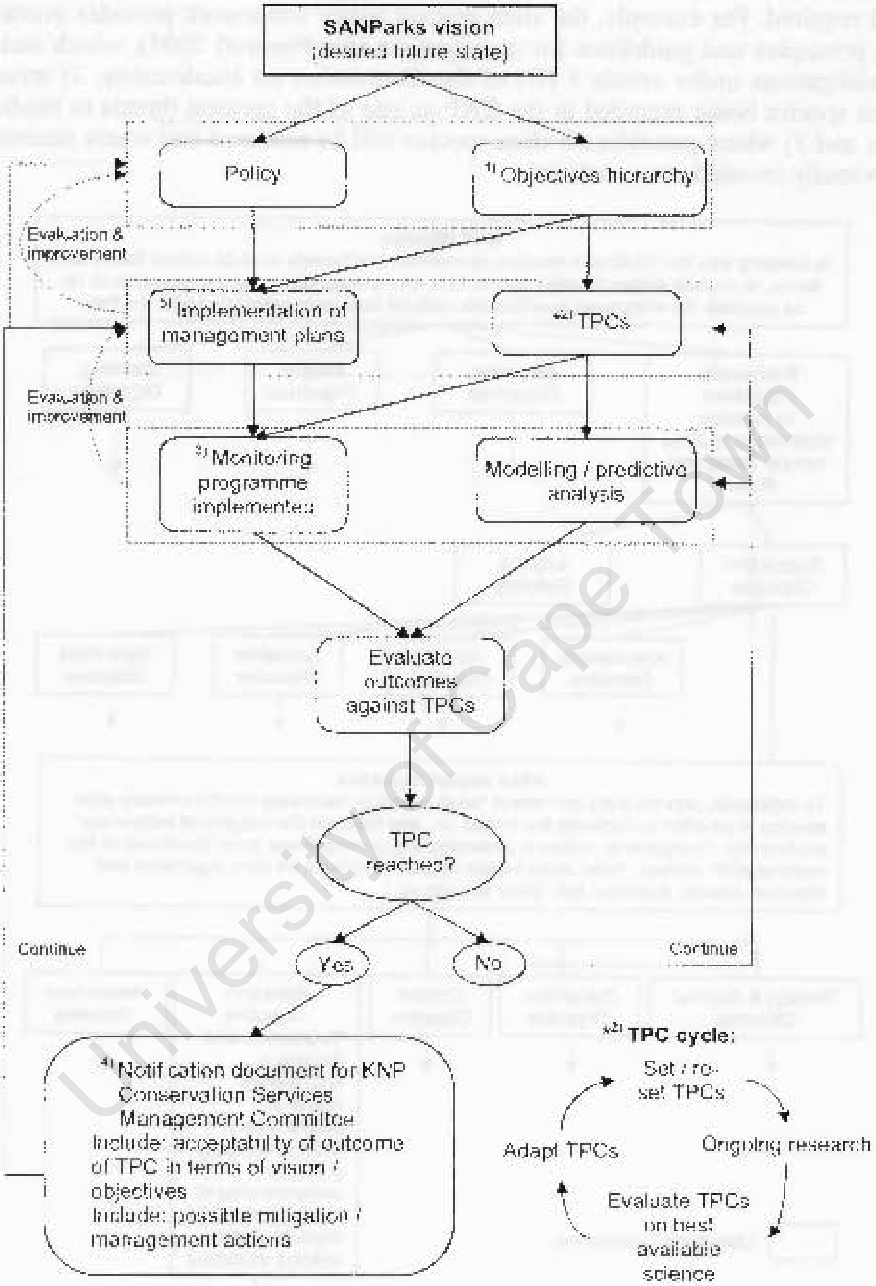

Fig. 2. The Strategic adaptive management system and component linkages, as used in the KNP. The framework contextualises the various components of the cycle, namely: 1) The KNP objectives hierarchy and policy, 2) Thresholds of Potential Concern, 3) Monitoring Programmes, 4) Responding to a TPC breach, and 5) Implementation of management action. The insert (*2) describes the TPC development, implementation and revision cycle within the broader SAM framework.

still required. For example, the alien species policy framework provides overarching principles and guidelines for management (see Foxcroft 2005), which include 1) obligations under article 8 (H) of the Convention on Biodiversity, 2) invasive alien species being regarded in the KNP as one of the greatest threats to biodiversity, and 3) where possible, all alien species will be removed and where necessary, previously invaded areas restored.

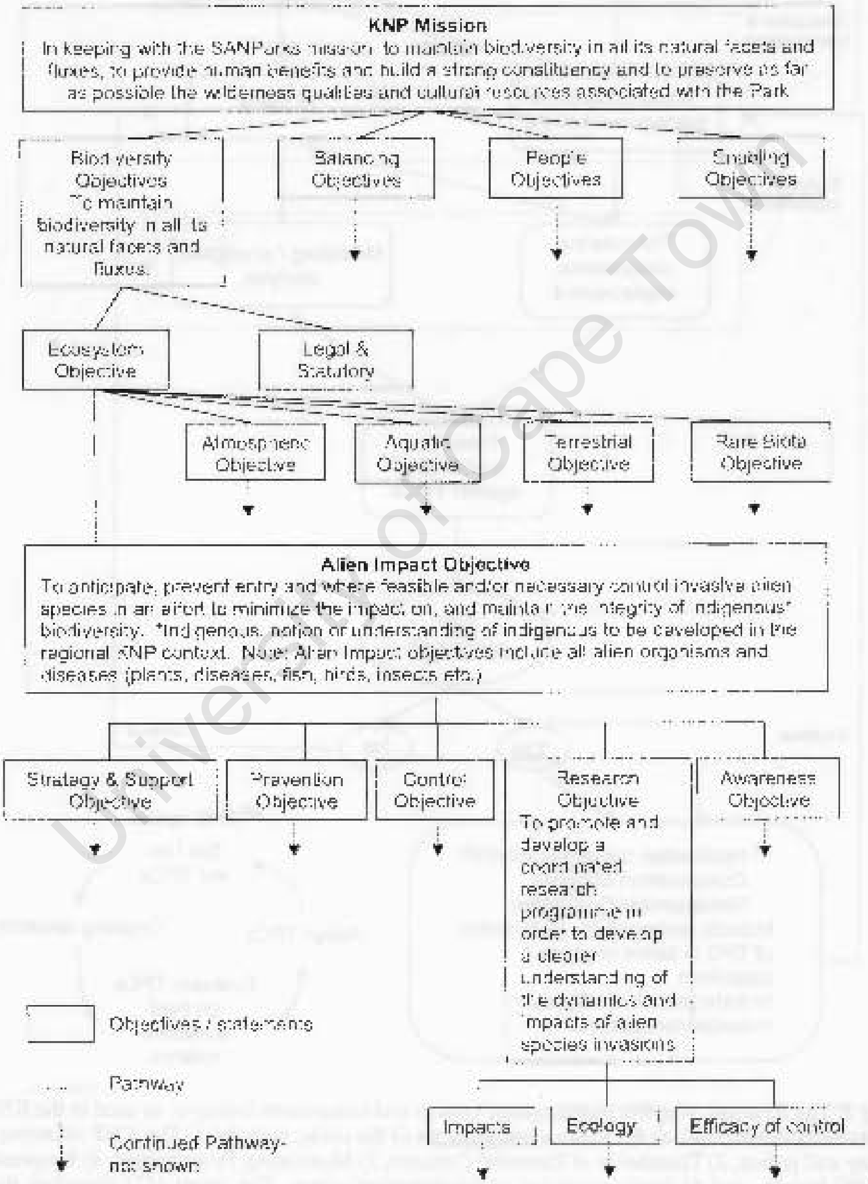

Fig. 3. A sample of the structure and wording of the invasive species component of the KNP objectives hierarchy.

2. Thresholds of Potential Concern (TPCs)

'Natural' variation or fluctuations are allowed to occur within a pre-determined upper and lower limit (in space and time). These limits or TPCs represent endpoints in a continuum of change, at which point active management is required (Biggs & Rogers 2003). In many instances the data to support these thresholds are limited and the TPCs are articulated as hypotheses, requiring testing and refinement (Biggs & Rogers 2003, Foxcroft 2004). Regular monitoring is required to establish if a TPC has been surpassed or breached. Once breached, an assessment is made as to the most appropriate intervention. Currently 20 TPCs have been developed for the major decision areas, including water flow and quality, fire and alien species. There are however, no lower thresholds for alien species, as alien species are a continued source of concern.

The invasive alien species TPCs are divided into three distinct management responses, relating to the invasion process or pathway. The First TPC targets new invasions or incursions within the KNP, as preventing new incursions will protect biodiversity from future any threats. This TPC is breached by either an imminent external threat (i.e. a species outside KNP, that has the potential to invade within 12 months), or the first occurrence of an alien species within the KNP. This TPC is based on the policy position that, 1) new alien species invasions contravene the SANParks mandate (Foxcroft 2005), 2) potential impacts far outweigh the risk of an alien species being benign (e.g. Mooney *et al.* 2005, and references therein), 3) the possibility of eradication is decreased with an increase in foci or population size (Rejmánek & Pitcairn 2002), 4) early intervention is cost effective (Rejmánek and Pitcairn 2002), and 5) a 12 month timeframe provides sufficient time to develop management strategies.

The second TPC targets increases in the distribution of an alien species already within the KNP, as such increases are likely to result in a range of negative impacts to biodiversity. By dividing the Park into grid cells (the size of which is currently being explored) that are routinely searched, changes in the distribution of alien species can be detected. A breach occurs when an alien species already present in KNP is recorded in a new cell and the new record is not in a cell adjoining the species' current distribution, or new cells represent a greater than 5% increase in the number of cells occupied previously, despite active intervention. This TPC is based on: 1) the ability to detect the spread of alien species early is crucial for effective management (Wittenberg & Cock 2001, 2005), e.g. once an invasion covers an area of 100ha, the chances for eradiation are minimal (Rejmánek & Pitcairn 2002), 2) while very few alien species that naturalize become invasive (see Williamson 1996), those that do often experience lag periods as a result of biotic barriers (Mack 1996). Some alien species overcome such lags as a result of propagule pressure, whereby a critical threshold in population size is reached (Sullivan *et al.* 2004). This point is followed by an exponential increase in the population which is seldom manageable (Wilkinson 1995, Chapman *et al.* 2001), and 3) the eradication of newly formed foci will increase the probability of containing the invasion at its current extent (Moody & Mack 1988).

The third TPC targets increases in the density of an alien species in the KNP. This TPC is stated as a hypothesis, as it is not yet operational, due in part to the lack of data on acceptable thresholds relating to density related impacts and the availability of efficient cost-effective monitoring protocols to detect such thresholds. Irrespective, this TPC will use a range of defined densities (being scattered, low, medium, and high) to determine breaches, as any increase in density of an alien plant can be used as a surrogate measure for an increase in biodiversity impacts. A TPC breach occurs when an alien plant species increases its density by two density classes or more in any cell (i.e. from scattered to medium density), or increases from medium density in any cell. This TPC is based on the assumption that increased density is likely to 1) have negative impacts on indigenous biodiversity, 2) be a reflection of a potential rapid expansion event, 3) require increased management, and 4) high densities are more likely to result in changes to ecosystem function and services (e.g. altered disturbance regimes; Mack & D'Antonio 1998).

A KNP review of the TPC process showed that breaches of the invasive species TPCs occurred more frequently than for any other management concern (26 of the 32 breached TPCs examined), highlighting the threat alien species posed to protected areas, which has enabled KNP management to gain a better appreciation of the problem.

3. *Monitoring and evaluating TPCs*

For the TPC process to function effectively, a monitoring system is required that allows data collection which is consistent with the reporting requirements of each TPC, through and within suitable monitoring timeframes (e.g. grid cells) or intervals. For example, certain TPCs may require annual data collection, while others may only need five year intervals, as changes in these systems are gradual, thereby preventing unnecessary monitoring.

4. *Responding to a TPC breach*

When a TPC is breached or preferably when modelling predicts that it will be breached, a notification plan is prepared detailing the nature of the TPC, predicted consequences of the breach, and the recommended actions required to reverse the breach. For example, the alien plant *Acacia decurrens* (Wendl.) Willd., a large tree, was recorded just outside the KNP boundary on the Sabie River and thus breached the first TPC. As this population consisted of a few individuals, a rapid response action was recommended and immediate eradication was initiated. In another example, the alien plant *Parthenium hysterophorus* L., an annual herb, increased its distribution in KNP from the currently mapped and managed area, and thus breached the second TPC. The recommended action was to immediately re-survey its extent within KNP. The survey revealed that *P. hysterophorus* was widespread and thus was not a suitable candidate for eradication. Subsequently the species was referred to the Working for Water Programme (see below) to control and manage all the known populations within KNP.

5. *Controlling alien plants within KNP*

The South African National Working for Water Programme (WFW) is one of the largest alien plant control initiatives to be undertaken, worldwide (van Wilgen 2004). Established in 1995, the Programme's aim is to control alien plants in watersheds to restore water flows, while creating employment for a large number of South Africa's unemployed. The people employed in this programme are given training both in the control of alien plants and their impacts as well as other life skills. The enormous benefit of the Programme is clearly evident in many areas of South Africa (van Wilgen 2004).

Working for Water provides approximately R20-30 million (approximately 2,7 4 million Euro) per annum to SANParks for the control of invasive alien plants across all 20 national parks in South Africa. A special unit within SANParks implements the WFW programme nationally. The annual funding provided to the KNP averages R5 million (675,000 Euro) per annum, which employs up to 500 people and has seen many of the rivers, e.g. the Sabie River, which were previously heavily invaded by alien plants, now at a maintenance level (i.e. where resource requirements are limited and the impact on the ecosystem is assumed to be negligible).

6. *Development of an alien species research programme within KNP*

The lack of a co-ordinated research programme for biological invasions in the KNP has been considered a shortcoming in the management of the Park (Foxcroft & Freitag-Ronaldson 2004). It is unlikely that all of the alien species that presently occur in the KNP will be eradicated or even controlled, and thus some are likely to become part of the landscape. A challenge therefore is to be able to identify and predict the negative impacts of alien species invasions, in particular changes in ecosystem functions and the flow-on effects of such changes (i.e. altered fire regimes, see Mack & D'Antonio (1998) and Gordon (1998) for further discussion).

A research priority framework for alien species has been developed which focuses on three focal research areas: 1) impacts (to biodiversity structure, composition and function), 2) ecology of invasions (i.e. to develop a predictive capacity of the dynamics of alien species based on their ecology), and 3) efficacy of control (i.e. to develop more effective and efficient controls, which minimise non-target impacts and lead to long-term rehabilitation of invaded sites). These research areas will also help to provide information for refining and developing future TPCs.

Managing alien plants within the New South Wales Park system

In New South Wales (NSW), there are over 600 protected areas encompassing 6.5 million ha of land, all of which are managed by the Parks and Wildlife Division (PWD) of the NSW Department of Environment and Conservation (Fig. 1). While the PWD does not have an adaptive management system like that used in the KNP or a system of TPCs, it is in the process of developing a park policy framework, which outlines all management areas, both biological and non-biological (e.g. assets). When it comes to managing alien plant species, this draft framework outlines a combination of site- and species-led management. Site-led management is based on controlling alien plants at sites of high conservation value (e.g. World Heritage areas), while species-led management is based on programs for a specific alien plant (e.g. *C. monilifera* subsp. *rotundata*, or where control is species-specific e.g. biological control). The underlying decisions on when to use each are determined by seven key management objectives (not in any order of priority), being 1) biodiversity conservation, 2) community/neighbour relations, where there is direct benefit from working with external partners to prevent or limit spread between protected areas and surrounding lands (e.g. see Dennis 2002), 3) asset management (e.g. cultural heritage values), 4) infrastructure management (e.g. controlling alien plants around picnic areas, camping grounds, walking tracks, and roads), 5) fostering research aimed at improved management and, 6) delivering broader strategic outcomes (e.g. actions in strategies like the National *C. monilifera* Strategy (ARMCANZ *et al.* 2000) or the *C. monilifera* Threat Abatement Plan (DEC 2006), and 7) alien plants which have potential impacts on human health. In addition, the management of alien plants in NSW may also be governed by legislation (e.g. NSW *Noxious Weeds Act 1993*).

There are more than 1380 naturalized alien plant species in NSW (Coutts-Smith & Downey 2006), 300 of which are considered to be invaders of natural ecosystems (Downey *et al.* in press) and thus are of concern for protected areas management. Given the large number of invasive alien plants and reserves, the management of alien plants is divided into two components, namely, 1) a centralized pest management unit, responsible for state-wide programs and policy, and 2) regional and local on-ground operations co-ordinated through regional pest management strategies and dedicated pest management officers.

While the TPC system has not been used in NSW, the invasion pathways the TPCs are based around have been addressed in a less formally conceptualized manner, through a co-operative governance approach. For example, the NSW Department of Primary Industries assesses new incursions (i.e. first TPC) across the state, and determines the course of management to be undertaken by other stakeholders in accordance with the NSW *Noxious Weeds Act 1993*. This system is not specifically aimed at protected areas, but rather the state as a whole. The regional pest management strategies in part encompasses the system described in the first and second TPC for KNP, by identifying new incursions that have the potential to impact on park values. The third TPC is not addressed however, as the NSW system has moved away from an assumption based approach, to measuring impacts on biodiversity (i.e. increase in density) to an actual impact measure (i.e. the biodiversity at risk), especially for wide-spread species (see below).

1. *State-wide management*

The focus for alien species management at a state-wide level in protected areas within NSW is currently directed through the Threat Abatement Planning (TAP) process for widespread species (see Downey 2003, Downey & Leys 2004). This process requires prioritization of alien plants for management, an understanding of their impact on biodiversity, as well as information on the best practice management (see below for further discussion).

2. *Regional management*

As resources (e.g. monetary and in-kind) are insufficient to control all alien species in all parks, a series of regional pest management strategies have been developed, which establish priorities and direct resources to areas where expected outcomes are the greatest (e.g. NPWS 2002, 2004). These regional strategies are currently being revised using an improved set of criteria, encompassing 12 management areas divided into four prioritized categories (low to very high). The management areas include biodiversity conservation, human health, new incursions, neighbour relations, cultural heritage, world heritage areas, recreation and aesthetic values, community backed programs, co-operative programs, community education, previous programs, and opportunistic events (e.g. after wildfires).

Developing a strategy for managing alien plant impacts on biodiversity

In a mini-review of alien plant management in Australia, Downey (this volume) argues that impacts on biodiversity are not adequately addressed, with the exception of some recent work by the PWD for widespread species. This work has led to a three stage assessment system, being the identification of 1) the alien plant species posing the greatest risk to biodiversity, 2) the biodiversity at risk from alien plants, and 3) an effective management strategy for alien plant species that pose the greatest threat to biodiversity – each of which is outlined briefly below.

1. *Identifying the alien plant species posing the greatest risk to biodiversity*
Of the 2800 naturalized plants in Australia (Groves *et al.* 2003), about half occur in NSW (see Coutts-Smith & Downey 2006). Of these, many do not pose a threat to Protected Areas as they are, for example, agricultural invaders. An assessment of the alien plant species that are naturalized in NSW was developed to determine the potential impact of naturalized alien plant to biodiversity. This assessment of the 1380 naturalized alien plants within NSW reduced this number to 300 species, by excluding all alien plants that only posed a threat in agricultural, wastelands and urban (e.g. roadsides) situations, and then all those species that were considered to be naturalized but not a threat or unlikely to pose a serious threat in the future were eliminated, using the categories outlined in Groves *et al.* (2003). These 300 species were ranked using a model which assessed current and potential distribution, the types and diversity of ecological communities invaded and the way in which biodiversity was impacted (e.g. ecosystem function, and ability to affect an entire community). This was then weighted against the total biodiversity present on a regional basis (see Downey *et al.* in press). The model predicted that approximately 90 alien plants posed significant concern for biodiversity conservation, suggesting that management strategies for protected areas should be focused on these alien species in the first instance. It must be noted that for many of these alien plant species some form of control currently occurs.

2. *Determining the biodiversity at risk from alien plants*
One of the primary objectives for managing protected areas is to ensure that the values contained within such areas are not eroded. While the major causes of biodiversity decline have been identified (see WRI *et al.* 1992), little has been done to determine the native biodiversity that is at risk (Downey this volume). Given that protected areas address the main cause of biodiversity decline, e.g. habitat destruction, biodiversity conservation in such areas must address the next major cause, being invasive alien species.

Historically, attempts to determine the impacts of alien species to native biodiversity have been either through specific scientific investigation (e.g. Weiss &

Noble 1984, French & Zubovic 1997, Vranjic *et al.* 2000), or reviews of such studies (e.g. Grice *et al.* 2004, Vidler 2004). However, a more comprehensive assessment is needed, that encompasses a broad range of biodiversity and a range of alien plant species. Recent work undertaken by the PWD involving two distinct approaches has enabled such assessments. The first process involved an examination of threatened species lists (see Coutts-Smith & Downey 2006), while the second involved the development of the Weed Impact to Native Species (or WINS) assessment process (see Downey 2006). These two new approaches have significantly increased the number of native species considered to be at risk from alien plant invasions within NSW (Downey, this volume, presents further discussion of these approaches).

3. *Determining an effective management strategy for alien plant species that pose the greatest threat to biodiversity*

Knowing which alien plants are posing a threat to protected areas and the biodiversity most at risk from such invasions provides the auspices for developing management strategies. For example, the Threat Abatement Planning (TAP) process developed under the NSW *Threatened Species Conservation Act 1995* (TSC Act) for alien species listed as Key Threatening Processes (KTP) has led to such a management strategy. A Threat Abatement Plan outlines a strategy to abate, ameliorate or eliminate the threat posed by the KTP to biodiversity, independent of land tenure. Based on the only alien plant TAP to date (i.e. *C. monilifera* TAP; see DEC 2006), the TAP contains five broad objectives, which aim to 1) develop a strategic framework for delivering control of the threat to areas of high conservation value (in terms of threatened biodiversity), 2) develop and promote best practice management, 3) monitor the effectiveness of control programmes in terms of the recovery of threatened biodiversity, 4) foster community education, involvement and awareness, and 5) identify and fill knowledge gaps where possible. In order to meet the first objective a two stage process was developed to determine and prioritise sites where the control of alien plants will have the greatest benefit for biodiversity. The first stage uses the four step WINS assessment process, being 1) literature review, 2) targeted workshops to survey land managers, 3) development and review of a list of native species at risk, and 4) model the final list (see Downey 2006 for further details). The second stage assesses the sites where these species occur for control based on the 1) ability to achieve effective control, 2) the actual impact of the alien species, and 3) condition of the species and the location (i.e. other threats present). Implementation of the *C. monilifera* TAP at the 169 priority sites for the conservation of 19 species and 26 ecological communities involves all levels of government and the community. Community groups (e.g. Landcare groups) play a pivotal role in management of alien plants in Australia, as well as helping to raise awareness across the broader community (see Atkins & Molloy 1993). There are approximately 600 community groups working along the coastline of NSW, many of these groups work on the control of *C. monilifera* subsp. *rotundata* and the restoration of previously invaded areas (both on- and off-park).

Comparison of the two approaches

While each agency developed a different approach to invasive alien plant management, comparisons of these approaches illustrate that each agency actually addressed similar management components in a different way, and what could collectively form a more comprehensive strategy. The KNP used a formalized management structure, emphasising 'learning by doing', where the specific management objectives are directed through a series of thresholds of potential concern (TPCs). The TPCs are based around acceptable upper and lower limits, within which 'natural' variation occurs, and in order to detect breaches monitoring is critical. Active intervention only occurs once a TPC has been breached. The alien species TPCs are an evolving process; as is the case for other TPCs and thus some management aspects of alien species management are yet to be established for KNP (e.g. the impacts on biodiversity of widespread alien species). On the other hand, the PWD opted for a more informal management system, involving a combination of state-wide and regional priorities which account for the objectives behind the first two TPCs developed for KNP, without specifically formulating a robust TPC for each or adopting a formal monitoring system. This is probably in part because the PWD works with other agencies in NSW to manage alien plants. In addition, the PWD has placed a greater emphasis on understanding and managing the impacts of widespread alien plants on biodiversity, through the development and implementation of strategies to identify and prioritise alien plant species, the native species at risk and sites for control. This process is not based on assumptions of impacts as is the case of the third TPC, but could be encompassed within a fourth TPC where some measure of the species at risk (e.g. a specific number) initiates a breach and a TAP is developed and implemented.

Irrespective, many aspects of management components are similar between the two organisations, specifically the need for additional data to make decisions, further research (including the evaluation of control programs), and involving the community and neighbours.

Conclusion

The threat posed by alien plants to the value of Protected Areas and their management cannot be overstated. This threat has resulted in development of many alien species management strategies as illustrated by the South African and Australian examples presented here, aimed at delivering the same outcomes. Both agencies have had to overcome a range of hurdles which include the limitations of the available data, an increasing number of alien plant species and competing priorities in order to resolve the vast management challenges associated with managing biodiversity and alien species within protected areas.

This comparison of the two approaches highlights the diversity of solutions that have been developed for managing alien plants in Protected Areas. These approaches both mirror each other and encompass issues not addressed by the other. The ideas presented here can be used as a model for establishing alien species management strategies for other Protected Areas.

Managing protected areas in the face of biodiversity loss poses substantial challenges. The solutions to these challenges are equally as complex and require a range of different strategies. It is anticipated that this chapter will be the beginning of collaborations between the KNP and PWD, aimed at developing a collective knowledge base for the management of alien species within Protected Areas.

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Seven decades of institutional learning: managing alien plant invasions in the Kruger National Park, South Africa

Llewellyn C. Foxcroft and Stefanie Freitag-Ronaldson

Abstract Long-term ecological and economic sustainability will ultimately determine the outcome of any conservation management programme. Invasive alien plants, first recorded in the Kruger National Park, South Africa, in 1937, are now recognized as one of the greatest threats to the biodiversity of this Park. Such plants have been managed in the Park since 1956, with control advancing mainly through a process of trial and error. Refinement of invasive plant management strategies has resulted in an understanding of the target plants' biology and ecology, herbicide use and herbicide-plant interactions, as well as the plant-insect interactions of biological control. Careful integration of different control methods has proved essential to ensure the most appropriate use of techniques to deliver the best possible results from the resources available and achieve long-term sustainability. We outline the development of control efforts and current control programmes and the process of their incorporation into the institutional memory of Kruger National Park over the last 7 decades.

Keywords Biological control, chemical control, institutional memory, invasive alien plants, Kruger National Park, mechanical control, South Africa.

Introduction

The Kruger National Park is situated in the eastern Limpopo and Mpumalanga Provinces of South Africa, bordered along its entire eastern side by Mozambique (Fig. 1). The Park extends 360 km from north to south and covers 20,000 km^2, making it one of the largest protected areas in the world. Kruger is bisected by seven major river systems, originating in the highlands to the west and draining a combined area of *c.* 88,600 km^2. The Park falls within the savannah biome of southern Africa (Scholes, 1997) and has been classified into 35 landscape types (Gertenbach, 1983).

Kruger National Park, although largely a roadless area under protection since its declaration as a National Park in 1898, has not escaped the increasing threats of biological invasions (Foxcroft & Richardson, 2003; Freitag-Ronaldson & Foxcroft, 2003). Invasive alien plants (naturalized alien plants that produce offspring, often in large numbers and at considerable distance from the parent plants and thus with the potential to spread over vast areas; Richardson *et al.*, 2000), probably already present in the Kruger National Park region prior to its gazettement, have established and dispersed along all major rivers and vast areas of upland vegetation. Stevenson-Hamilton recognized invasive alien plants as a concern almost 7 decades ago (Stevenson-Hamilton, 1937) when management was not based on research and science but on a practical understanding of the environment (Rogers & Bestbier, 1997). Unfortunately, little was done to address the problem until the 1950s, and even then this was insufficient to curtail the invasions.

The first six alien plant species were recorded in 1937 as 'troublesome weeds' (Table 1A; Obermeijer, 1937), and this initial list has been periodically updated (Table 2). Currently, 372 alien plant taxa have been recorded in the Park (Foxcroft *et al.*, 2003; Table 2). This includes two transformer species (transformer species are invasive plants that change the character, condition, form or nature of ecosystems over a substantial area; Richardson *et al.*, 2000; Table 1B), 125 invasive species, and 223 species that are either naturalized (meaning alien plants that reproduce consistently and sustain populations over many life cycles but do not necessarily invade natural, semi-natural or human-made ecosystems) or casual aliens (alien plants that may flourish and even reproduce occasionally in an area, but that do not form self-replacing populations; Foxcroft *et al.*, 2003). The most prevalent invasive species include two terrestrial invaders and three species of free-floating aquatic macrophytes (Table 1C; Foxcroft & Richardson, 2003).

History of control efforts

The first management efforts in the Park were aimed at the eradication of species such as Persian lilac *Melia*

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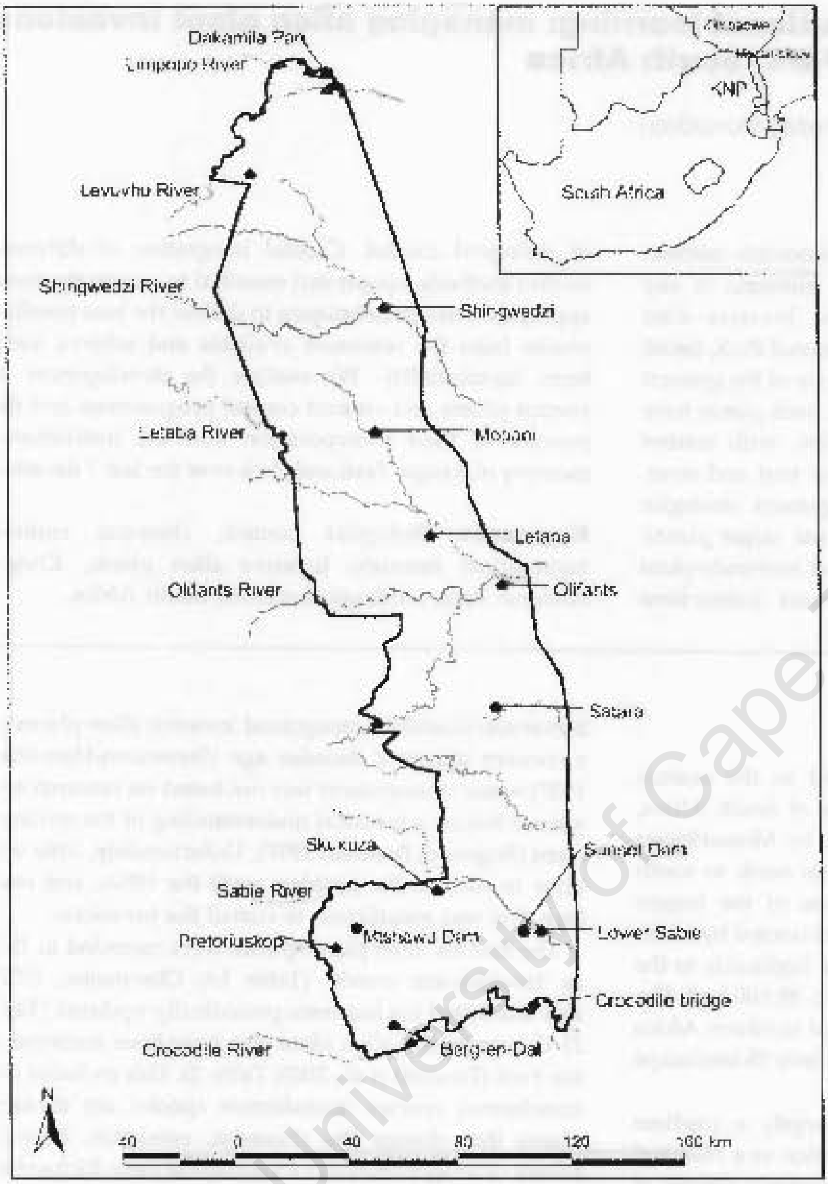

Fig. 1 Map of the Kruger National Park, indicating the main rivers and larger tourist camps. Also shown are specific dams and pans mentioned in the text. The inset shows the location of the Park (KNP) in South Africa.

azedarach L. on the Sabie, Crocodile and Nsikasi Rivers This was done by boring holes into the trunks and filling these with paraffin (Joubert, 1986) and in 1957 through mechanical means (Macdonald & Gertenbach, 1988; Fig. 2). Chemical control of invasive alien plants in the Park initially developed slowly but later became the main control method and focus of research. During the 1960s the herbicide KOP 250 (2,4,5,-T) was tested and proved effective (Joubert, 1986), resulting in the formal introduction of herbicides into the control of alien plants. Numerous herbicide trials followed over the ensuing years, with herbicides also used to control woody shrubs, aquatic weeds, bush thickening and road verge encroachment. Nevertheless, these often failed to provide adequate control of the plants and in some areas resulted in erosion and other impacts, especially along firebreaks and fences (Joubert, 1986).

By 1985 10 species (Table 1D) were thought to have been successfully eradicated, with the eradication of a further 14 species considered possible (Macdonald & Gertenbach, 1988). However, of the 10 species considered eradicated, six still require ongoing control efforts today. Whether failure to eradicate these species was because of later reintroductions or, more likely, a lack of continuity in control efforts, is not specified in available reports (Foxcroft *et al.*, 2003). We believe the latter reason more plausible as eradication is extremely difficult under any scenario (Panetta & Timmons, 2004).

During 1982–1995 control operations were conducted by the Park's dedicated alien plant clearing team

Table 1 Examples of invasive alien plant species in the Kruger National Park. Groups of species are also cross-referenced to specific discussion points in the text.

Cross ref.	Text reference	Species	Common name	Habitat
A	First alien plant species recorded	*Chenopodium ambrosioides* L.	Wormseed/goosefoot	Ruderal
		Cocculus hirsutus (L.) Diels	Cocculus	Ruderal
		Boerhavia diffusa L.	Erect boerhavia	Ruderal
		Gomphrena celosioides Mart.	Prostrate globe amaranth	Ruderal
		Argemone mexicana L.	Yellow-flowered Mexican poppy	Ruderal
		Tagetes minuta L.	Khaki bush	Ruderal
B	Species considered to be transformer species	*Lantana camara* L.	Lantana	Terrestrial
		Opuntia stricta Haworth Haworth.	Sour prickly pear	Terrestrial
C	Currently the most prevalent species	*Lantana camara* L.	Lantana	Riparian
		Opuntia stricta Haworth Haworth.	Sour prickly pear	Terrestrial
		Chromolaena odorata (L.) R.M. King & H. Rob.	Chromolaena	Riparian
		Azolla filiculoides Lam.	Red water fern	Free-floating aquatic macrophyte
		Eichhornia crassipes (Mart.) Solms	Water hyacinth	Free-floating aquatic macrophyte
		Pistia stratiotes L.	Water lettuce	Free-floating aquatic macrophyte
D	10 species considered to have been eradicated by 1985	*Salix babylonica* L.	Weeping willow	Riparian
		Acacia dealbata Link.	Silver wattle	Riparian
		Senna didymobotrya (Fresen.) Irwin & Barnaby	Peanut-butter cassia	Riparian
		Caesalpinia pulcherrima (L.) Schwartz	Pride of Barbados	Riparian
		Opuntia aurantiaca Lindl.	Jointed cactus	Terrestrial
		Ipomoea purpurea (L.) Roth	Morning glory	Riparian
		Nicotiana glauca R.C. Graham	Wild tobacco	Riparian
		Tecoma stans (L.) Kunth	Yellow bells	Riparian
		Bidens pilosa L.	Common blackjack	Ruderal
		Salvinia molesta D.S. Mitchell	Kariba weed	Free-floating aquatic macrophyte
E	Species for which approved biocontrol agents have been released	*Azolla filiculoides* Lam.	Red water fern	Free-floating aquatic macrophyte
		Eichhornia crassipes (Mart.) Solms	Water hyacinth	Free-floating aquatic macrophyte
		Lantana camara L.	Lantana	Riparian
		Opuntia stricta Haworth Haworth.	Sour prickly pear	Terrestrial
		Pistia stratiotes L.	Water lettuce	Free-floating aquatic macrophyte
		Salvinia molesta D.S. Mitchell	Kariba weed	Free-floating aquatic macrophyte
		Sesbania punicea (Cav. Benth)	Red sesbania	Riparian

consisting of 10 people, with occasional assistance from rangers' labour teams. Work performance was coarsely measured by recording the number of plant stems removed, focusing mainly on *Lantana camara* and *Opuntia stricta*. In this period, 6,889,515 stems were removed, and a further 8,579,314 stems were removed during 1996–1999 (Freitag-Ronaldson & Foxcroft, 2003). During the latter period a geographic information system was first used to capture the extent of clearing operations, which amounted to approximately 92,688 ha. This represents only 16% of the total area (590,295 ha) invaded by alien plants in the Park but is still essential to the long-term success of the control operations (Freitag-Ronaldson & Foxcroft, 2003) as these areas are regularly followed up.

In 1997 the National Working for Water (WFW) programme launched its first alien plant control project in the Park, with the sponsorship of ZAR 3 million from the Royal Netherlands Government and ZAR 6 million from the Poverty Relief fund of the South African Government. This enabled the employment of up to 1,000 unemployed people, focusing only on clearing invasive alien plants. The project has continued to the present, with a total of around ZAR 60 million (*c.* USD 8.5 million) being spent on control efforts in the Park to the end of the 2006/2007 financial year. These massive

Table 2 Records of alien plant species in Kruger National Park, arranged chronologically (from Foxcroft & Richardson, 2003; Freitag-Ronaldson & Foxcroft, 2003).

Total no. of species	Additional number of species	Source
6	6	Obermeijer (1937)
32	26	Codd (1951)
43	11	Van der Schijff (1957)
76	33	Van der Schijff (1969)
150	74	Gertenbach (1985)
156	6	Macdonald & Gertenbach (1988)
202	46	Anon (1995)
214	12	Anon (1997b)
360	146	Foxcroft (1999)
362	2	Foxcroft (2000)
366	4	Foxcroft (2001a)
370	4	Foxcroft *et al.* (2003)
372	2	Foxcroft (2004)

management efforts, built upon the foundations of the Park's own alien plant clearing programmes, have led to the current situation in which invasive plant population abundances are nearing maintenance levels, with annual follow-up operations being implemented. However, should these follow-up operations lapse, experience has shown that the system will revert to its former densely invaded state (Freitag-Ronaldson & Foxcroft, 2003).

Biological control

Biological control is the intentional use of populations of upper trophic level organisms, commonly referred to as natural enemies, to suppress populations of target invasive alien plant species. The introduction of a new species from one country to another is not without inherent risks. However, South Africa's Agricultural Research Council Plant Protection Research Institute (ARC-PPRI) is regarded as one of the top biocontrol research organizations in the world (Klein, 2001) and permission for biocontrol agent release needs to be given by both the National Department of Agriculture and the Department of Environmental Affairs and Tourism prior to release anywhere in South Africa (Klein, 2001). The ARC-PPRI is the lead partner in biocontrol efforts in Kruger National Park and the use of any such agents is only considered after all necessary national research, testing, screening and permissions have been granted. These stringent pre-release processes have resulted in an absence of non-target effects on any indigenous species in either the Park or elsewhere in South Africa (Klein, 2001).

In Kruger the first biological control agent (*Neohydronomus affinis*; Coleoptera: Curculionidae) was introduced by ARC-PPRI for the control of *Pistia stratiotes* at Dakamila Pan in the far northern Pafuri region in 1985 (Cilliers *et al.*, 1996; Martin & Foxcroft, 2001). This marked another significant milestone for the management of invasive plants and led to the development of integrated control programmes in the Park. Since 1985, 16 biological control agents have been introduced into the Park for the control of seven alien plants (Table 1b; Martin & Foxcroft, 2001) with research predominantly focused on long-term post-release

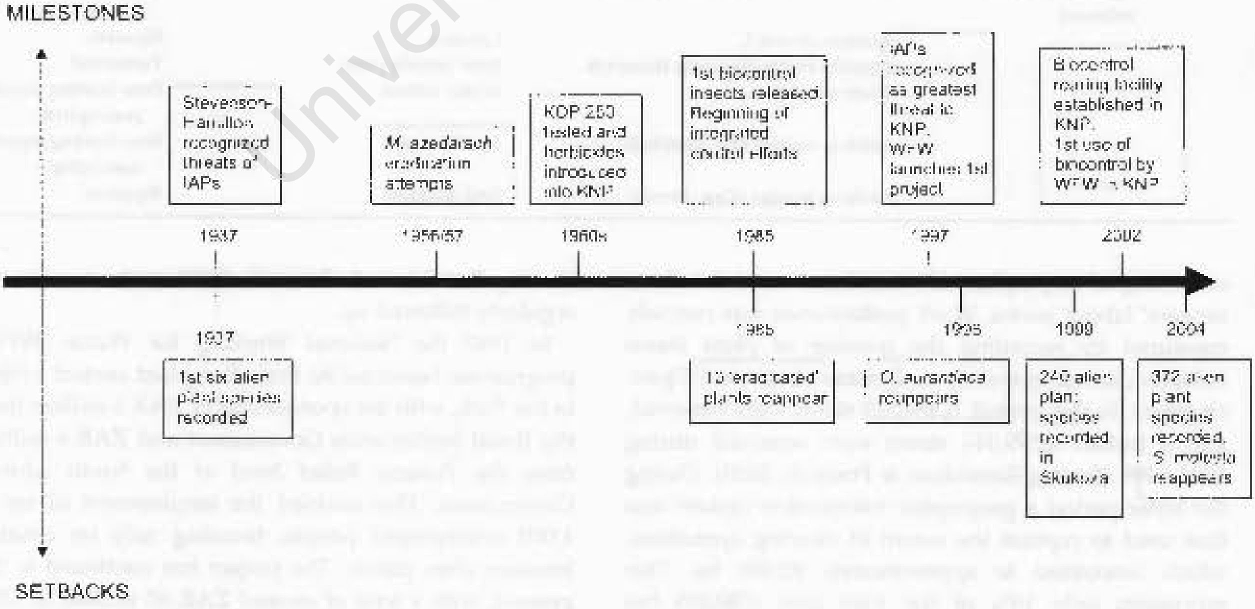

Fig. 2 Time line indicating milestones and setbacks during the management of alien plants in Kruger National Park (KNP) over the last 7 decades. IAPs, Invasive Alien Plants; WFW, Working for Water.

evaluation of plants under biological control, allowing a greater understanding of the insect-host interactions (Cilliers *et al.*, 1996; Lotter, 1997; Hoffmann *et al.*, 1998a,b). Although no specific studies were undertaken on whether or not there have been non-target effects, the long-term monitoring programmes provided opportunities to make the types of observations that would have detected any such effects. To date, none have been apparent. This was largely facilitated through a partnership between the Park, ARC-PPRI and the University of Cape Town.

The introduction of biological control has not been without problems. The often slow increase of insects, as well as the cyclic seasonal fluctuations, has received criticism from those not conversant with the functioning of biocontrol. The Park has been on the brink of abandoning certain biocontrol efforts when pressures to provide a quick chemical solution have been overwhelming, e.g. at the favoured tourist site of Sunset Dam near Lower Sabie (L.C. Foxcroft, S. MacFadyen & C.J. Cilliers, unpubl. data). Nevertheless, biological control has and will continue to play a major role in the control of aquatic weeds (e.g. *P. stratiotes*, *Azolla filiculoides* and *Salvinia molesta*) that are inherently aggressive and difficult to control. Biological control has provided long-term management options that effectively save the Park substantial resources and is also now recognized as one of the most cost-effective ways of managing invasions of alien plants (van Wilgen *et al.*, 2001) with self-perpetuating populations of the control agent maintaining the abundance of the host weed plant at acceptable levels.

Role of staff in importing and distributing alien plants

Park staff played a major role in facilitating alien plant invasions in Kruger National Park (Foxcroft, 2001b; Foxcroft & Richardson, unpubl. data). In the past, Park staff unwittingly introduced exotic species into cultivation in tourist camps and staff villages for ornamental and other uses. Their subsequent escape into the surrounding indigenous vegetation highlights the role of intentional introductions as foci of future invasion, a situation not unique to the Park. For example, Foxcroft *et al.* (2006) documented how tourist lodges in the Ngorongoro Conservation Area, Tanzania, are landscaped with ornamental alien plant species that pose a significant future threat to the surrounding areas.

Current control efforts

Kruger National Park's 1997 biodiversity conservation management review, using a SWOT-type analysis (Strengths, Weaknesses, Opportunities and Threats), identified invasive alien species as one of the greatest ecosystem threats (Anon. 1997a) ahead of other traditionally recognized concerns such as poaching, fire and large mammal control. This was backed by widespread evidence from across the Park and a developing knowledge of invasion biology (Rejmánek *et al.*, 2006). In essence, little institutional learning and management adaptation to invasive alien plant threats had taken place in the Park since Stevenson-Hamilton first raised his concerns in 1937. Nevertheless, the 1997 review also marked the time when the organization acknowledged and internalized the fact that given time and limited resources, invasive alien plants will establish to the detriment of indigenous biodiversity. Foxcroft & Richardson (2003) and Freitag-Ronaldson & Foxcroft (2003) partly ascribed the failure of the Park to manage early plant invasions to the lack of integration of alien plant control into overall management structures, which failed to recognize the long-term threats at the time.

Alien plants are currently controlled by a combined effort involving the Park (through its Invasive Alien Biota section and rangers) and the nationally funded WFW programme. WFW is particularly instrumental in management of riverine invasions, focusing on chemical and mechanical control of species such as *L. camara*, *Chromolaena odorata* and others. Collaboration with provincial WFW structures remains essential in coordinating operations at the catchment and landscape levels.

The Park has developed a biocontrol rearing facility in Skukuza, primarily for rearing the cochineal biocontrol insect *Dactylopius opuntiae* (Homoptera: Dactylopiidae) that is mass-released throughout the 66,000 ha *O. stricta* invasion within the Park and neighbouring areas. WFW operational teams have adopted this new control option as an alternative to manually spraying herbicides. This marks a significant development in the long-term effective management of *O. stricta* in the Park and in the expanding scope of WFW operating procedures.

Control of invasive species also requires the management, mitigation and, where possible, prevention of propagule distribution. Thus recognition of the main vectors and pathways of dispersal are critical. In Kruger the invasion of riparian habitats far exceeds that of any other habitat and is directly linked to the extensive invasions in the upper catchments to the west of the Park (Foxcroft *et al.*, 2007). Until satisfactory and sustained efforts are made in managing the plant invasions in the state-owned and private upper watershed areas, long-term control efforts will, at best, only provide temporary relief.

Impacts of invasive species

Within the Park indigenous species may be eliminated or extensively replaced with invasive plant species or associated complexes (Holmes & Cowling, 1997) but the direct negative impacts on biodiversity have not been investigated. However, it is implicitly assumed that such impacts are happening, and are therefore undesirable in the National Park context (IUCN, 2000; Freitag-Ronaldson & Foxcroft, 2003). The lack of research to quantify the negative impacts of invasive plants has been a shortcoming of the Kruger National Park programme (Foxcroft & Freitag-Ronaldson, 2005).

Structural ecosystem diversity includes landscape, habitat, population and genetic structure (Noss, 1990) and invasive species have effects at all these levels. The Park is structurally an island amidst vast and varying landscape uses and has been invaded to varying extents by numerous alien plant species (Foxcroft & Richardson, unpubl. data). Alien plant species are hypothesized to cause alternative landscape patterns to emerge, frequently with severe follow-on effects. Although not rigorously tested in the Park, Lotter & Hoffmann (1998) give an account of the impact of *O. stricta* on the vegetation structure. They showed that in an area densely invaded by *O. stricta* the vegetation was significantly altered, with *O. stricta* substantially outnumbering the indigenous plants. In a similar manner, species with allelopathic properties, such as parthenium *Parthenium hysterophorus*, which has invaded the southern region of the Park, may inhibit or prevent the establishment of indigenous species in its close proximity (Reinhardt *et al.*, 2004).

Institutional learning: internalizing the experience

It appears that little of the experience gained through the management of invasive species was internalized in Kruger National Park for at least the first 6 decades. The slow response to increasing invasions over time have resulted and will continue to result in a costly and continuous management programme. Clearly, slow, insidious ecosystem impacts are not as obvious and do not generate the immediate and large response that sizeable infrequent disturbances do (Parsons *et al.*, 2005), a reality that managers must now explicitly take into account. In Kruger this gradual increase in awareness, support and planning has only occurred in the last 10 years.

Efforts have been made to record and document the invasion history in the Park, providing an institutional memory and record of learning for future managers. However, the learning taking place both within the Park and internationally needs to be further internalized in the future, and we contend that: (1) Management must fully embrace the inherent risks and challenges associated with biological invasions by providing appropriate resources; an issue that has already received attention. (2) A well documented and annotated database and reference system must be maintained, including all invasive species distribution records, management history, research, monitoring and the myriad other activities that are taking place. (3) Setting of objectives (both short- and long-term), drafting of implementation plans, long-term monitoring programmes and research are key issues that require integration and adaptive feedback loops to develop an overall, institutional approach to biological invasions.

Kruger National Park has made substantial advances in integrating the science and management of invasive species into a learning framework (Foxcroft & Richardson, 2003; Freitag-Ronaldson & Foxcroft, 2003). Termed Strategic Adaptive Management, the process is embraced as a framework of managed learning, which steers strategic action to achieve desired endpoints in a complex ecosystem (Salafsky *et al.*, 2001; Biggs & Rogers, 2003). Adaptive management has been successfully used in natural resource management in general (Salafsky *et al.*, 2001; Biggs & Rogers, 2003; Smit, 2003) and invasive species management specifically (Tu, 2001; Towns, 2003). In Kruger this approach has helped articulate and elevate the threats, catalyze a broader understanding, and implement appropriate structured responses to invasions of alien plants. We suggest that reviewing and capturing previous management attempts, successes, and probably more importantly, failures, are important steps in improving future operations.

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Biographical sketches

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APPENDICES

Part 2- Alien plant lists for the Kruger National Park.

2.1 Table: Ornamental alien plant species recorded per camp in Kruger National Park, indicating the number of camps in which each species has been recorded, as well as mode of introduction (Chapter 4). Species names, authorities and indications of naturalization are based on Foxcroft *et al.* (2003). Evidence of cultivation means that the taxon was intentionally introduced, propagated, irrigated and tended to. Evidence of naturalization means that the species has naturalised out side of staff gardens and tourist rest camps. It might happen that the species naturalized (naturalized, sensu Pyšek *et al.* 2004) in the village environment, not necessarily in the natural landscapes. * indicates that the species is invasive in KNP.

APPENDICES

Part 2- Alien plant lists for the Kruger National Park.

2.2 Table: Distribution and nestedness of alien plant species between camps (Chapter 4).

Appendix 2.1 Table: Ornamental alien plant species recorded per camp in Kruger National Park, indicating the number of camps in which each species has been recorded, as well as mode of introduction. Species names, authorities and indications of naturalization are based on Foxcroft *et al.* (2003). Evidence of cultivation means that the taxon was intentionally introduced, propagated, irrigated and tended to. Evidence of naturalization means that the species has naturalised out side of staff gardens and tourist rest camps. It might happen that the species naturalized (naturalized, sensu Pyšek *et al.* 2004) in the village environment, not necessarily in the natural landscapes.
* indicates that the species is invasive in KNP.

Species	Family	Common name	Date of first record	Number of camps in which the species was recorded	Cultivated ?	Evidence of naturalization?
Acalypha wilkesiana Mull. Arg.	Euphorbiaceae	copper leaf	1949	1	Yes	No
Acanthus mollis L.	Acanthaceae	bear's breeches	1999	1	Yes	No
Agave attenuata Saml-Dyck	Agavaceae	soft-leaved agave	1999	7	Yes	No
Agave sisalana Perrine	Agavaceae	sisal	1965	5	Yes	Yes*
Agave vivipara L. (*A. angustifolia* misapplied in SA)	Agavaceae	narrow-leaved sisal/ century plant	1999	2	Yes	Yes
Ageratum conyzoides L.	Asteraceae	invading ageratum	1949	3	Yes	Yes*
Ageratum houstonianum Mill.	Asteraceae	Mexican ageratum/ floss flower	2000	2	Yes	Yes*
Ajuga reptans L.	Lamiaceae	carpet bugleweed	1999	1	?	Yes
Alocasia sp.	Araceae	elephant's ear	1999	2	Yes	Yes
Alpinia zerumbet (Pers.) Burtt & Smith	Zingiberaceae	shell ginger	1999	12	Yes	Yes
Alpinia zerumbet 'variegata'	Zingiberaceae	variegated shell ginger	1999	8	Yes	Yes
Alstroemeria peregrina L.	Amaryllidaceae	Peruvian lily	1999	1	Yes	Yes
Alternanthera denticulata	Amaranthaceae	large purple	2003	4	Yes	Yes

R.Br.		alternanthera				
Alternanthera ficoidea (L.) R. Br. ex R. & S.	Amaranthaceae	purple Alternanthera/ Joseph's coat	1999	2	Yes	Yes
Alternanthera pungens H.B.K.	Amaranthaceae	khaki bur weed	1950	1	No	Yes
Amaranthus spinosus L.	Amaranthaceae	thorny pigweed	1952	1	No	Yes*
Anthurium andraeanum Linden	Basellaceae	flamingo lily	1999	1	Yes	No
Antigonon leptopus H.& A.	Polygonaceae	coral creeper	1951	6	Yes	Yes*
Archontophoenix cunninghamiana H. Wendl. & Drude	Arecaceae	king palm/ bangalow palm	1999	1	Yes	No
Argemone mexicana L.	Papaveraceae	yellow-flowered Mexican poppy	1932	4	No	Yes*
Argemone ochroleuca Sweet subsp. *ochroleuca* (= *A. subfusiformis* GB.Ownby)	Papaveraceae	white-flowered Mexican poppy	1952	1	No	Yes*
Aristolochia elegans Mast.	Aristolochiaceae	Dutchman's pipe/ calico flower	1950	6	Yes	Yes*
Arundo donax L.	Poaceae	giant reed/ Spanish reed	1953	1	Yes	Yes*
Asclepias curassavica L.	Asclepiadaceae	scarlet milkweed/ bloodflower	1991	2	Yes	Yes*
Aspidistra elatior Bl.	Convallariaceae	cast iron plant/ milky way	1999	1	Yes	No
Asplenium nidus L.	Aspleniaceae	bird's nest fern	1999	1	Yes	No
Axonopus fissifolius Chase (= A. affinis)	Poaceae	carpet grass	1999	1	Yes	Yes
Bambusa balcooa Roxb.	Poaceae	giant bamboo/	1988	1	Yes	Yes

		balcooa bamboo				
Bambusa multiplex (Lour.) Raeusch. ex Schult. & Schult. f. (= *B. glaucescens*)	Poaceae	hedge bamboo/ Chinese dwarf bamboo	1999	3	Yes	Yes
Bambusa vulgaris Schrad. ex J. C. Wendl.	Poaceae	common bamboo	1995	1	Yes	Yes
Bauhinia purpurea L.	Caesalpiniaceae	butterfly orchid tree	1951	1	Yes	Yes
Bauhinia variegata L.	Caesalpiniaceae	orchid tree	1951	1	Yes	Yes
Bauhinia X *blakeana* S. T. Dunn.	Caesalpiniaceae	fragrant orchid tree	1999	1	Yes	Yes
Beaumontia grandiflora Wall.	Apocynaceae	Easter lily vine/ herald's trumpet	1999	1	Yes	No
Begonia X *tuberhybrida*	Begoniaceae	wax begonia/hybrid tuberous begonia	1999	1	Yes	No
Belamcanda chinensis (L.) DC	Iridaceae	leopard lily/blackberry lily	2000	1	Yes	Yes
Bidens biternata (Lour.) Merr. & Sherff	Asteraceae	five leaved-blackjack/ nose stud bur	1949	1	No	Yes
Bidens pilosa L.	Asteraceae	common blackjack	1975	1	No	Yes*
Bougainvillea glabra Choisy	Nyctaginaceae	paper flower	1952	1	Yes	No
Bougainvillea spectabilis Willd.	Nyctaginaceae	bougainvillea	1952	9	Yes	No
Brachychiton populneus (Schott & Endl.) R. Br.	Sterculiaceae	bottle tree	1952	1	Yes	Yes
Breynia disticha J.R. & G. Forst.	Euphorbiaceae	snowbush	1999	1	Yes	Yes
Bromelia spp.	Bromeliaceae	bromeliad	1999	1	Yes	No
Browallia americana L.	Solanaceae	amethyst violet/ Jamaican forget-me-	1999	1	Yes	Yes

		not				
Brugmansia arborea (L.) Lagerh. (= *Datura arborea, D. cornigera*)	Solanaceae	angel's trumpet	1999	1	Yes	Yes
Brunfelsia pauciflora (Cham. & Schltdl.) Benth.	Solanaceae	yesterday, today & tomorrow	1999	3	Yes	No
Bryophyllum daigremontianum (Raym.-Hamet & E.P. Perrier) Berger (= *Kalanchoe daigremontiana*)	Crassulaceae	good luck plant/ mother of millions	1999	12	Yes	Yes*
Bryophyllum delagoense (Eckl. & Zeyh.) Schinz. (= *Kalanchoe delagoense, K. tubiflora*)	Crassulaceae	chandelier plant/ mother of millions	1988	12	Yes	Yes*
Bryophyllum gastonis-bonnieri Raym.-Hamet & H. Perrier	Crassulaceae	donkey ears/ life plant	2001	4	Yes	Yes
Bryophyllum pinnatum (Lam.) Oken	Crassulaceae	air plant	2001	3	Yes	Yes
Caesalpinia decapetala (Roth) Alston	Caesalpiniaceae	Mauritius thorn/ Mysore thorn	1961	1	No	Yes*
Caesalpinia pulcherrima (L.) Schwartz	Caesalpiniaceae	pride of Barbados	1949	1	Yes	Yes
Cajanus cajan (L.) Millsp.	Papilionaceae	pigeon pea	1996	1	Yes	Yes
Calathea sp.	Marantaceae	rattlesnake plant	1999	1	Yes	No
Calliandra brevipes Benth.	Mimosaceae	fairy duster tree	1999	1	Yes	Yes
Callisia repens (Jacq.) L. (= *C. elegans*)	Commelinaceae	striped creeping inch plant	1999	16	Yes	Yes*
Callistemon sp.	Myrtaceae	bottlebrushes	1999	1	Yes	No

Callistemon viminalis (Sol. ex Gaertn.) G. Don ex Loudon	Myrtaceae	weeping bottlebrush	1999	1	Yes	No
Campsis grandiflora (Thunb.) K. Schum.	Bignoniaceae	Chinese trumpet vine	1999	1	Yes	No
Canna indica L.	Cannaceae	canna/ Indian shot	1999	9	Yes	Yes
Cannabis sativa L.	Cannabaceae	dagga/ marijuana/ hemp	1981	2	No	Yes*
Capsicum frutescens L. (= C. minimum)	Solanaceae	bird's eye chili/ bird pepper/ cayenne	1991	7	Yes	Yes
Cardiospermum grandiflorum Swartz	Sapindaceae	balloon vine	1995	4	Yes	Yes*
Cardiospermum halicacabum L. (= *C. corindum*)	Sapindaceae	heart pea/ lesser balloon vine	1953	2	Yes	Yes*
Carica papaya L.	Caricaceae	pawpaw/ papaya	1988	7	Yes	Yes
Caryota mitis Loureiro	Arecaceae	clustered fish-tail palm	1999	1	Yes	No
Caryota urens L.	Arecaceae	common fish-tail palm	1999	1	Yes	No
Catharanthus roseus (L). G. Don. (= *Lochnera rosea*)	Apocynaceae	graveyard flower/ Madagascar periwinkle	1951	11	Yes	Yes
Ceiba pentandra (L.) Gaertn.	Bombacaceae	kapok tree/ silky cotton tree	1999	1	Yes	No
Cereus jamacaru DC.	Cactaceae	queen of the night	1988	2	Yes	Yes
Cestrum diurnum L.	Solanaceae	inkberry/ day jessamine	1999	1	Yes	Yes
Chamaedorea elegans (Mart.) Liebm. ex Oersted	Arecaceae	parlour palm	1999	1	Yes	No
Chenopodium album L.	Chenopodiaceae	white goosefoot	1950	2	No	Yes
Chenopodium ambrosioides	Chenopodiaceae	wormseed goosefoot	1930	1	No	Yes

L.						
Chenopodium polyspermum L.	Chenopodiaceae	many-seeded goosefoot	1949	1	No	Yes
Chromolaena odorata (L.) R.M. King & H. Rob.	Asteraceae	chromolaena/ triffid Weed	1997	1	No	Yes*
Chrysanthemum spp.	Asteraceae	daisies	1999	1	Yes	No
Cinnamomum camphora (L.) Siebold	Lauraceae	camphor tree	1999	2	Yes	No
Citharexylum spinosum (= *C. quadrangulare*)	Verbenaceae	fiddlewood	1999	1	Yes	No
Citrus aurantiifolia (Christm.) Swingle (= *Limonia aurantiifolia*)	Rutaceae	lime	1978	1	Yes	No
Citrus limon (L.) Burm.f.	Rutaceae	lemon	1988	7	Yes	No
Citrus sinensis (L.) Osbeck (= *C. aurantium* var. *sinensis*)	Rutaceae	sweet orange/ Valencia orange/ navel	1952	1	Yes	No
Clerodendrum sp.	Verbenaceae		1999	1	Yes	No
Clerodendrum splendens G. Don ex James.	Verbenaceae	flaming glory bower	1999	1	Yes	Yes
Clerodendrum thomsoniae Balf.	Verbenaceae	bleeding heart	1999	1	Yes	No
Clitoria ternatea L.	Papilionaceae	butterfly pea	1951	3	Yes	Yes
Codiaeum variegatum (L.) Bl.	Euphorbiaceae	gold spot/ croton	1999	1	Yes	No
Coffea arabica L.	Rubiaceae	Arabian coffee/ coffee tree	1999	1	Yes	No
Colocasia esculenta (L.) Schott	Araceae	elephant's ear/ taro	1999	5	Yes	Yes
Commelina benghalensis L.	Commelinaceae	Bengal wandering Jew	1953	1	Yes	Yes

Cordyline fruticosa Goepp. (= *C. terminalis*)	Agavaceae	ti plant	1999	1	Yes	No
Cortaderia selloana (Schult.) Asch. & Graebn	Poaceae	pampas grass	1995	2	Yes	No
Costus speciosus (J. Koenig) Smith	Zingiberaceae	crepe ginger	1999	7	Yes	Yes
Cryptostegia grandiflora (Roxb.) R. Brown	Asclepiadaceae	rubber vine	1996	2	Yes	Yes
Cyathea australis (R. Br.) Domin.	Cyatheaceae	rough tree fern	1999	1	Yes	No
Cycas circinalis L.	Cycadaceae	queen sago	1999	1	Yes	No
Cycas revoluta Bedd.	Cycadaceae	king sago	1999	1	Yes	No
Datura ferox L.	Solanaceae	large thorn apple	1993	1	No	Yes*
Datura inoxia Mill.	Solanaceae	downy thorn apple	1991	1	No	Yes*
Datura stramonium L.	Solanaceae	common thorn apple	1953	2	No	Yes*
Delonix regia (Bojer ex Hook.) Raf. (= *Poinciana regia*)	Caesalpiniaceae	flamboyant	1952	4	Yes	No
Dichorisandra thyrsiflora Mikan f.	Commelinaceae	blue ginger	1999	1	Yes	Yes
Distictis buccinatoria (DC.) A. Gentry	Bignoniaceae	Mexican blood-trumpet	1999	1	Yes	No
Dracaena fragrans (L.) Ker.-Gawl (= *D. deremensis*)	Dracaenaceae	palmillo/ striped dracaena	1999	1	Yes	No
Dracaena marginata Lam.	Dracaenaceae	tricolor/ dragon tree/ sanderiana	1999	1	Yes	No
Duchesnea indica (Andr.) Focke	Rosaceae	wild strawberry/ false strawberry	1999	1	Yes	No
Duranta erecta L. (= *D. repens*)	Verbenaceae	golden dewdrop/ forget-me-not-tree/	1953	1	Yes	Yes

		pigeon berry				
Dypsis lutescens (H. Wendl.) Beentje & Dransf. (= *Chrysalidocarpus lutescens*)	Arecaceae	yellow bamboo palm/butterfly palm	1999	1	Yes	No
Encephalartos ferox Bertol. f.	Zamiaceae	Zululand cycad	1999	1	Yes	No
Epidendrum obrienianum Rolfe	Orchidaceae	scarlet orchid	1999	1	Yes	No
Epipremnum pinnatum (= E. aureum)	Araceae	golden pothos/ marble queen	1999	1	Yes	No
Eriobotrya japonica (Thunb.) Lindl.	Rosaceae	loquat	1988	1	Yes	Yes
Erythrina pallida Britton	Papilionaceae	pink coral tree	1999	1	Yes	No
Eugenia uniflora L.	Myrtaceae	pitanga/ Surinam cherry	1991	1	Yes	Yes
Euphorbia heterophylla L.	Euphorbiaceae	dwarf poinsettia	1950	1	Yes	Yes
Euphorbia leucocephala Lotsy.	Euphorbiaceae	snow flake	1999	1	Yes	Yes
Euphorbia pulcherrima Willd. ex Klotzsch	Euphorbiaceae	poinsettia	1954	2	Yes	Yes
Flaveria bidentis (L.) Kuntze	Asteraceae	smelter's bush/ yellowtop	1953	1	No	Yes*
Gardenia jasminoides Ellis	Rubiaceae	Cape jessamine	1953	1	Yes	Yes
Grevillea robusta A. Cunn.	Proteaceae	Australian silky oak/ silver oak	1952	1	Yes	No
Hamelia chrysantha Jacq.	Rubiaceae	fire bush	1999	1	Yes	No
Hedera helix L.	Araliaceae	English ivy	1999	1	Yes	Yes
Hedychium coccineum Sm.	Zingiberaceae	red ginger lily	1999	2	Yes	Yes
Hedychium coronarium J. Koenig	Zingiberaceae	butterfly ginger/ white ginger lily	1999	2	Yes	Yes
Hedychium gardnerianum Ker	Zingiberaceae	kahili ginger lily	1999	2	Yes	Yes

Gawl						
Helianthus annuus L.	Asteraceae	sunflower	2000	1	Yes	Yes
Heliconia sp.	Heliconiaceae	false bird of paradise	1999	1	Yes	No
Hibiscus rosa-sinensis L.	Malvaceae	Chinese cotton rose/ rose of China	1969	2	Yes	No
Hibiscus schizopetalus (Mast.) Hook.	Malvaceae	coral hibiscus	1999	1	Yes	No
Holmskioldia sanguinea Retz.	Verbenaceae	Chinese hat plant/ cup-and-saucer-plant	1999	5	Yes	No
Homalocladium platycladum (F. J. Muell.) L. H. Bailey	Polygonaceae	tapeworm plant	1999	1	Yes	No
Howea belmoreana (T. Moore & F. Muell.) Becc.	Arecaceae	belmore sentry palm	1999	1	Yes	No
Hoya carnosa (L. f.) R. Br.	Asclepiadaceae	wax plant/ Hindu rope plant	1999	1	Yes	No
Hylocereus undatus (Haw.) Britt. & Rose	Cactaceae	night-blooming cereus	1996	4	Yes	Yes
Hymenocallis littoralis (Jacq.) Salisb.	Amaryllidaceae	spider lily	1999	1	Yes	Yes
Hypoestes phyllostachya Baker	Acanthaceae	polka dot plant	1999	4	Yes	Yes
Impatiens walleriana Hook. f.	Balsaminaceae	busy Lizzy	1999	1	Yes	Yes
Ipomoea alba L.	Convolvulaceae	moonflower	1993	2	Yes	Yes*
Ipomoea purpurea (L.) Roth	Convolvulaceae	morning glory	1988	1	Yes	Yes
Ipomoea tricolor Cav.	Convolvulaceae	heavenly blue/ blue star	1998	1	Yes	Yes
Iresine herbstii Hook.	Amaranthaceae	blood leaf	1999	1	Yes	Yes
Ixora coccinea L.	Rubiaceae	flame of the woods	1988	1	Yes	Yes
Jacaranda mimosifolia D. Don	Bignoniaceae	jacaranda	1969	2	Yes	Yes

Jatropha podagrica Hook.	Euphorbiaceae	buddah belly plant/ gout plant	1995	1	Yes	No
Justicia brandegeana Wassh. & L. B. Sm.	Acanthaceae	shrimp plant	1999	1	Yes	No
Kalanchoe beharensis Drake	Crassulaceae	velvet leaf	1995	4	Yes	Yes
Lagerstroemia indica L.	Lythraceae	pride-of-India/ crepe myrtle	1995	3	Yes	Yes
Lantana camara L.	Verbenaceae	lantana	1940	9	Yes	Yes*
Leucaena leucocephala (Lam.) de Wit	Mimosaceae	leucaena/ wonder tree/ giant wattle	1995	1	Yes	Yes
Ligustrum vulgare L.	Oleaceae	common privet	1988	1	Yes	Yes
Liriope muscari (Decne.) L.H.Bail.	Convallariaceae	lily turf	1999	1	Yes	No
Liriope muscari 'variegata' (Decne.) L.H.Bail.	Convallariaceae	variegated blue lily turf	1999	1	Yes	No
Litchi chinensis Sonn.	Sapindaceae	litchi	1999	1	Yes	No
Livistona chinensis (Jacquin) R. Brown ex Martius	Arecaceae	Chinese fountain palm/ Chinese fan palm	1999	1	Yes	Yes
Luffa aegyptiaca Mill.	Cucurbitaceae	sponge gourd/ loofah	1999	1	Yes	No
Macfadyena unguis-cati (L.) A.H. Gentry	Bignoniaceae	cat's claw creeper	1995	6	Yes	Yes
Malvaviscus arboreus var. *mexicanus* Schlectend.	Malvaceae	Turk's cap/ fire dart/ wax mallow	1999	1	Yes	No
Mangifera indica L.	Anacardiaceae	mango	1951	9	Yes	Yes
Manihot esculenta Crantz.	Euphorbiaceae	bitter cassava/ manioc/ tapioca	1999	1	Yes	Yes
Maranta leuconeura erythroneura E. Morr.	Marantaceae	ten-commandments	1999	1	Yes	No
Megaskepasma	Acanthaceae	Brazilian red-cloak	1999	1	Yes	No

erythrochlamys Lindau						
Melia azedarach L.	Meliaceae	Persian lilac/seringa	1948	1	Yes	Yes*
Mimosa pigra L.	Mimosaceae	giant sensitive plant	1999	1	?	Yes*
Mirabilis jalapa L.	Nyctaginaceae	four-o'-clock	1953	1	Yes	Yes
Momordica charantia L.	Cucurbitaceae	bitter cucumber/ bitter melon	1999	1	Yes	Yes
Monstera deliciosa Liebm.	Araceae	delicious monster/ Swiss cheeseplant	1999	6	Yes	Yes
Morus alba L.	Moraceae	white mulberry/ common mulberry	1995	2	Yes	Yes
Musa X *paradisiaca* Linnaeus	Musaceae	banana/ plantain	1999	2	Yes	No
Mussaenda frondosa L.	Rubiaceae	flag bush	1999	1	Yes	No
Myriophyllum aquaticum (Vell.) Verde	Haloragaceae	parrot's feather	1989	1	Yes	Yes*
Nandina domestica Thunb.	Berberidaceae	heavenly bamboo	1999	1	Yes	Yes
Neomarica caerulea (Ker-Gawl.) Sprague	Iridaceae	blue walking dietes	1999	1	Yes	?
Nephrolepis exaltata (L.) Schott	Davalliaceae	sword fern/ Boston fern	1999	11	Yes	Yes
Nerium oleander L.	Apocynaceae	oleander	1988	2	Yes	Yes*
Nothoscordum gracile (Ait.) Stearn	Alliaceae	onionweed/ Stearn slender false garlic	1959	1	?	Yes
Odontonema strictum Kuntze	Acanthaceae	firespike	1999	1	Yes	No
Opuntia imbricata (Haw.) DC	Cactaceae	imbricate prickly pear	1996	1	?	Yes
Opuntia stricta (Haworth.) Haworth	Cactaceae	sour prickly pear/ Australian pest pear	1953	1	Yes	Yes*
Pandanus baptistii hort. Veitch ex Misonne	Pandanaceae	variegated screw-pine	1999	1	Yes	No
Pandanus utilis Bory	Pandanaceae	common screw-pine	1999	1	Yes	No
Parthenium hysterophorus L.	Asteraceae	parthenium/congress	1991	1	No	Yes*

		weed/ feverfew				
Passiflora edulis f. *flavicarpa* Degen	Passifloraceae	guavadilla/ yellow passion fruit	2003	8	Yes	Yes*
Passiflora edulis Sims	Passifloraceae	purple granadilla/ purple passion fruit	1988	2	Yes	Yes
Pedilanthus tithymaloides (L.) Poit.	Euphorbiaceae	jacob's ladder/ devil's backbone	1969	1	Yes	Yes
Pennisetum purpureum Schumach.	Poaceae	elephant grass/ Napier grass	1958	1	Yes	No
Pennisetum setaceum (Forssk) Chiov.	Poaceae	fountain grass	1953	3	Yes	Yes
Peperomia marmorata Hook.f.	Piperaceae	silver heart	1999	1	Yes	No
Pereskia aculeata Mill	Cactaceae	Barbados gooseberry/ pereskia	1999	2	Yes	No
Persea americana Mill.	Lauraceae	avocado	1953	3	Yes	No
Philodendron bipennifolium Schott	Araceae	horsehead philodendron	1999	1	Yes	No
Philodendron bipinnatifidum (= *P. selloum*)	Araceae	lacy tree philodendron	1999	2	Yes	No
Phlebodium aureum L. (= *Polypodium aureum*)	Polypodiaceae	gold-foot fern/ rabbit's foot fern/ blue fern	1999	8	Yes	Yes
Phoenix roebelenii O'Brien	Arecaceae	dwarf date palm/ pygmy date palm	1999	1	Yes	No
Phytolacca dioica L.	Phytolaccaceae	belhambra	1952	1	Yes	Yes
Pilea cadierei Gagnep. & Guillaum.	Urticaceae	aluminium plant	1999	1	Yes	No
Pilea microphylla (L.) Liebm.	Urticaceae	artillery plant	1999	1	Yes	Yes
Pistia stratiotes L.	Araceae	water lettuce	1977	1	Yes	Yes*

Plumeria rubra L.	Apocynaceae	frangipani	1954	2	Yes	Yes
Pontederia cordata L.	Pontederiaceae	pontederia/ pickerel weed	1990	1	Yes	Yes*
Psidium guajava L.	Myrtaceae	guava	1949	5	Yes	Yes*
Ptychosperma macarthurii (H. Wendl.) Nichols	Arecaceae	hurricane palm/ Macarthur palm	1999	1	Yes	No
Pyrostegia venusta (Ker-Gawler) Miers	Bignoniaceae	golden shower/ flame trumpet vine	1996	1	Yes	No
Ricinus communis L.	Euphorbiaceae	castor-oil plant	1953	3	No	Yes*
Rosa spp.	Rosaceae	roses	1999	1	Yes	No
Roystonea regia (Kunth) Cook	Arecaceae	Cuban royal palm	1999	1	Yes	No
Sabal palmetto (Walt.) Lodd. ex JA & JH Schultes	Arecaceae	common palmetto/ blue palmetto	1999	1	Yes	No
Salvia microphylla Benth.	Lamiaceae	cherry sage/ wild watermelon	1999	1	Yes	Yes
Sanchezia nobilis Hook.f.	Acanthaceae	noble sanchezia	1999	1	Yes	No
Sansevieria trifasciata hort. ex Prain	Agavaceae	mother-in-law's tongue	1999	1	Yes	No
Schefflera actinophylla (Endl.) Harms	Araliaceae	Australian cabbage tree/ Queensland umbrella tree	1999	6	Yes	Yes
Schefflera arboricola Hayata	Araliaceae	dwarf umbrella tree	1999	1	Yes	Yes
Senna bicapsularis (L.) Roxb (= *Cassia bicapsularis*)	Caesalpiniaceae	rambling cassia/ butterfly cassia	1992	2	?	Yes*
Senna didymobotrya (Fresen.) Irwin & Barnaby (= *Cassia didymobotrya*)	Caesalpiniaceae	peanut-butter cassia	1961	1	Yes	Yes*
Senna occidentalis L. (= *Cassia occidentalis*)	Caesalpiniaceae	coffee senna	1952	1	?	Yes*